THE POTATO
IN HEALTH AND DISEASE

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FOREWORD

It seems advisable, in view of the greatly extended field covered by this edition of the book, that the direct responsibility of each author should be indicated, though for the book as a whole the responsibility is, of course, a joint one. Dr T. P. McIntosh is responsible for Chapters I to VII covering the varied botanical aspects of the potato plant, Chapter XIII and for Appendix II which records the general characters of the chief commercial varieties and the characteristics of the sprouts. The late Mr W. M. Findlay was responsible for the cultural information included in Chapters IX, X, XII and XIV. Dr Whitehead is responsible for the Introduction, for Chapters XV to XXIX dealing with animal pests and potato diseases, for Appendix I concerning Fungicides and the compilation of References to the Literature on pests and diseases.

The authors are indebted to many friends for material and help. In particular they wish to express their indebtedness to Dr W. Black, B.Sc., F.R.S.E., Scottish Society for Research in Plant Breeding, Edinburgh, for writing Chapter VIII on Potato Breeding; and to Mr J. W. West, B.A. (Cantab.), Dip.Agric. (Cantab.), of the Scottish Agricultural Machinery Testing Station, Howden, Mid-Calder, for contributing Chapter XI on Potato Machinery. They are also indebted to Dr J. G. Hawkes, M.A., of Birmingham University, for the considerable assistance he gave in dealing with the many difficulties encountered in writing Chapter II. Mr H. Whitby, B.Sc., Assistant Secretary, Department of Agriculture for Scotland, and Mr O. I. Beilby, M.A., B.Litt., Advisory Officer in Agricultural Economics, Department of Agriculture for Scotland, have collaborated in the revisal of Chapter I, and to them also the authors are very grateful. Thanks are due to Mr G. L. Turner and Mrs B. Banes for the assistance they have given in compiling the Index.

In the matter of illustrations of pests and diseases, also, the authors are indebted both to personal friends and to Her Majesty's Stationery Office. In particular to the following: Professor H. W. Miles and Mrs M. Miles, M.Sc., of Wye

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CONTENTS

INTRODUCTION

THERE is no agricultural crop plant which possesses so wide an appeal as the potato. Interest in the crop is shared by growers of very different types, comprising not only the specialist farmer who relies mainly upon this crop for a livelihood and who keeps abreast of every modern development of potato breeding and cultural practice, but also the average arable farmer, to whom the crop is important, though not very much more so than any other he can select for his " root break." It also includes the market gardener and any man, whatever his profession, who has a few square yards of land to cultivate in his spare time.

Even if the amateur is sometimes unable to point with pride to a large yield in tubers, he is rarely at a loss to find some aspect of his potato crop to serve as a topic of conversation. Indeed, the " monstre " potato vies with the weather, the vegetable marrow and the fish which just escaped the angler's gaff, as an antidote for melancholia and a lucrative subject for the professional humorist. What other agricultural crop plant can boast of an almost affectionate nickname known to townsman and countryman alike ? Certainly not wheat which, as the " staff of life," can be set against the wild form of the oat plant as rather a subject for moralising ; and no one, since the time of the late Dr Johnson, has dared to be facetious about cultivated oats.

The fact is, of course, that the potato is deservedly popular because it insists on yielding several times its own weight of produce, whatever liberties are taken with it, and however abysmal the ignorance of the grower. Few growers indeed, however recently initiated into the art of cultivating the land, will admit to any doubts of their ability to grow potatoes ; yet the enormous difference between the crop at its best and the average yield throughout the country is sufficient evidence either that the crop is too often grown under quite unsuitable conditions, or is handled all too frequently in an incompetent manner. Therein lies the need for a book in which the knowledge, at present scattered through many inaccessible scientific journals, can be summarised and discussed in relation to the many practical problems with which the grower is confronted.

THE POTATO PLANT.—What is this plant, then, which forms perhaps the staple food in some countries and is important in almost all ? In its main external features it is familiar to everybody, yet many mistakes in cultivation would be avoided if the grower really grasped the nature of the plant he is trying to grow.

Like all green plants it can be looked upon as a factory in which "raw" chemicals are converted into food, part of which is used up during growth and part set aside to provide for the needs of the plant in the following year. The roots not only act as an anchor but also as a means of absorbing the mineral part of the food from the soil ; for both these reasons, therefore, cultivation must strive to assist in root development. The remainder of the food, *i.e.* the carbon, comes from the carbon dioxide of the atmosphere, which enters the leaves through special breathing pores (stomata) and, under the influence of light, is combined with water brought up from the roots to form sugars. These sugars are then united in various proportions with some of the elements brought up from the roots to form the many kinds of proteins which make up the living substance of the plant. The excess sugar, which is not immediately required for this purpose, is stored up during the day in the form of starch, but at night the starch is re-converted to sugars and transported to all actively growing parts of the plant. The surplus then passes down the stem or haulm to the tubers, which are underground stems modified to act as warehouses for just this purpose of storing up excess food, as starch, until the following spring. Other things being equal, it is clear that it is the size of the canopy of leaves rather than the height of the stem which determines the output of sugars (and hence of starch) for the swelling tubers. The stem or haulm, in fact, merely serves to carry the leaves apart from each other so that all can develop to the full and receive the maximum benefit from whatever light is available.

Sugar formation in the leaves can only occur with an adequate temperature and in light of sufficient intensity. At temperatures between 55° F. and 77° F. the rate of sugar production increases rapidly with rise of temperature, but above and below these points its production becomes progressively less. Hence the potato plant is more efficient in temperate climates than in either tropical or subarctic conditions; and even in temperate climates it is less efficient in early spring than in the height of summer. Sugar production is influenced in much the same way by light—increasing with the amount of light up to a maximum beyond which any further intensity of light fails to stimulate any increase in sugar production. The optimum light intensity, as with other physiological conditions, varies with the kind of plant, but as a rough guide in the case of potatoes it may be assumed that, so long as the light intensity on a summer day is not reduced by more than one-third when the sky is overcast, there will be no falling off in sugar formation. In winter, however, the light intensity may be no more than one-third that of summer, and sugar production is then barely sufficient for maintenance and leaves no surplus to be stored up as starch in the tubers. This is the reason why the potato cannot usually be grown successfully for tuber formation in winter, even in a heated glasshouse, unless special means are employed for artificial lighting.

The action of light on growth is a complex one, for although it is essential for sugar production and hence for continued growth, its direct action is to retard rather than to stimulate growth. The truth of this is known to any potato grower who has compared the long, spindly sprouts resulting from sprouting tubers in the dark, with the plump, sturdy sprouts developing in the seed-box in a well-lighted room. One important practical result of sprouting in the light is the shortness of the intervals between the "nodes" on the sprouts, from which arise the fibrous roots and the underground stems (stolons) which ultimately swell to form tubers. A well-sprouted tuber secures an advantage in the early development of the underground parts over the spindly-sprouted or unsprouted tuber and this results in an increased yield.

The ability of some kinds of potato to form tubers appears to be influenced by light, quite apart from its direct effect upon growth or on sugar production. The potato of Peru and Bolivia in South America, or *Solanum andigenum*, as the botanists call it, consists mainly of types which produce satisfactory crops of tubers only under the short-day conditions existing in the Andes. When grown under European conditions of light, the plants may grow luxuriously but seldom yield good crops. Different varieties of the European potato react differently to external conditions, such as temperature and light, as well as other conditions less well understood, and it is because of these differences in reaction that potato types are classed conveniently as first earlies, second earlies and maincrop varieties. Although, therefore, there is a measure of agreement in these respects between the varieties of any one class, they are quite distinct from each other in many features; the varieties Arran Pilot and Sharpe's Express, for instance, are clearly distinct although they are both first earlies. Even within the same variety it is possible to find fairly substantial variations both in form and reaction to environment: Sharpe's Express, for example, varies from a coarse upright habit, which flowers freely and matures relatively late, to a spreading type, generally without flowers, which is definitely earlier in maturity. Apart from such variations, however, it is true to say that a variety shows constant differences from another variety in very many respects, and it is for this reason that the grower should make himself thoroughly familiar with the varietal characters described later in this book.

What is the cause of these differences, both great and small? To find the answer we must examine the inner structure of the plant in some little detail. The potato plant is built up of enormous numbers of minute cells, each cell consisting of a box of dead material known as cellulose containing the living substance or protoplasm. Each tiny cell is connected with others by strands of this same protoplasm so that the protoplasm of root, tuber, stem, leaves, flowers and berries is really continuous; the whole object in grafting is to unite the protoplasm of scion and stock, and it is only when this is accomplished that further growth of the scion takes place. Yet each cell is a separate unit which appears to be controlled in many ways by a central portion of the protoplasm known as the nucleus. The nucleus has a somewhat different composition from that of the ordinary protoplasm of the cell, and is of particular interest to us in that it contains minute granules which pass through a succession of changes when a young cell divides into two, as happens repeatedly during the growth of the plant. At one stage in cell division the granules are arranged as a network which gradually separates into a number of small rods or *chromosomes*. These split lengthways and the two halves of each chromosome pass to opposite ends of the dividing cell, so that when division is completed by the formation of a cellulose wall across the middle of the cell, each daughter-cell is provided with a nucleus derived from the original one in this way.

Now, the remarkable point about all this is the fact that most, if not all, of the hereditary qualities which distinguish one variety from all others are carried in the chromosomes of the nucleus, so that every cell receives a complete sample of all these qualities. That is the reason why all the tubers of a

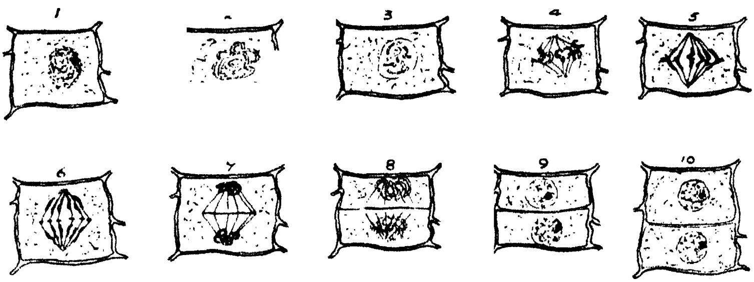


FIG. 1.—Showing Successive Stages in Cell Division.

variety produce similar plants which can at once be recognised as belonging to one and the same variety, the only exceptions being those known as "sports."

In the sexual parts of the flower (pollen grains and ovules) the number of chromosomes is halved, so that on fertilisation, *i.e.* the union of the contents of the male pollen from the stamens with the female ovules in the pistil, the full chromosome number is restored. The essence of "cross-breeding" is to mix the qualities obtained from one parent with those of the other, and it is clear that this is accomplished by the union of the two different sets of chromosomes. In simple cases of inheritance, all the plants resulting from such crossing will contain the qualities of both parents, although some may not be able to express themselves in the progeny, *e.g.* the quality of "shortness" may be present in one parent and that of "tallness" in the other; the result of union will be either to produce plants of medium size or the one parent will dominate the other so that all the progeny will be short or tall. The possibilities are thus very varied, even in the simplest cases of inheritance, when one remembers the vast number of "qualities" which may be inherited. In the case of the potato, the apple, and many other plants, however, the position is much more complicated owing partly to the mixed origin of modern varieties of these plants, so that the seedlings obtained from a cross will not only differ from both parents but even from each other. The question of the hybridising of species of *Solanum* is discussed later in this book, but sufficient has been said to show the enormous difficulties to be confronted in the raising of new varieties of the potato.

It will be remembered that all the cells of the plant are enclosed in cell-walls, so that the only food substances which can enter the plant must be either in gaseous or liquid form, for these alone can penetrate through the cell-walls. Fortunately, such substances are present in abundance under normal conditions of cultivation for, as has already been pointed out, the plant utilises the carbon dioxide of the atmosphere and the mineral salts dissolved in soil water as raw materials for food. There is little or nothing that the grower can do to influence the intake of the carbon dioxide by the leaves, and the problems of cultivation are essentially those of providing adequate minerals in the soil and the proper conditions for their absorption by the roots. These minerals, in solution in soil water, enter the plant through the outer cells of the fibrous roots, especially near the tips where the cells are drawn out to form threads or hair-like structures known as "root-hairs." Any cultural operation, therefore, which increases the number of fibrous roots and root-hairs will, to that extent, benefit the plant; while any lack of care resulting in damage to these delicate structures will have a corresponding adverse effect upon the growth of the plant and the produce obtained from it. The maintenance of a good tilth has an important function in allowing the free movement of air between the particles of soil, without which the roots are unable to respire; for in "packed" or in waterlogged soil the plant roots suffer from lack of air just as surely as do cattle in badly ventilated buildings. The movement of food materials through the plant takes place along special conduit tubes which form the vascular strands visible in the angles of the stem when this is cut across. The tubes conveying the sugars from the leaves, or from the sprouting tubers, are elongated living cells which together form the phloem or bast. Those which transport the mineral salts in solution from the soil together make up the xylem or wood ; most wood cells differ essentially from the living phloem in being empty of protoplasm and in having their walls strengthened to serve as additional support for the haulm. Both wood and phloem form continuous strands throughout the whole plant and anything breaking this continuity will result in the death of the plant. Damage caused by an implement or a horse hoof during cultivation are obvious ways in which the wood and phloem may be irretrievably injured, but a less obvious one is the effect of parasitic fungi and bacteria. These often completely block the passage of watery salts through the wood, with the result that the plant suffers from a typical " wilt " disease. Sometimes the phloem is attacked, *e.g.* by the Leaf-Roll virus, with consequent inhibition of sugar movement from the leaves, which then assume a rolled appearance. The various brown, rusty spots, streaks or rings which sometimes occur in the tuber flesh are also often due to the effect of disease upon the phloem strands of the tuber. Similarly, the veinal streaks which affect potato foliage are due to the death of the phloem and the tissues immediately around them, whilst the brown or yellow spots characteristic of certain foliage diseases are, on the other hand, caused by the death of small groups of the ordinary living cells which make up the bulk of the leaf tissue.

CHAPTER I

INTERNATIONAL POSITION OF THE POTATO AND THE SIGNIFICANCE OF THE CROP IN BRITISH AGRICULTURE

WORLD WAR II had a remarkable effect on the agriculture of most countries, particularly the combatant countries. International trade in potatoes (though never important in relation to production) was considerably reduced for a time while the acreage in countries which were not the scene of actual fighting considerably increased. In the United Kingdom, for instance, where the necessity to build up reserve supplies to replace bread grain from overseas was fully recognised, the potato acreage increased by 90 per cent. and production by 93 per cent. comparing the mid-war with pre-war years.

Before the war the consumption of potatoes in Great Britain was comparatively low, being about half a pound per head per day. In most other countries consumption was much higher. During the war, however, consumption per head in this country increased by about 60 per cent. and has since been maintained at about this level except for a short period at the end of 1947 and the beginning of 1948, when the relatively low production of the 1947 crop forced the Government to introduce potato rationing at the rate of 3 lb. per head per week.

Although the war thus brought the potato into special prominence and largely obscured the normal interplay of economic forces, these latter still remain and may be expected to come again into full operation. For this reason, therefore, a brief study of the pre-war picture of the potato industry will serve a useful purpose in setting the crop in its normal perspective.

THE POTATO AS A WORLD CROP IN PRE-WAR YEARS.—There is no need to emphasise the importance of the potato as a food for mankind. In most countries it forms a regular and considerable part of the human diet and, in addition, is also used for the feeding of livestock. Some countries, notably Germany, use potatoes extensively in the manufacture of farina, starch and alcohol. In Great Britain, however, the difference in the value of potatoes for human consumption and for manufacturing processes was too great to allow of profitable crops being grown specifically for the latter purpose; such potatoes, also, as were fed to livestock were those which could not normally be sold for human consumption. Of the more important world crops, potatoes give the greatest weight of produce per acre, as can be seen from Table I below.

TABLE I

World Acreage and Production of Potatoes, Wheat, Maize, Rice and Oats

(From *F.A.O. Handbook of Agricultural Statistics*, 1946)
Average of five years 1935-1936 to 1938-1939

Crop.	Acreage (000).	Production (000 tons).	Yield (tons per acre).
Potatoes	52,280	143,021	2·74
Wheat	414,600	158,380	0·38
Maize	216,690	117,994	0·54
Rice *	206,100	149,381	0·72
Oats	138,840	62,237	0·45

* 1935-1936 to 1939-1940 annual average.

It is beyond the scope of this book to consider the crop in different countries in any detail, but it is clear from the data given in Table II that both the acreage under potatoes and the productivity varies widely from country to country. Generally the northern European countries show a high yield per acre, whereas Argentine, U.S.A., Turkey, Italy, Hungary, Rumania and Yugoslavia have only a low productivity; and even Canada produces less than half the yield per acre obtainable in the United Kingdom or Eire. The final column in Table II relates production in the various countries to their human population and shows the quantity of potatoes produced per head per week for all purposes—human consumption, seed, stock-feed and industrial use.

INTERNATIONAL TRADE IN POTATOES IN PRE-WAR YEARS. —While the world acreage devoted to potatoes, so far as it was measurable, was distinctly less than that of wheat, maize, rice or oats (see Table I), it was nevertheless so large as to make it appear at first sight strange that there was so little international trade in this commodity. The main reasons for this, however, are not far to seek. Not only were many countries self-sufficient as regards potatoes, but the transport costs of the crop were heavy relative to the value, due both to its bulk and the liability to deteriorate during long journeys unless special care is taken in storage. Further, restrictions on international trade were caused by the stringent regulations adopted by many countries.

TABLE II

Acreage and Production in Various Countries

(From *F.A.O. Handbook of Agricultural Statistics*, 1946)
Average of five years 1935-1936 to 1938-1939

Country.	(Acreage 000).	Production (000 tons).	Yield (tons per acre).	Production per head (lb. per week).
Argentine	311	710	2·3	2·4
Australia	114	345	3·0	2·2
Austria	520	2,840	5·5	18·3
Belgium	383	3,130	8·2	16·2
Canada	516	1,725	3·3	6·6
Czechoslovakia	1,879	9,982	5·3	28·1
Denmark	188	1,277	6·8	14·9
Eire	328	2,632	8·0	37·8
Finland	213	1,303	6·1	15·6
France	3,489	15,353	4·4	15·8
Germany	7,160	49,172	6·9	31·0
Hungary	729	2,133	2·9	10·2
Italy	1,038	2,703	2·6	2·7
Japan	293	1,592	5·4	1·0
Netherlands	323	2,698	8·4	13·7
Norway	127	880	6·9	13·1
Poland	7,312	27,864	3·8	34·8
Rumania	669	1,975	3·0	4·3
Spain	1,126	4,580	4·1	7·9
Sweden	325	1,785	5·5	12·2
Switzerland	120	707	5·9	7·3
Turkey	136	178	1·3	0·5
United Kingdom	720	4,898	6·8	4·4
England and Wales	461	3,124	6·8	3·3
Scotland	134	951	7·1	8·2
Northern Ireland	125	823	6·6	27·3
U.S.A.	3,033	9,522	3·1	3·2
U.S.S.R.	17,569	57,166	3·3	14·6
Yugoslavia	646	1,384	2·1	3·9

Such international trade as did occur was largely the result of special circumstances. If the trade was in potatoes for human consumption it was usually due either to that indefinable quality, "public taste," or to the desire of the importing country to extend the season beyond that possible with home-grown supplies. The influx of " earlies " to this country from the Channel Islands, the Canaries, Malta and Spain was probably due, in varying degrees, to both these reasons. Similarly, Belgium exported large quantities of early varieties to Germany, and quite half the total crop of Dutch earlies found a market in the Rhineland, Belgium and Great Britain. Some Mediterranean countries looked to the East for the partial disposal of their exportable crop, and Italy and Malta found such an outlet in the western provinces of India. In a few cases practically the whole crop was grown for export. Tasmania, for instance, shipped most of her potato produce to Victoria and New South Wales, while Bermuda found a ready market for the whole of her crop in New York. Similarly, the Channel Islands and the Canaries relied upon Great Britain for the disposal of practically all their potato crop.

As regards trade in *seed tubers*, international restrictions were usually very severe, owing to the risk of introducing diseases into the importing country. Such trade was in any case the result of a reputation, slowly built up in the importing country, for the health and vigour of the stocks produced in the country of origin. This, and the ease with which a reputation can be lost, cannot be brought too often to the notice of seed-potato growers. Scotland and, more recently, Eire and Northern Ireland in this way developed a valuable export trade in " seed " with England and the Channel Islands, and with countries outside the British Isles, particularly with Spain, South Africa, France and the Canaries. Lincolnshire was the only English county with an export trade in " seed " ; whilst Wales, notwithstanding a rapid development in the production of high-grade seed, still figured only as a large importer. The Canadian maritime Provinces of New Brunswick and Prince Edward Island supplied practically the whole seed requirements of Bermuda, which country, as we have seen, re-exported the produce of this seed almost entirely to New York. Italy appears to have built up her pre-war seed-trade with India on the fact that her potato varieties were better suited to Indian climatic conditions than were those grown in Great Britain, although the market price and the shorter ocean voyage may also have contributed.

THE POTATO AS A BRITISH CROP IN PRE-WAR YEARS.—

The importance of the potato in British agriculture before the war can be assessed from the data given in Table III, in which the acreage and productivity of the main crops grown in this country are compared.

TABLE III

Acreage and Production of the more Important Crops grown in Great Britain

(Average of five years 1935-1939)

Crop.	Acreage (000).	Production (000 tons).	Yield (tons per acre).
Wheat	1,838	1,664	0·91
Barley	931	781	0·84
Oats	2,154	1,716	0·80
Potatoes	595	4,075	6·85
Turnips and Swedes	771	10,501	13·62
Mangolds	228	4,172	18·30
Sugar Beet	344	3,031	8·81
ss (for Hay)	1,731	2,353	1·36
Total Arable	12,045	...	...
Permanent Grass	17,322	...	...

Potatoes are definitely less productive, measured by tonnage per acre, than other root crops, but even so the value of the output of potatoes in Great Britain, *i.e.* the value of that part of the produce sold off the farm or consumed in the farm household, amounted to an annual average of about £67,000,000 in the three years 1947 to 1949 or nearly 9 per cent. of the value of the total agricultural output. The comparison with other crops grown for human consumption, however, should not be pressed too far, for potatoes frequently receive favoured treatment both as regards manures and the fertility of the land selected for this crop and, further, a much greater weight of " seed " is planted per acre for the potato crop than is the case with any other crop grown on British farms.

While the above Table III indicates the importance of potatoes in relation to other crops in this country as a whole, before the war there were significant variations in its importance on individual farms in different parts of Great Britain. Apart from certain specialised potato-growing districts, such as the Ayrshire and Wigtownshire coasts and the Boston district of Lincolnshire, which have particularly suitable soils and where potatoes are grown on large acreages (and often for a number of years on the same ground), the acreage occupied by potatoes on the individual farm varied considerably. It ranged from perhaps 100 acres on a 450-acres highly arable farm to half an acre, or less, on a farm in a typical grazing district. The great bulk of the potato crop was grown in the more arable counties of the east, from Angus in the north to Kent in the south. In 1935 the following eight counties provided 53 per cent. of the total acreage under potatoes in Great

TABLE IV

Average Yield of Potatoes in Five-Year Periods from 1886 to 1949, in Tons per Acre

The Five-Year Period.	England and Wales.	Scotland.
1885-1889	5·9	5·8
1890-1894	5·9	5·4
1895-1899	6·1	5·8
1900-1904	5·6	6·0
1905-1909	6·2	6·4
1910-1914	6·2	6·6
1915-1919	6·2	6·2
1920-1924	6·1	6·8
1925-1929	6·5	6·8
1930-1934	6·5	6·9
1935-1939	6·8	7·1
1940-1944	7·1	7·1
1945-1949	6·8	7·2

Britain, viz. Lincolnshire (109,865 acres), Yorkshire (51,161 acres), Cambridge (40,828 acres), Lancashire (34,790 acres), Norfolk (21,417 acres), Cheshire (19,109 acres), Angus (18,628 acres), Perth (17,117 acres).

The tendency to revert to grass, which was so evident after the last war, of course, was most pronounced in areas with a pastoral rather than an arable tradition : Wales, for instance, reduced the arable acreage from 51,000 in 1870 to 20,000 in 1930. As regards potatoes, however, the effect was to redistribute rather than to reduce the total acreage ; indeed, the total acreage under potatoes increased somewhat during the past fifty years. It is interesting to note also that the yield per acre showed a steady improvement, particularly in Scotland, as is illustrated by the data in Table IV.

This increase in production, however, did not quite keep pace with the increase in population ; the production per head of the population in Great Britain in 1891 amounted to some 217 lb. and in 1931 to about 205 lb. The figures could not, of course, be accepted as sufficient evidence of a marked decline in the consumption of potatoes in pre-war years. The change in the age structure of the population, the quantities fed to livestock, and the balance of import and export of the crop would all need to be considered before any definite opinion on this point would be justified.

Unfortunately, the yield per acre was by no means so steady as the market, for fluctuations of 15 per cent. up to 20 per cent. from year to year were not uncommon. There being no alternative outlet for the excess crop in a good growing year (for the practical difficulties in the way of establishing factories for processing proved insuperable), the farmer was compelled to dispose of his produce at an extremely low market price, or to feed the bulk of it to his livestock. The experience of several " glut " years, with their consequent low prices, which accentuated the depression to which agriculture had recently become accustomed, was an important factor leading to the establishment of the Potato Marketing Scheme in 1934. Under this Scheme a Marketing Board, elected by the whole body of potato growers, was set up, with the main function of regulating supplies of ware potatoes reaching the market in this country in such a manner as to reduce any undue fluctuation in prices, both during any one season and between different seasons. Put very briefly, the methods adopted to secure this stability in prices were : (1) the regulation of imports which amounted to about 6 per cent. of the total home production (this was not, of course, a power exercised by the Board but by the Government, as part of their policy of assisting organised marketing) ; (2) the regulation of the acreage under potatoes by allotting a " basic " acreage to each grower and imposing penalties if an acreage in excess of this figure was planted ; (3) the compulsory sales of " ware " through authorised merchants, and the forbidding of sales on commission ; (4) the regulation of supplies by enforcing standards of the size of tubers sold for human consumption, the minimum size being increased in " glut " periods and decreased when the demand began to exceed supplies ; (5) the building up of reserves of capital to enable the Board to intervene, when prices became uneconomically low for any reason, by themselves purchasing surplus stocks; and (6) the investigation of alternative outlets for potatoes and the establishment of an intelligence service, particularly of market forecasts, to serve as a guide to those engaged in the potato trade.[1]

WAR DEVELOPMENTS IN GREAT BRITAIN.—The Ministry of Food assumed control of the potato industry after the outbreak of war and the functions of the Potato Marketing Board were largely suspended. Prices at each stage of sale were controlled and subsidies were introduced to enable consumers' prices to be kept at a reasonable level. The acreage restriction for growers was also removed and everything possible, including the prohibition of too early lifting, was done to increase production. The industry was now better regulated than ever before, and steps were taken to reduce wastage to a minimum. Potato growing could be undertaken without risk of serious financial loss. On the debit side, however, there was a shortage of potassic manures. The effects of this shortage were nevertheless minimised by the placing of potatoes amongst the priority crops.

THE POST-WAR POSITION.—Many European countries have increased their acreage now that the ravages resulting from the war have been made good. The acreage in Europe (excluding the U.S.S.R.) increased from 22 million in 1946 to 24 million in 1948 and the production of potatoes now slightly exceeds pre-war. In the United Kingdom, however, owing to the greater availability of alternative foodstuffs the area under potatoes has gradually tended to drop from the peak acreages grown in 1943 and 1944 of around

[1] For very comprehensive and detailed studies of the potato market in this country in pre-war years, the reader is referred to:

(*a*) *Report on the Marketing of Potatoes in England and Wales.* (Economic Series No. 9, Ministry of Agriculture and Fisheries, 1926.)

(*b*) *Report on the Marketing of Potatoes in Scotland.* (H.M. Stationery Office, 1933.)

(*c*) *Organisation of Potato Marketing.* (Economic Series No. 34, Ministry of Agriculture and Fisheries, 1931.)

(*d*) *Factors affecting the Price of Potatoes in Great Britain*, by Ruth L. Cohen, University of Cambridge School of Agriculture (1930).

(*e*) *The Potato Marketing Scheme*, by Ruth L. Cohen, Agricultural Economics Research Institute, Oxford.

1,400,000 (or about double the pre-war figure) to 1,308,000 in 1949.

In the longer term, as the food position improves, potato production may decrease, but with the provision of guaranteed markets and assured prices for the main farm products, including potatoes, given under Part I of the Agriculture Act, 1947, combined with the Government's undertaking not to impose quantitative limitations in the case of potatoes (and certain other farm products) for as long ahead as one can see, the potato grower may face the future with every confidence.

Frequently, the cultivation (using the term in its widest sense) of the crop is insufficiently studied, with the result that yields are unsatisfactory. Enormous losses are incurred each year by the depredation of diseases and pests; but while complete freedom from these can seldom be expected, modern research has provided means by which much can be done to restrict losses. Indeed, as regards virus diseases and their control, the importance of which can hardly be exaggerated, it may be stated quite definitely that farming practice lags seriously behind present knowledge. The judicious selection of the proper variety to grow, and the special care necessary for individual varieties, are matters which growers frequently ignore. The "roguing" of potato stocks to eliminate diseases or plants not true-to-type is often left to hired specialists, thus adding to the costs of production, whereas with a little study and direction this could easily be done by the grower himself or one of his regular employees. Those engaged in the potato trade, merchants as well as growers, do not always appear to realise that potatoes are living bodies, readily injured by rough handling, overheating or chilling, and that injuries, however small, often enable rotting organisms to enter and destroy the tissues. The proper handling and storage of the potato crop is therefore of great importance and merits serious study. The economic use of the potato as stock-food involves a knowledge of balanced rations, of precautions to be used in feeding, and of converting the tubers into silage if there is reason to believe that they may not be consumed until late summer. It is imperative, therefore, that the grower should be familiar with the most up-to-date information on the whole aspect of feeding potatoes to stock.

Much of the most recent knowedge of improvement in cultural practice is readily available to growers, whereas what may be called the more technical aspects of potato growing, such as varietal characteristics and disease control, are less accessible. These considerations, together with the need for economy of space, have determined the treatment of the present work, largely restricting it, as has already been said in the Introduction, to such information as is either not available at all or, if so, occurs only in the form of articles in scientific journals published in this and other countries.

CHAPTER II

COUNTRY OF ORIGIN OF THE POTATO; INTRODUCTION INTO EUROPE; SYSTEMATIC POSITION, INCLUDING AN ACCOUNT OF OTHER TUBER-BEARING *SOLANUMS*; THE POTATO PLANT; AND POTATO VARIETIES

COUNTRY OF ORIGIN

WHENCE came the potato? Since its introduction into Europe, the question of the country of origin has excited much speculation. The various theories may be roughly classed as those based on fact and fiction respectively. Those relating to countries outside South America are now, for instance, regarded as fallacious, and in this category must be included the theory that the plant came from Virginia.

The problem of determining the country of origin of any plant may be approached by historical or by biological methods. A settled system of agriculture has generally been necessary for the development of civilisations, nomadic races having contributed little towards progress. All plants were wild prior to cultivation by primitive peoples, and it is most likely that the countries of origin of crop plants are associated with the centres of ancient civilisations. These latter can be explored and the evidence of the habits and agriculture of the peoples may be studied. Further, records of travel frequently offer information of value. Biologically, the countries of origin of plants are studied by investigating the botanical and other characters of the plants themselves and also the distribution of closely allied forms. This latter method is based on the fact that the number, range and diversity of forms of a given plant increase as the centre of origin is approached.

Many botanists have surveyed the possible countries of origin of the potato, and nowhere outside South America has any evidence been found that the plant was cultivated prior to the discovery of that continent. Tuber-bearing species of *Solanum* have been found outside South America, in Mexico, Guatemala and the U.S.A. for instance; but although the tubers of these species are sometimes eaten by the natives, there is no record that they have ever been cultivated, a fact probably associated with the greater productivity of other food plants in these regions. According to Salaman,[1, 3] the potato was first mentioned in literature by Juan de Castellanos in his *Historia del Nuevo Reino de Granada* (1536; published 1886). Castellanos describes the first encounter by a European with the potato, which occurred in the native village of Sorocotá, about 7° N. latitude, not far from the Spanish town of Vélez in Colombia. Pedro Cieza de Leon found the potato in 1538 growing, generally at great heights, in Colombia, Ecuador and Peru. In his *The Chronicle of Peru* (1550) Cieza has left a record of his journeys and observations. Safford [2] has pointed out that along the coasts of Peru and North Chile there are old cemeteries in which mummies are found, accompanied not only by desiccated plants but also funeral vases, some of which depict the foods of ancient inhabitants. Dried potatoes have been found in these cemeteries, and funeral vases depicting potatoes have been obtained in abundance in North Peru. Salaman [3] has dealt very thoroughly with the archæological data, more especially with the pottery which has been excavated during the last forty years. Drake encountered the potato in the Isle of Mocha, off the coast of Chile, in 1577, and Cavendish also found it in St Mary's Isle, near Concepcion in Chile, in 1587.

Historical data appear to suggest, therefore, that the country of origin of the European potato might lie within the territory embraced by Chile, Peru, Bolivia, Colombia and Ecuador. Salaman contends that at the time of the original introductions the transport difficulties were such as to make it almost impossible for tubers to have been brought to Europe from Chile in time for planting, and believes, therefore, that the potato must have come, not from Chile, but from the northern countries of South America. It should be remarked, however, that a lengthy voyage does not necessarily exclude the possibility of the potato having been brought from Chile:

[1] Dr R. N. Salaman, Masters Lectures, 1936. "The Potato in its Early Home and its Introduction into Europe," *Journ. Roy. Hort. Soc.*, 1937.

[2] W. E. Safford, "The Potato of Romance and Reality," *Journal of Heredity*, 1925.

[3] Dr R. N. Salaman, *The History and Social Influence of the Potato*, 1949.

apart from true seed, many potato varieties can develop secondary tubers on their sprouts during storage, and such tubers make it possible to carry the potatoes over a season without any planting. Salaman and Hawkes [1] maintain that evidence derived from herbarium specimens proves beyond a doubt that the earliest types of potatoes grown in W. Europe and England were typical *S. andigenum* forms, *i.e.* forms found in the Northern Andes.

Quite a different conclusion has been reached by another biological line of approach. In this connection, the most important contributions have been made by Russian scientists who sent botanical expeditions to America, commencing in 1925. These scientists explored a great part of South and Central America and found that extraordinary variations existed in the native forms of the potato. These affected all its characters and led to the identification of a whole series of new species. Cultivated potatoes were found throughout the range of the Andes mountains in Venezuela, Colombia, Ecuador, Peru, Bolivia and north Argentina, whilst they were also encountered in the coastal plains of Chile and in the island of Chiloé as far south as the 45th parallel. In general the cultivated potatoes of South America are confined to the cool temperate belts of the Andes and south-central Chile, though some sorts occur at an altitude of up to 14,000 ft. in a zone where frosts are frequent and others at about 6-8000 ft. where the climate is almost subtropical. It was found that the natives cultivated many different species of potatoes, some of which seem to have been grown from the earliest times. The Peru-Bolivian region of the Lake Titicaca basin seems to have been the centre of origin of the cultivated potatoes, and it is here that one finds the greatest number of species and the greatest diversity of genic material. Some of the most ancient civilisations, such as the Tiahuanaco and the Inca cultures coincided in their origins with this area, and there is reason to believe that these peoples cultivated the potato from the earliest times. A second, though subsidiary, focus of diversification of the cultivated potato lies in Chile, in the zones mentioned above. In this region it was cultivated at the time of the conquest by the Araucanian Indians. Of the cultivated species most differ

[1] Dr R. N. Salaman and J. G. Hawkes, "The Character of the Early European Potato," *Proc. Linn. Soc. of London*, 1949.

substantially from, and only two show resemblances to the potato of Europe. Of these two, one is found in the Peru-Bolivian centre and the other in South Chile. The characters of the first are more primitive than those of the second, but an interesting and further difference between the two is their differential reaction to the length of daylight. Just as plants are specially adapted to varying conditions of temperature and humidity, so also have they specific light requirements. The length of day during the growing period is short at the Equator and increases with the latitude. Thus, during the course of evolution, plants have become specialised as regards short-day requirements in Equatorial regions, while farther from the Equator other types, requiring longer days, have come into being. In their native habitats the Peru-Bolivian species (which, stretching as it does through the Andes from Venezuela to north Argentina, might better be named the Andean species) and the Chilean species seem to crop equally well. In northern Europe, however, the Andean species crops poorly unless the conditions of illumination are artificially reduced to twelve hours or less daily. The primitive nature of the Andean potatoes and above all their short-day requirements have convinced the Russians that they constitute a different species from the ordinary European potato, *Solanum tuberosum*, and they have accordingly named it *S. andigenum*. The less primitive characters of the Chilean potatoes and particularly their long-day requirements have guided them to consider that the original home of the European potato is Chile ; these Chilean potatoes they therefore call *S. tuberosum*, distinguishing the European sorts derived (as they suppose) from the original Chilean ones as *S. tuberosum* var. *europaeum*. This conclusion is disputed by Salaman,[1] who contends that, historical reasons apart, types of *S. andigenum* exist which have fairly long-day requirements and that by breeding and selection, plants indistinguishable from *S. tuberosum* may be obtained. Indeed, he is unwilling to concede species rank to *S. andigenum*. Hawkes[2] has suggested that the two should be united under

[1] Dr R. N. Salaman, " The Potato in its Early Home and its Introduction into Europe," *Journ. Roy. Hort. Soc.*, vol. lxii, pp. 61-77, 112-23, 153-62, 253-66. 1937.

[2] J. G. Hawkes, " Potato Collecting Expeditions in Mexico and South America. II. Systematic Classification of the Collections," *Bull. Imp. Bur. Pl. Breed. Genet.*, Cambridge, 1944.

the name *S. tuberosum* and should be given rank as geographical sub-species. The Andean short-day forms would be called *S. tuberosum* subsp. *andigenum*, the Chilean forms *S. tuberosum* subsp. *chileanum*. The European potatoes would remain as before, simply as *S. tuberosum*. In this way we should not be committing ourselves to the tacit acceptance of either of the two opposing theories of origin of the European potato as we do when speaking of *S. andigenum* for the Andean forms and *S. tuberosum* for the Chilean ones. However, since these nomenclatural changes have not yet been validly published botanically, we shall continue here to speak of *S. andigenum* and *S. tuberosum* sensu strictu (*i.e.* in the narrow sense) to denote the Andean and Chilean tetraploid complexes respectively.

The statement that long-day types may be obtained from short-day forms by breeding and selection is correct and there is cogency in the argument about the transport difficulties at the time of the original introduction. On the other hand, the Russian thesis cannot be entirely ignored. The weight of available evidence, however, favours Salaman's view.

Species hybridisation is likely to complicate the question in future, for types derived in this way will contain characters inherited from plants of widely different origin.

The Introduction of the Potato into Europe

It is certain that there were two independent introductions. The first was into Spain. Salaman,[1] on the basis of historical record, dates this introduction at about 1570. From Spain, potatoes found their way to Italy, from which country they were sent to some other parts of Europe, and ultimately two tubers were given in 1588 to the botanist Clusius in Vienna by Philip de Sivry, Prefect of Mons. They were first described by Caspar Bauhin in his *Phytopinax*, published in 1596, and later by Clusius in 1601 in the *Rariorium Plantorum Historia*. Clusius, however, had the potatoes before Bauhin, and both descriptions were made from the same continental group of potatoes that originally came to Spain, as indicated above. A second introduction occurred about 1586 when tubers were brought to England, by whom cannot be stated with any

[1] Dr R. N. Salaman, *The History and Social Influence of the Potato*. 1949.

TABLE V

The Systematics of Wild and Cultivated Potatoes, constituting the subsection Hyperbasarthrum *of the section* Tuberarium *of the genus* Solanum, *investigated in the Living State* *

Series.	24 Chromosomes.	36 Chromosomes.	48 Chromosomes.	60 Chromosomes.	72 Chromosomes.
Conicibaccata . .	...	...	S. colombianum [4]		
Etuberosa . . .	S. fernandezianum [3]				
	S. brevidens [3]				
Bulbocastana . .	S. Bulbocastanum [7]				
Cardiophylla . .	S. lanciforme [7]	S. cardiophyllum [7]			
Pinnatisecta . .	S. sambucinum [7]				
	S. Jamesii [7, 11]				
Commersoniana .	S. Boergeri [10]	S. Commersonii [10]			
	S. chacoense [1, 8]	S. Millanii [1]			
	S. Emmeae [1]	(triploid form)			
	S. Garciæ [1]				
	S. gibberulosum [1]				
	S. Henryi [10]				
	S. Horovitzii [1]				
	S. jujuyense [1]				
	S. Knappei [1]				
	S. laplaticum [1]				
	S. mechonguense [1]				
	S. mercedense [10]				
	S. Millanii [1]				
	S. Ohrondii [10]				
	S. Parodii [1]				
	S. saltense [1]				
	S. Schickii [1]				
	S. sorianum [10]				
	S. tarijense [2]				
Acaulia . . .	...	...	S. acaule [2, 9]		
			S. depexum [1]		
Demissa . . .	S. verrucosum [7]	...	...	S. edinense [13]	S. demissum [7]
				S. Salamanii [7]	
				S. semidemissum [7]	

Longipedicellata		S. vallis mexici [7]	S. ajuscoense [7] S. Antipoviczii [7] S. Fendleri [11] S. longipedicellatum [7] S. malinchense [7] S. tlaxcalense [7]		
Polyadenia	S. polyadenium [7]				
Cuneoalata	S. platypterum [2] S. glanduliferum [1]				
Tuberosa— i. Wild species	S. Abbottianum [9] S. Arrac-papa [9] S. Ballsii [1] S. Berthaultii [2] S. Bukasovii [9] S. canasense [9] S. catarthrum [9] S. Lechnoviczii [9] S. multidissectum [9] S. pampasense [9] S. punoense [9] S. simplicifolium [1, 2] S. Soukupii [9] S. Vavilovii [9]	S. Magha [3]			
ii. Weed species	S. anomalocalyx [2] S. brevimucronatum [2] S. calcense [9] S. fragariæfructum [9] S. lapazense [2]		S. Herreræ [9] S. leptostigma [3] S. Molinæ [3] S. subandigenum [2] S. sucrense [2]		
iii. Cultivated species	S. Ajanhuiri [2] S. Ascasabii [5] S. Cardenasii [2] S. goniocalyx [9] S. Kesselbrenneri [5] S. Phureja [2] S. Rybinii [4] S. stenotomum [2, 9] S. Yabari [9]	S. Chaucha [2, 9] S. Juzepczukii [2, 9] S. mamilliferum [9] S. tenuifilamentum [2, 9]	S. andigenum [1, 2, 4, 5, 6, 7, 9, 12] S. tuberosum [3] (s. str.)	S. curtilobum [2, 9]	

* Only includes distribution records for specimens of the species investigated in the living state, *i.e.* records from herbarium specimens only are not noted.
[1] Argentina. [2] Bolivia. [3] Chile. [4] Colombia. [5] Ecuador. [6] Guatemala. [7] Mexico. [8] Paraguay. [9] Peru. [10] Uruguay. [11] U.S.A. [12] Venezuela
[13] Unknown, probably produced artificially.

certainty. The plants grown from these had white tubers and light purple flowers, as distinct from the coloured tubers and dark purple flowers of those described by Clusius. The English potato was described by the botanist Gerard in his catalogue in 1596 and in his *Herball* in 1597. It is probable that there were subsequent introductions, but these would be unlikely to create the same interest as the initial plants, the potato being no longer a novelty. It is, moreover, certain that with the introduction of Early Rose from U.S.A. in the nineteenth century fresh "blood" was obtained from South America, as this variety, which had its origin from a South American plant, was used largely by British and American breeders.

THE SYSTEMATIC POSITION OF THE POTATO[1]

The potato belongs to the natural order *Solanaceæ* and is, therefore, related to many well-known plants such as tobacco, tomato, egg plant and nightshades. The order includes many species in the warmer and tropical parts of the globe and is represented in northern regions only by a few temperate species. Numerous tuber-bearing species of the genus *Solanum* have been studied in the living condition. These are found mainly in South America, but some occur also in Central America, Mexico and south-western U.S.A.

A scheme showing the chromosome number of many wild and cultivated species is set out in Table V. It will be noted that all species occur within five groups, forming what is known as a polyploid series, the chromosome number of each of which is divisible by 12. We therefore speak of 12 as being the basic number for the series, and assume that the first-formed species were 24-chromosome types or diploids, evolution proceeding in the order of sequence of increasing chromosome number.

It is assumed that the 36 chromosome or triploid species were formed either as hybrids between those with 24 and 48 chromosomes or from the union of unreduced with reduced gametes in a diploid species or between two hybridising diploid

[1] For further information the reader is referred to: *Potato Collecting Expeditions in Mexico and S. America. II. Systematic Classification of the Collections*, by J. G. Hawkes, Ph.D., Imp. Bureau of Plant Breeding and Genetics. June 1944.

species. An example of the former type is the cultivated species *S. Juzepczukii* formed as a hybrid between the wild tetraploid *S. acaule* and a form of the cultivated diploid *S. stenotomum*. The latter process is illustrated by species such as *S. cardiophyllum* and *S. Commersonii*, both of which species possess only diploid relatives. Tetraploids would have occurred when the chromosome complement of diploids was doubled, as can be done artificially in the laboratory by the use of colchicine. Pentaploids, like triploids, may have originated in two ways. They may have been formed as hybrids between a hexaploid (2n = 72) and a tetraploid (2n = 48) species, as was probably the case with *S. Salamanii* and *S. semidemissum*, or as a result of the union of non-reduced triploid with reduced tetraploid gametes, as is assumed to have occurred in the formation of *S. curtilobum* in South America, where no hexaploid species is known.

The problem of the origin of the only hexaploid species, *S. demissum*, is rather obscure, since the closest related species from which it might have been formed is *S. verrucosum*, a diploid. The other related species, *S. semidemissum*, was in all probability formed from *S. demissum* rather than the other way round. It would be theoretically possible to obtain a hexaploid by chromosome duplication in a triploid, but so far no one has discovered the triploid ancestor of *S. demissum*, if it ever existed. Neither has any related tetraploid been discovered which might have formed a link in the production of this species.

A knowledge of the chromosome numbers of these wild potato species gives us an indication of the possible ancestors of the cultivated potato and rules out the possibility that a mutation from *S. Commersonii* and *S. Maglia*, both triploids, could have produced the cultivated potato plant as was at one time conjectured. The possibility of either of these two species having been the direct ancestor of the potato is now definitely excluded by virtue of their chromosome number.

NOTES OF SOME TUBER-BEARING SPECIES OF *SOLANUM* OTHER THAN *S. TUBEROSUM*

Interest in the tuber-bearing species, other than *S. tuberosum*, is twofold. First, are they themselves worthy of cultivation and, secondly, have they any value for plant breeding and the improvement of cultivated varieties? In Europe, no species can compete with *S. tuberosum* for cropping, hence the interest in this Continent concerns almost entirely their value for breeding. European varieties show differences in disease-resistance, frost-resistance, maturity, dormancy period and composition of tubers, but the wild and primitive cultivated species show a much greater range of variation in all these qualities, and, in particular, some are disease- and frost-resisting to a very high degree.

Potatoes are classified botanically in the genus *Solanum* L., but the tuberiferous species constitute only a very small portion, not more than 10 per cent. of this genus, which in all comprises some 2000 species. Potatoes come within the sub-section *Hyperbasarthrum* of the section *Tuberarium* and are distinguished, in addition to the fact that most produce tuberiferous stolons, chiefly by the pedicel or flower-stalk bearing a joint or articulation that is not situated right at its base. Within this sub-section are included about 200 wild and 20 cultivated species. Some of these, especially the wild ones, appear at first glance to bear no affinities to the cultivated potato as we know it in Europe.

Sub-section *Hyperbasarthrum* has been further divided into some 13 groups or series. Those that have been studied in the living state are included in Table V. A short description of each series, together with notes on those species that are of most importance for potato breeders is given below.

Series I. *Juglandifolia* Rydb.

Here belong certain species that are only just beginning to be studied in the living state. They do not bear tubers or stolons, are rather distinct morphologically and probably would not hybridise with the cultivated potato. The following species are included: *S. juglandifolium*, *S. ochranthum* and *S. lycopersicoides*.

Series II. *Conicibaccata* Bitt.

Species with elongated-oval to long conical berries are placed in this series. Probably not all the species bear tubers; those types studied so far in the living state possess 48 somatic chromosomes but have not yet been crossed with any other tuber-bearing species. *S. oxycarpum*, *S. colombianum* and *S. violaceimarmoratum* are the best-known members of the series.

Series III. *Etuberosa* Juz.

The chromosome number of the species so far studied in this non-tuberiferous Chilean series is $2n = 24$. The species are distinguished by the very low pedicel articulation and the absence of stolons and tubers. One species studied in England, *S. brevidens* seems to be highly resistant to sap-transmissible viruses. The well-known species *S. etuberosum* also belongs here.

Series IV. *Bulbocastana* Rydb.

Two Mexican species, *S. Bulbocastanum* and *S. morelliforme*, with stellate corollas and simple leaves are grouped here. The former species is a diploid blight-resister but has so far resisted all attempts at crossing with other types whilst the latter has not yet been studied in the living state.

Series V. *Cardiophylla* Buk.

This may prove to be an important group of species since the two so far tested are blight-immune. Unfortunately they will not hybridise, so far as is known, with other species, though it is possible that some success might be obtained with *S. lanciforme* (2n = 24). *S. cardiophyllum* (2n = 36) sets no fruit at all and is apparently quite sterile. The species are characterised by dark green shining leaves and stellate buff or cream-coloured flowers.

Series VI. *Pinnatisecta* Rydb.

Closely related to *Cardiophylla*, differing in the non-shining leaves and white corolla. Only one species of this series, *S. Jamesii*, has been studied so far in the living state. It is said to resist Colorado beetle but few hybrids have yet been made between it and other species.

Series VII. *Commersoniana* Buk.

The three series with stellate corollas mentioned above are all confined to Mexico and Central America. *Commersoniana* also possesses a stellate corolla but is confined to South America. Here are included such well-known species as *S. Commersonii* and *S. chacoense*, together with the numerous related diploid micro-species given in detail in Table V. *S. chacoense* has been of value in breeding for resistance to Colorado beetle, and some of the other species show some degree of resistance to frost.

Series VIII. *Acaulia* Juz. et Buk.

This is one of the most interesting series, comprising two frost-resistant species, *S. acaule* and *S. depexum*. They are distinguishable morphologically by the flattened rosette habit, almost invisible pedicel articulation and extremely short corolla lobes. All forms of both species possess 48 somatic chromosomes and are highly resistant to frost.

Series IX. *Demissa* Buk.

This Mexican series is undoubtedly the most important from the point of view of breeding varieties resistant to blight, frost and Colorado beetle. Its best-known species, *S. demissum*, has been used more than any other as a basis for breeding for blight resistance. Besides the hexaploid *S. demissum* we have the pentaploid *S. Salamanii*, *S. edinense* and *S. semidemissum*, and the diploid *S. verrucosum*.

Series X. *Longipedicellata* Buk.

The geographical distribution of *Longipedicellata* is also Central Mexico spreading northwards into the southern states of the U.S.A. The species possess a certain degree of blight resistance, though not so much as *Demissa*. They are distinguished by the chromosome number (2n = 48; 36 in the hybrid species *S. vallis-mexici*), rather long pedicels (though this character is not always easy to determine), and the circular corolla with large acumens standing out sharply from it. The species grouped here are *S. longipedicellatum*, *S. Antipoviczii* (including *S. neoantipoviczii*), *S. ajuscoense* (including *S. candelarianum*), *S. malinchense*, *S. tlaxcalense*, *S. stoloniferum* *S. Fendleri* and the triploid *S. vallis-mexici*.

Series XI. *Cuneoalata* Hawkes.

This small series from South America includes the species *S. infundibuliforme*, *S. platypterum*, *S. xerophyllum* and *S. glanduliferum*. It is distinguished chiefly by the wedge-shaped wings on the central stalk or rhachis of the leaf. The chromosome number in the species investigated is $2n = 24$. So far no valuable characters have been discovered in this series, though there is a possibility that some may prove to be drought-resistant since they were found growing in very dry situations.

Series XII : *Polyadenia* Buk.

This is a monotypic series represented by only one species, *S. polyadenium*, which is distinguished by dense glandular pubescence and unpleasant odour. This species is chiefly noteworthy for its resistance to Blight and Colorado beetle but unfortunately will not form hybrids with any other.

Series XIII. *Tuberosa* Rydb.

Tuberosa comprises wild and cultivated species, including our European domestic sorts. It is characterised in a negative way by the absence of the special features that distinguish the series mentioned above. It is, in fact, a very wide grouping of species about many of which we do not know enough to classify them according to their affinities with any degree of accuracy. The plants always bear tubers (under the appropriate environmental conditions) and possess a rotate corolla and globular berries. The polyploid series in the wild species of this group is represented from diploid to tetraploid, whilst amongst the cultivated potatoes we have diploid to pentaploid types. Such well-known species as *S. Maglia*, *S. andigenum* and *S. tuberosum* are placed in this series.

Special Uses of the Wild and Primitive Cultivated Potatoes in Breeding

All the primitive cultivated species are susceptible to Blight (*Phytophthora infestans*). Some forms of *S. andigenum* are perhaps more resistant to infection than our European varieties but their resistance is only a matter of degree, and it is extremely doubtful whether they would be of any use as parents for breeding Blight-immune varieties. Far more important are certain Mexican wild species, some of which exhibit total immunity and others a high degree of resistance. The immune species are *S. demissum* (certain varieties are, however, susceptible), *S. lanciforme*, *S. cardiophyllum*, *S. Bulbocastanum* and *S. polyadenium*. The highly resistant ones are *S. semidemissum*, *S. verrucosum*, *S. Antipoviczii*, *S. ajuscoense*, *S. longipedicellatum*, *S. vallis-mexici*, *S. tlaxcalense*, *S. malinchense* and *S. Salamanii*.

Commercial varieties have now been produced in Great Britain, the U.S.A. and Germany that derive their immunity from *S. demissum*, which is by far the best species to use in this respect. There are several different strains or physiological races of the Blight organism and the commercial varieties so far produced only possess immunity from the common strain which is the least virulent. However, the parent wild species is immune from all races so far discovered, and breeders are now working to produce varieties resistant to the other strains too.

Resistance to virus diseases has only recently been worked on and is complicated in that different types of resistance may be found. We may have the partial sort of resistance where varieties do not contract virus diseases or do so only very slowly in the field but are sometimes quite susceptible when infected artificially. In the second place there are all the varying degrees of intolerance, culminating in field immunity, when infection is restricted to necrotic local lesions, and a top necrosis results on grafting with an infected scion. Immunity here is a sort of supersusceptibility, where the tissues of the host plant die and so prevent further spread of the disease. There is also a true immunity reaction where the virus cannot be recovered from the plant after having been transferred to it. The top-necrotic reaction to potato virus " X " has already been demonstrated in domestic varieties by Cockerham,[1] whilst Schultz *et al.*[2] have shown the presence of true immunity to this virus in the U.S.D.A. seedling 41956, which was derived from crosses between domestic types and a native Chilean variety that was generally supposed to have conferred the immunity factors. Resistance to virus " Y " has been found in Mexican and South American wild species, such as some lines of *S. demissum*, *S. malinchense* and *S. simplicifolium*. In Germany also, breeding work for virus resistance is based partly on lines with South American parentage.

In the high mountainous regions of South America the potato has for ages been grown at altitudes of 12-13,000 ft. This is a zone with frequent frosts at the beginning and end of the growing season. Three cultivated species, *S. Juzepczukii*, *S. curtilobum* and *S. Ajanhuiri*, grown in this region withstand frosts of −5° to −6° C. Species of the *Acaulia* group ascend

[1] G. Cockerham, *Ann. Appl. Biol.*, vol. xxx, pp. 105-8, 1943.
[2] E. S. Schultz *et al.*, *Amer. Potato J.*, vol. xiv, pp. 124-7, 1937.

still higher, even up to 14,000 ft., and withstand temperatures of $-10°$ C. Frost resistance is also to be found in *S. demissum*, *S. semidemissum*, *S. edinense*, *S. Henryi*, *S. Ohrondii*, *S. Commersonii*, *S. Millanii*, *S. Bukasovii* and *S. Abbottianum*. Plant breeders have chiefly made use of the species *S. demissum*, *S. acaule* and *S. curtilobum*. Both *S. curtilobum* and *S. demissum* will hybridise easily with European varieties but hybrids with *S. acaule* are more difficult and not so satisfactory.

Resistance to other fungus and to bacterial diseases has also been demonstrated among the wild potato species, whilst eelworm (*Heterodera rostochiensis*) resistance has been reported by Ellenby.[1] Resistance to Colorado beetle has been demonstrated by various workers in *S. chacoense*, *S. Henryi*, *S. polyadenium*, *S. Jamesii*, *S. demissum*, *S. acaule* and *S. verrucosum*. The most promising parental material is obtained from *S. demissum* and *S. chacoense*.

The ecological properties of the tuber-bearing species are such that types suitable for the tropical and subtropical belts of the world may be evolved from them, whilst others may contribute to the production of drought-resistant varieties. Some of the diploid cultivated species, such as *S. Rybinii*, *S. Cardenasii*, *S. Phureja* and others mature early, possess no dormancy period in the tubers and grow in lower subtropical altitudes in the Andes. Certain wild species, such as those included in the series *Cuneoalata* grow under conditions of extreme drought and may be of value in breeding for this property in domestic varieties.

Work has also been done with the wild and primitive cultivated species on protein and vitamin content, but though the results indicate promise not enough fundamental work has been done on this subject to make them quite certain.

It has been determined that, in the absence of male sterility, successful hybridisation between species does not depend on chromosome numbers but largely on the taxonomic nearness of the species concerned in the cross. With the exception of *S. Rybinii*, the 24 and 36 chromosome species have hitherto produced no promising hybrids. According to Bukasov,[2]

[1] C. Ellenby, *Empire Journ. Exp. Agric.*, vol. xiii, p. 158, 1945.

[2] S. M. Bukasov, "Interspecific Hybridisation in the Potato," *Bull. Acad. Sci.*, U.S.S.R., 1938.

crosses between species differing in chromosome number are usually successful if the chromosome numbers are multiples ($2n = 24$, 48 or 72). The triploid species are very difficult to cross with other species. Of the pentaploid species one, *S. curtilobum*, crosses with the diploids and tetraploids, while another, *S. semidemissum*, does not. The hexaploid *S. demissum* will cross reciprocally with *S. tuberosum*.

So far, it has not been possible by crossing wild species together to produce a cultivated species, either a known one or a new one. High yields must, therefore, be introduced from the cultivated species. Hybrids of the short-day cultivated species are usually low yielders in the temperate zones, where high-yielding hybrids can be obtained only by crossing with *S. tuberosum*. In this way satisfactory new varieties may be obtained in the first generation of crosses between *S. andigenum* and *S. tuberosum* or in the back-crosses. Hybrids of wild species usually require three or more back-crosses with *S. tuberosum* before forms suitable for commerce are produced. In view of the sterility of many of the F_1 hybrids from interspecific crosses and the fact that any offspring they produce may have the wild chromosomes predominating, the use of the F_2 hybrid generation in breeding is rarely to be recommended and back-crosses with *S. tuberosum* are usually to be preferred. Repeated back-crossing with the same variety is not such a profitable line to follow as that of using a different variety each time a back-cross is made. Diploid by tetraploid (*S. tuberosum*) crosses often produce tetraploid progeny which may be fertile. This has been observed in crosses of both *S. Rybinii* and *S. phureja* with *S. tuberosum*. Hybridisation between three or more species is sometimes the only practical way of combining two species that do not cross directly.

The practical success which has followed interspecific hybridisation of potatoes in Great Britain, the U.S.A. and the U.S.S.R. augurs well for the extension of the range of cultivation and usefulness of an already highly important crop plant.[1]

Potato breeding is discussed in Chapter VIII.

[1] For further information, see J. G. Hawkes, "The Indigenous American Potatoes and their Value in Plant-breeding," *Empire Journal of Experimental Agriculture*, January 1945.

THE POTATO PLANT

No study of potato varieties should exclude some preliminary knowledge of the general characteristics of the plant.

At the outset, it should be noted that differences exist between plants derived from true seed and from tubers respectively. A true seed produces a seedling with a definite tap-root and two or occasionally three ovate cotyledons. Because of the climatic conditions, such a seedling does not develop well in Europe unless grown under glass during its initial period of existence. A good seedling will, nevertheless, crop as well as a plant derived from a seed tuber. The latter type has no tap-root or cotyledons and begins from an eye, or bud, on the sett. This is the type of plant with which the grower has to deal and which must now be considered.

The Root System

All roots on the potato plant are adventitious and arise in groups of three or four at the nodes of the underground stem or stolon. The system is distributed mainly in the upper layers of the soil, but individual roots may penetrate deeply into the subsoil. Although roots may form on the cut surfaces of tubers, tubers themselves do not bear normal roots. Frequently, however, at each side of a basal eye a depression is found and arising from the centre of this is a small rootlet. Such depressions and rootlets are more common in deep-eyed potatoes than in shallow-eyed varieties.

The Aerial Stem

The above-ground stem of the potato is herbaceous and erect in the early stages of growth, but later becomes more spreading. The thin-walled cells of the pith can be recognised readily in the centre of a cross section. In the lower parts of the stem the pith generally breaks down leaving a hollow ; the nodes, however, are always solid. The vascular cylinder of the young stem consists of isolated groups of bundles corresponding chiefly to the angles of the stem, but in older tissue they unite to form a closed cylinder round the pith. The vascular cylinder thus formed is the principal track for the conveyance of water and food material ; it can be traced continuously from the root or sett into each leaf and stolon

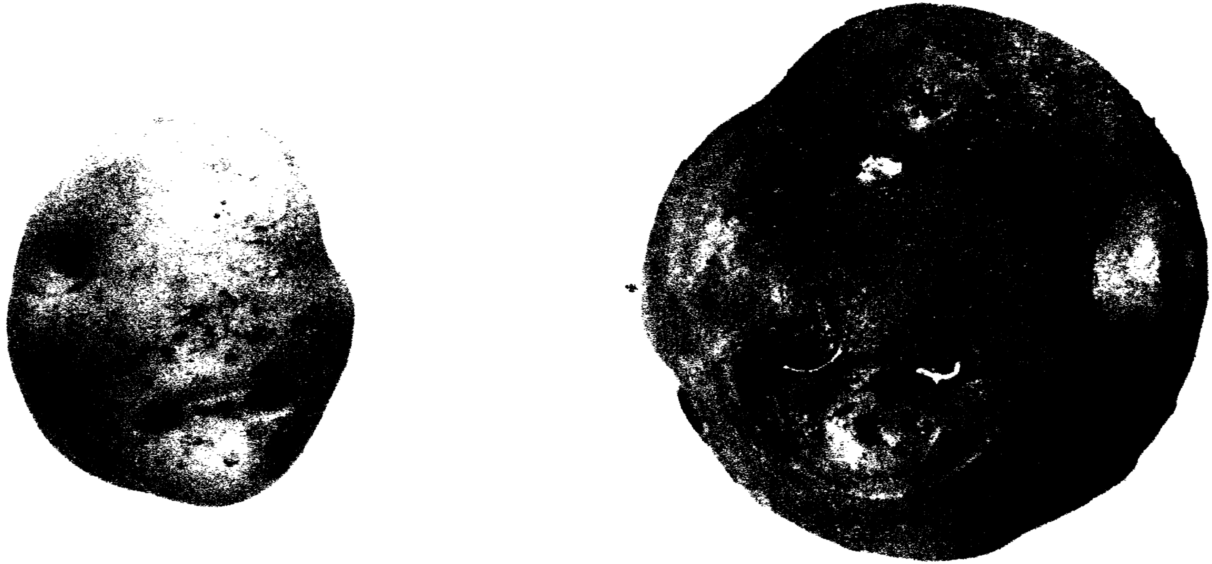


FIG. 2.—Tubers showing rootlets and depressions at the sides of basal eyes.

and through the heel-end into each tuber. The cortex of the stem consists partly of thin-walled and partly of thicker-walled cells. Below the epidermis the colouring matter of the stem is to be found in one or two layers of cells; the colour is green if these cells contain chlorophyll alone; in coloured stems the chlorophyll is partly obscured by a pigment dissolved in the cell sap. The epidermis, or outermost layer of cells, is always more or less pubescent, *i.e.* hairy.

The stem is normally triangular in cross section, except at the nodes, where it is round. At each angle of the triangle the margins are drawn out to form wings (Fig. 9), which originate in pairs at the base of each leaf and are decurrent unequally on the stem, one extending for one internode the other for two internodes. The portion of the stem covered with soil has no wings, is round in cross section and normally solid.

THE LEAF

The first leaves are more or less entire. Later they become more compound and irregularly pinnate, opposite pairs of large leaflets alternating with smaller ones (secondary leaflets). The leaves are arranged on the stem in a spiral, usually to the left up the plant. At its junction with the stem, the leaf encircles the latter for nearly one-third of the circumference. Two stipule-like growths are to be found at the base of all normal leaves; these are half-moon shaped and encompass the stem. Young potato leaflets are thickly covered with hairs, some of which are long and straight, others being shorter and glandular. The mature leaflet has relatively fewer hairs. Stomata, or pores, are found on both surfaces, but they are more abundant on the lower.

THE FLORAL PARTS

The inflorescence is a cyme (Fig. 15). The flower stalk, or peduncle, terminates the growth of the stem and is pushed to one side by an axillary shoot from the penultimate or sometimes the ultimate leaf which continues the growth in length of the stem (see Fig. 14).

There are five partially united sepals. The petals are also united, the corolla being tubular with five lobes. Radiating from the centre of the flower are five rays or ribs. These rays are collectively known as the "star," and consist mainly of vascular bundles. There are five stamens which are alternate with the corolla lobes and are attached to the tube. The stamens have orange or yellow anthers which in some varieties are tinged in certain places with red or violet. The latter are larger than the filaments, and, until maturity, they form a close column round the style. Each anther has two lobes, and each lobe consists of two pollen sacs which open by means of a single pore situated at the apex. There are two completely fused carpels forming a two-celled ovary with a single style and bi-lobed stigma. The ovary is superior and the placentation axile. The potato "plum," "seed ball" or "apple" is a berry, round, two-celled and many-seeded, containing sometimes up to 500 seeds.

The Tuber and Stolon

Shortly after the potato haulm appears above ground, stolons develop in the axils of the scale leaves on the underground portion of the stem. These stolons lengthen for several internodes and ultimately swell at their tips to form tubers. The tubers and stolons, being modified stems, present a typical stem structure, the tissues having undergone the same process of development as those of the stems. The change from stolon to tuber is quite abrupt. According to Artschwager,[1] in the young tuber extensive cell division takes place in the pith and much less in the outer cortical region; hence the vascular tissue in passing from stolon to tuber bulges outward and is to be found not far from the skin. Later growth results from active division of cells lying between the cortex and the pith, divided into two unequal parts by the narrow vascular ring; these become the chief starch-containing cells. On cutting a mature tuber it is easy to recognise the vascular cylinder which lies roughly about one-eighth of an inch below the skin. This cylinder encloses a large amount of storage tissue and the pith, while externally there are more storage cells and the cortex. While the tuber is expanding fine strands of vascular bundles are formed amongst the pith and storage cells; the bundles can be clearly traced entering the heel end of the tuber from the stolon and sending branches into each eye. The pith forms the central part of the tuber

[1] E. Artschwager, "Studies of the Potato Tuber," *Journ. Agric. Res.*, vol. xxvii, p. 4, 1924.

and it is broadest near the middle; it gives off lateral branches which communicate with the eyes and it terminates with the apical eye. The entire tuber is covered with a corky skin, from six to ten cells deep; this skin is pitted with lenticels (breathing pores) which, under certain conditions, become quite visible as white dots owing to a proliferation of their tissue.

Morphologically the tuber is a shortened, thickened stem with scale leaves, and in the axils of these leaves lie the eyes. Each eye is a collection of buds lying more or less in a depression. The number of buds in each eye may be greater, but the normal is three. Actually, the eye is a lateral branch with undeveloped internodes. Thus it will be seen that the tuber is a branched shoot system and not a simple shoot. At the rose end, or apex, of the tuber the eyes are more crowded than at the heel, or stolon, end.

POTATO VARIETIES

What is a potato variety? If the history of any variety be traced, it will be found that all stocks have had a common origin in one plant which, in turn, was derived from a true seed. Vegetative variations occur occasionally in the potato; for example, Field-Marshal is a variation of Up-to-Date. When plants are propagated by seed tubers, however, the characters of a variety, and even of a variant, remain for all practical purposes constant from season to season. This constancy in vegetative reproduction is the chief characteristic of varieties.

There is no record of a multiplicity of varieties having been brought to Europe at the time of the original introductions, and it would appear that the majority of existing varieties have been derived from a few initial types. This remarkable fact can be explained only on the assumption that the original types were not only self-fertile but also of a very mixed nature. For a long period after the introduction of the potato there was no mention of different varieties. According to Davidson,[1] Rye, an Irish writer, in his work *Considerations on Agriculture* (1730), was the first to refer to British varieties, and he described five types. After this, reference to varieties became fairly

[1] W. D. Davidson, "History of Potato Varieties," *Journ. Department of Agriculture, Dublin*, vol. xxxiii, No. 1, 1935.

frequent. In *The Agriculturists' Manual*, published in 1836 by Messrs P. Lawson and Son, Edinburgh, there appears a classified list of 146 varieties. According to Davidson, the most outstanding of the old varieties were: The Black Potato (before 1730), Cluster (1765), Apple (about 1768), Red-nosed Kidney (about 1775), Manly (before 1776), Ox Noble (before 1787), Lumper (before 1808), Cups (before 1808), Ashleaf (about 1813), Regent (before 1841), Fluke (1841), Rocks (before 1856), Myatt's Ashleaf (about 1853), Paterson's Victoria (1863), Nicol's Champion (1876) and Magnum Bonum (1876). To this list should be added Early Rose (1867) because of its very great influence, directly or indirectly, as a parent of many later and important varieties; also Maincrop (1876), of which Golden Wonder is a variant, is entitled to a place of honour. Of the more modern varieties the following are outstanding: Duke of York (1891), Up-to-Date (1893), British Queen (1894), Epicure (1897), King Edward (1902), Great Scot (1909), Majestic (about 1911) and Arran Chief (1911). The most successful of the most recent introductions are: Kerr's Pink (raised 1907 and marketed in 1915), Arran Banner (1927), Arran Pilot (1931), Gladstone (1934), Dunbar Standard (1936) and Home Guard (1941). Numerous new varieties, however, are now appearing on the market and it will be some time before their merits and popular favour can be assessed. Of particular interest are the varieties registered by the Department of Agriculture for Scotland. Included in these are two —Orion (Smith) and Pentland Ace (Scottish Society for Research in Plant Breeding)—which are immune from the common form of Blight.

The outstanding characteristics demanded of a good variety are: good cropping capacity, disease resistance, good cooking quality, good shape, good keeping quality, capacity of the foliage to fill the drill except where intercropping with other plants is practised, absence of long stolons, and, as regards the normal British Market, white flesh and the absence of deep purple pigment throughout the tuber skin. For special purposes different qualities are sometimes required. In the crisp trade, for instance, yellow-fleshed varieties are popular. Without a fair share of these qualities no variety has any chance of success. Varieties, however, differ in other respects, some for instance maturing at different periods of the growing season. These differences are important in commerce and varieties are classified as first-earlies, second-earlies, early maincrops and lates. No two varieties are identical either physiologically or in external characters, and it is because of the peculiarities of each variety that the ability to differentiate the various sorts is so important. The merits of any variety can be appreciated only if the stocks are pure, and purity can be obtained, and maintained, only if the grower has knowledge sufficient to enable him to identify the various sorts.

CHAPTER III

INTERVARIETAL DIFFERENCES IN THE POTATO FOLIAGE

POTATO varieties have been elaborated through generations of cross-breeding; even the seeds of self-set berries of all popular varieties carry many characters in a blended state and give rise to plants which differ amongst themselves and are distinct from the parent. It is not easy for the expert to find seedlings which he cannot readily distinguish from one another; but all conditions prevail, ranging from plants which differ widely to those which are very similar. Differences, which appear not only in grosser features, but also in detail, are not confined to form, but extend also to physiological and chemical qualities.

Many characters, *e.g.* flower and tuber colours, are little affected by environment, for all practical purposes remain constant and are, therefore, of first importance in differentiating varieties. Others, *e.g.* leaf and tuber shapes, are affected more by environment and, depending on the conditions of growth, fluctuate about a mean and have thus only a relative value. Nevertheless, as the modifications of any character are normally of the same degree for all varieties grown in similar conditions, relative differences are very important. Most characters, whether relative or otherwise, express themselves variously in different varieties, so that, while generally appearing, they are pronounced in some, weak in others and intermediate in many. Thus leaflets may be described as large, small and intermediate. It is the extremes, the pronounced and weak expression of the character—in this instance the large and small leaflets—which are most helpful in the field.

Since the study of varieties on the basis of individual differences is tedious and difficult, anything conducing to a more systematic approach to the subject is helpful. Some characters are very frequently associated. The recognition of these makes it possible for the student to view the plant as a whole and to think in terms of differences between plants and groups of varieties instead of differences in individual parts of plants. Thus foliages may be grouped into types; with these maturity and tuber characters are often associated. A whole range of character expressions is connected with the appearance of colour in the tuber cork. Certain sprout features are associated with characters found in the above-ground plant. As these characters are all so helpful, the student is recommended, once he has read the sections dealing with intervarietal differences, to study the section (Chapter VI) dealing with the subject of associated characters.

While potato characters are very constant, on no account should abnormalities resulting from diseases, physiological disturbances and other agencies be ignored.

Certain diseases modify normal foliage characteristics and make identification difficult. A few, such as Blight, destroy the foliage; others, such as some virus diseases, while not destroying the foliage, modify to a large extent the typical appearance of the leaves and reduce not only the flowering but the size of individual flowers. Injury induces rigidity and it is difficult, for instance, to distinguish an injured King George plant from one of British Queen. Folding of the leaflets may be conditioned either by certain diseases, mineral deficiency or injury. In the evening most varieties show "sleep" movements, the upper and younger leaflets folding and becoming more upright, giving the plant a distinctive appearance. These factors should all be taken into account if mistakes are to be avoided, and the student is advised to study diseases, particularly virus diseases, concurrently with varieties. Finally, it must be emphasised that environment, *i.e.* climate, soil and manuring, affects the expression of individual characters and that, therefore, the complete mastery of varieties can be obtained only through studies of plants grown in various places and in different seasons.

FOLIAGE

All varieties may be identified with certainty by their foliage alone during the summer months. Foliage differences appear immediately the first leaves emerge from the soil. Arran Peak may, for instance, be rogued early by having regard to the dark colouring of its initial leaves. Identification of varieties is easiest, however, when the foliage is well grown, about the flowering stage, differences being then most marked. No hard and fast classification of the above-ground parts is possible since an endless number of types exists. Considering the foliage as a whole, the most that can be done is to define certain types and so to describe them that those interested will have less difficulty in the identification of varieties and the recognition of impurities in crops.

In summer, identification is governed largely by general appearance: the skilled observer recognises varieties by general appearance without regard to the various characters. This composite impression is very difficult to define because it is not produced by a few characters but by many, some of which are difficult to describe. However, the essential features of the various combinations are :—

1. The contour of the foliage.
2. The relative height of the stems.
3. The number, branching and colouring of the stems.
4. The size, number and set of leaves.
5. The distribution, size, shape, number and colour of the leaflets.
6. The profusion and colour of flowers.

The foregoing are modified by environment but essentially they are hereditary characters and are transmitted by vegetative propagation. We propose to consider here eight standards or groups. Many varieties cannot be classed, while other groups, with a limited number of varieties in each, might be defined. Once the student has grasped the principle of recognising varieties by their resemblances to those with which he is familiar, however, he may profitably attempt to construct other groups himself.

Group 1.—Type: Duke of York (Fig. 3)

(All early varieties)

Salient Features.—Low growing; spreading; stems weak; leaves long, open and drooping; leaflets long, narrow and light coloured.

Duke of York.	Early Rose.	Puritan.
Dunbar Yeoman.	Immune Ashleaf.	Reading Russet.
Edzell Blue.	Mr Breese.	Witchhill.
Entente Cordiale.	Ninetyfold	

FIG 3—Foliage Habit typical of Group 1 Varieties Spreading and drooping.
FIG 4—Foliage Habit typical of Group 2 Varieties Spreading with vigorous basal foliage.
FIG 5—Foliage Habit typical of Group 3 Varieties Upright with drooping tops

FIG. 6.

FIG. 7.

FIG. 8.

FIG. 6.—Foliage Habit typical of Group 4 Varieties. Upright; tops not so rigid as in Group 6.
FIG. 7.—Foliage Habit typical of Group 5 Varieties. Upright and open.
FIG. 8.—Foliage Habit typical of Group 6 Varieties. Upright with rigid tops. (*Note.*—Some varieties in this group have less rigid tops than others.)

GROUP 2.—TYPE: BRITISH QUEEN (FIG 4.)

Salient Features.—Taller than group 1; bushy and spreading; stems more robust than in group 1; branching; basal foliage vigorous; tops fairly stiff; leaf and leaflets more rigid than in group 1.

(*a*) Flowers white; foliage dark:—
Ballydoon, British Queen, Dr McIntosh, King George, Majestic, Rogue like British Queen and Rogue like King George.

(*b*) Flowers coloured; foliage dark:—
Arran Pilot, Catriona and May Queen.

(*c*) No flowers; foliage dark:—
Arran Luxury and Rogue like May Queen.

(*d*) Flowers coloured; foliage light:—
Bobbie Burns, Craigs Bounty, Early Market, Field-Marshal, Glenshee, Craigs Snow-white, Tinwald Perfection and Up-to-Date.

GROUP 3.—TYPE: KING EDWARD (FIG. 5)

Salient Features.—Medium to tall; upright; little obvious branching; leaves drooping; characteristic drooping tops; seldom flowering.

Epicure.	Lymm Gray.	Rogue like Epicure.
Evergood.	Prizetaker.	Royal Kidney.
King Edward.	Red King.	St Malo Kidney.

GROUP 4.—TYPE: GREAT SCOT (FIG. 6)

Salient Features.—Medium to tall; upright; stems robust; little obvious branching; leaves rather drooping; lacking characteristic tops of group 3 varieties.

Abundance.	Craigs Alliance.	John Bull.
Arran Banner.	Craigs Defiance.	Magnum Bonum.
Arran Chief.	Craigs Royal.	Orion.
Bellahouston	Great Scot.	Rogue like Great Scot.
Ben Lomond.	Irish Queen.	The Baron.

GROUP 5.—TYPE: KEPPLESTONE KIDNEY (FIG. 7)

Salient Features.—Tall, very upright and open; stems robust and highly coloured; internodes long; very little branching; leaf open, mid-ribs coloured.

Cardinal.	Kepplestone Kidney.	Red Ashleaf.
Edgecote Purple.	Long Blue.	Tawny.

GROUP 6.—TYPE: KERR'S PINK (FIG. 8)

(All late varieties)

Salient Features.—Tall; upright; foliage dense, compact and vigorous; stems very robust, branched apically and coloured; leaves fairly open and rigid, more numerous than in group 5 varieties and evenly distributed from base to top; midribs coloured.

Arran Victory.	Kerr's Pink Substitute.	Shetland.
Flourball.	Peerless.	Shamrock.
Gregor Cups.	Red Letter.	Sir Rufus.
Kerr's Pink.	Ryecroft Purple.	

Group 7.—Type: President

(All late varieties)

Salient Features.—Medium to tall; upright; leaves making an acute upper angle with stem; leaves rigid; leaflets dull, secondaries few.

Arran Cairn.	Blue President Rogue.	Marconi.
Blue Grey.	General.	President.

Group 8.—Type: Eclipse

Salient Features.—Varieties in this group have light green foliage with matt and somewhat wrinkled leaflets. In other respects the varieties may differ and indeed, as with Early Market, can be placed in other groups.

Early Market.	Rogue like Eclipse.
Eclipse.	Stirling Castle.

THE CONTOUR

The foliage contour may be described as spherical when the growth is equal in all directions. Such a contour is typical of many early varieties. Later types show a more abundant growth upwards, hence the typical profile becomes more rectangular and modified according to the vigour of the apical or basal foliage. Kerr's Pink and Golden Wonder present a long, whereas Great Scot and Arran Chief show a short rectangular profile. The dense apical foliage of such varieties as Sharpe's Express distinguishes them from varieties in groups 1 and 2.

THE STEM

Stems differ according to variety in the following respects: height, colour, frequency, branching, thickness and solidity, peculiarities of wings, straightness, nodes and internodes, and pubescence.

(*a*) *Height.*—The stem height is associated largely with maturity: in early varieties the stems are normally not tall; in late types they may be very tall; while varieties of intermediate maturity have stems of intermediate height.

(*b*) *Colour.*—The stem colour is of great use in the diagnosis of varieties. Some, *e.g.* Fortyfold and Harbinger, always have green stems, but colour appears in most varieties. This is due to a pigment which produces a range of colours from pale brownish red to deep purple. Differences exist not only in the intensity of colour but also in its distribution : thus the stems of British Queen and King George are reddish-brown at the base, those of Champion and Arran Peak mottled purple, those of Di Vernon red-purple, those of Epicure and King Edward tinged pink, and those of Arran Chief and Abundance tinged blue-purple especially at the base. In many instances the stem is markedly coloured at the base of the leaf, this being a special feature of Peachbloom, Buchan Beauty, Lord Tennyson and certain other varieties whose tubers have coloured cork. The colouring, however, is not confined to this type of variety. In a few varieties the colour is found both in the superficial cells and the vascular tissue. Very frequently the stem colour intensifies as the season advances, hence young plants cannot be compared with old. Varieties with coloured tuber skins generally have coloured stems ; there is, however, no absolute correlation between stem and tuber-skin colours : Fortyfold, with coloured tubers, has green stems, while Eclipse and International Kidney, white-tubered varieties, have coloured stems.

(*c*) *Frequency.*—Varieties differ greatly in the extent of stem development, some, like Arran Pilot, Rocks and Champion, having many stems and others, such as Golden Wonder and President, having only a moderate number. Most varieties are intermediate as regards this character, but those at the opposite ends of the scale in numbers can be separated very readily.

(*d*) *Branching.*—Branching in some respects is of less importance than other stem characters. It is variable, often hidden by the leaves, and may be expressed in the general habit of the plant. Two types, viz., basal and apical, are readily recognisable. Basal branching is typical of group 2 varieties, while apical branching is typical of those in group 6. Some varieties, *e.g.* Arran Comrade, Home Guard and Great Scot, show practically no branching.

(*e*) *Strength, Thickness and Solidity.*—Generally, early varieties which tend to droop have weak stems. This drooping character is doubtless due to want of firmness in the tissues, but it may also in part be attributed to the thin nature of these stems. Thin stems, however, are not always weak: the variety Champion has thin but strong, upright stems. Late varieties usually have thick stems. The robustness of the stems, or the reverse, is a useful diagnostic character.

Reference has already been made to the breaking down of the pith in the internodal tissue of all but the upper parts of the aerial stem. This leaves the stems hollow, a condition which is easily determined if the stem is cut across between two nodes. The pith does not, however, invariably break down and the varieties, Eclipse and Carisbrook Castle, whose stems are solid until maturity is almost reached, are outstanding exceptions.

(*f*) *The Wings.*—These can be of considerable use diagnostically. In some varieties, *e.g.* John Bull, they are inconspicuous, while in others, *e.g.* Majestic, they are broad. Some varieties, Arran Chief and Arran Peak, for example, have waved wings (Fig. 9), while others, *e.g.* King Edward, have straight wings (Fig. 9), and others again, *e.g.* Fortyfold, have wings which are waved at the top and straight towards the base of the plant. When the stems are coloured the wings are usually also coloured, but there are exceptions: Di Vernon, Arran Peak and Peachbloom are examples of the combination, coloured stems and green wings; in Cardinal and Edgecote Purple the wings and stems are similarly coloured; and in Yam the wing is usually darker than the stem.

(*g*) *The Straightness of the Stem.*—The great majority of varieties have fairly straight stems, hence the zigzag stems of such varieties as President, John Bull, Arran Cairn and Blue Grey are outstanding. Continental varieties show this feature to a greater degree than British.

(*h*) *Nodes and Internodes.*—The nodes may be used at times in distinguishing varieties. The varying characters are colour and size. In many varieties the stem colour does not pass through the nodal tissue, so that the latter is greener than the remainder of the stem. This condition is well illustrated in Eclipse. There are, however, other varieties, *e.g.* Arran Victory and International Kidney, in which the nodal tissue is as highly pigmented as the internodal tissue. A few varieties are distinguished by their swollen nodes, a feature specially prominent in Summit.

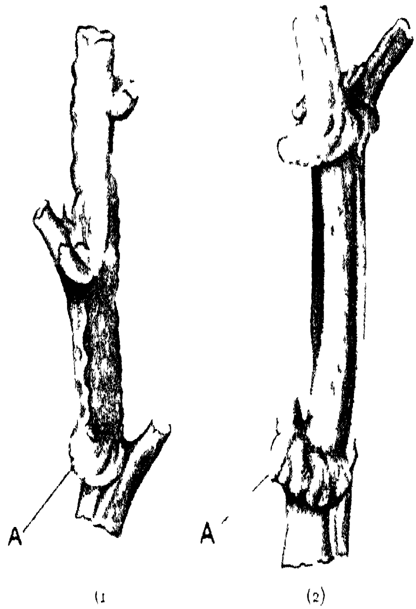


Fig. 9.—Potato Stems showing (1) waved wing and (2) straight wing.
A, Stipule-like growths.

The length of the internodes is a varietal character. In some varieties (*cf.* group 2) the basal internodes are short, leading to a crowding of the leaves at the bottom of the stems; in others, *e.g.* Immune Ashleaf and Sharpe's Express, the reverse condition holds and the leaves are more crowded at the apex. Generally, internodes are fairly uniform, long, as in such varieties as Golden Wonder and Kepplestone Kidney, and short as in Arran Comrade and Northern Star.

(*i*) *Pubescence.*—The stem hairs are usually most conspicuous at the base. Varieties differ as regards the frequency of these, however, and this character corresponds roughly with the hairiness of the tuber sprouts. Thus Ballydoon, British Queen, Di Vernon and Duke of York have hairy stems, while Arran Chief and John Bull have almost glabrous stems.

LEAVES

The leaves of varieties differ in the following characters: frequency, size, set on stem, openness, number of primary leaflets, number and position of secondary leaflets, and the pubescence of the midribs and stipule-like growths.

(*a*) *Frequency.*—The leaf frequency is an important diagnostic character. When leaves are numerous the plant presents a compact appearance, but where they are few an entirely different aspect is produced. Arran Comrade is typical of the first and Red Ashleaf of the second type. Where the characteristic is of service, the differences are so obvious that counting is unnecessary.

(*b*) *Size.*—Leaves may be long, short, broad or narrow. Up-to-date, Immune Ashleaf and Arran Consul are varieties with exceptionally long leaves; Eclipse, Northern Star, President and Blue Grey are short-leafed; while leaves of intermediate length are found in varieties such as Great Scot, Kerr's Pink and King Edward. The length of the leaf is generally more helpful than the width, but on occasion the latter may be useful: Dargill Early may, for example, be distinguished from Myatt's Ashleaf, which it closely resembles, by its broader leaf.

(*c*) *Set on Stems.*—This is an important feature, the outstanding characteristic of which is the presence of or want of rigidity in the leaf midrib. Where the midrib is rigid (Fig. 13, A) the leaf forms a more or less definite angle with the stem. In the varieties of group 7 the upper angle between stem and leaf is usually small; in others, *e.g.* Kerr's Pink and Dunbar

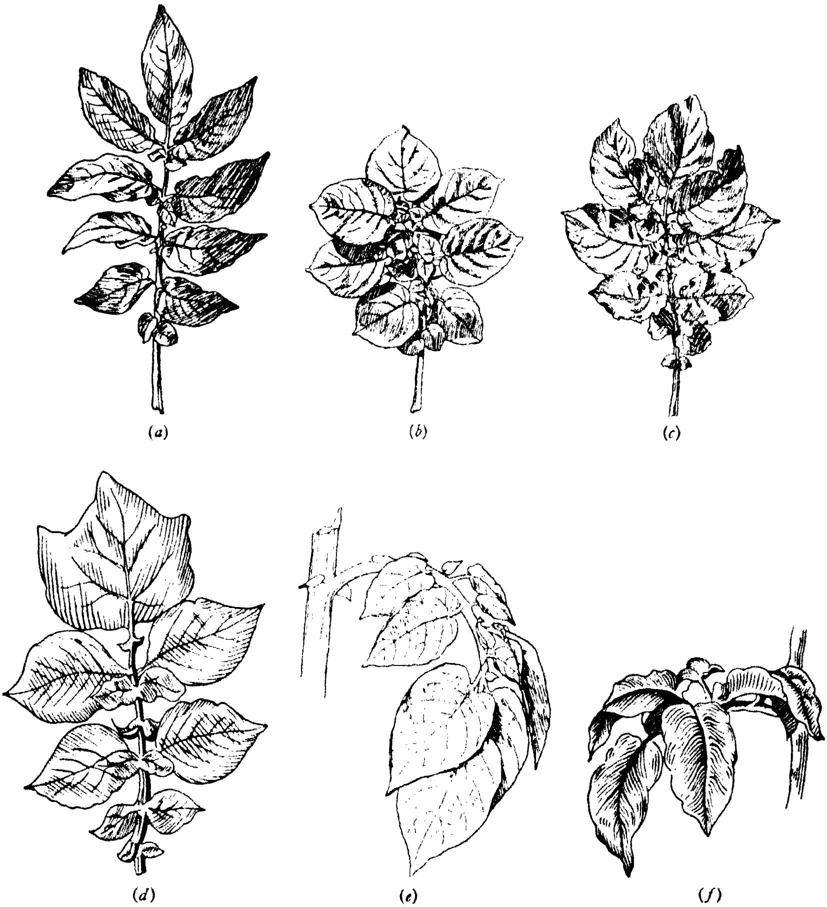


FIG. 10.—Potato Leaves.

(*a*) Open leaf with few secondaries; (*b*) close leaf with numerous secondaries; (*c*) leaf showing marginal waviness of leaflets; (*d*) leaf showing terminal leaflet fused with two lateral leaflets; (*e*) drooping leaf; and (*f*) leaf showing arched leaflets.

Cavalier, although the midrib is quite rigid, the angle is greater. On the other hand, the midrib may not be rigid and may droop (Fig. 10*e*), in which case an entirely different appearance is produced; drooping leaves are characteristic of varieties in group 1.

(*d*) *Openness of the Leaf.*—Figs. 10*a* and 10*b* illustrate open and close leaves. An open leaf is characterised by large intervals between the leaflets and the absence of large and crowded secondary leaflets. Open leaves are typical of the varieties in group 1, of Arran Consul, Champion and many other sorts. Where the opposite conditions prevail the leaf is termed close. Intermediate forms occur, but open leaves can always be distinguished from close leaves. The closeness of a leaf depends mainly on the frequency and size of the secondary leaflets as, for example, in the varieties Sharpe's Express and Lochar, but in some varieties it is due to the overlapping of the primary leaflets, the Alness and Irish Queen being varieties with close leaves due to this cause.

(*e*) *Number of Primary Leaflets.*—Varieties may be grouped as having numerous or few primary leaflets. In the former class occur such varieties as Up-to-Date, Sharpe's Express, Di Vernon and Immune Ashleaf, while of the latter Blue Grey, President and Ally are typical examples.

(*f*) *Number and Position of Secondary Leaflets.*—These are useful discrimination characters. Some varieties, such as Di Vernon, Gladstone and Sharpe's Express, have numerous secondaries (Fig. 10*b*), whereas in others, such as Ally, Arran Pilot and Alness, there are few (Fig. 10*a*). The general absence of secondaries on the midrib between the terminal and last pair of leaflets is characteristic of varieties such as Ally, Arran Luxury and Champion. The majority of secondary leaflets originate on the leaf midrib. Often, however, they appear at the junction of the leaflet petiole and the midrib, and when this occurs the leaflet appears to point towards the base of the leaf instead of outwards. Such leaflets are frequent in Arran Peak and Rhoderick Dhu. The presence of leaflets on the leaflet petiole is a common characteristic. These are sometimes referred to as tertiary leaflets and are common in Dunbar Rover, Dargill Early, Arran Banner and White City.

(*g*) *Colour of Midribs.*—The midrib colour can at times be helpful. Many varieties possess green midribs but in most some colour appears. Differences may be observed both in colour distribution and its tone. Colour is commonly found only at the base of the midrib and at the bases of the leaflet petioles; but, on occasion, the whole midrib may be coloured. Many colour tones are found, ranging from pale reddish-brown to deep-purple. Intense colouring at the base of the leaflet petiole and the base of the midrib, including, as regards the latter, both upper and lower surfaces, is characteristic of Dean, Lord Tennyson, Rector and Buchan Beauty, in which the tuber colour is located in the cork. Midrib colour is most highly developed in young leaves and faint colour often disappears with age.

(*h*) *Pubescence of Midribs.*—It has been pointed out previously that the upper surface of the midrib is invariably hairy. The condition of these hairs is sometimes helpful. British Queen, for instance, can be distinguished from King George, and Witchhill from Puritan, by the more upright hairs of the first-mentioned of each couple, the hairs of the last-mentioned being much more hooked.

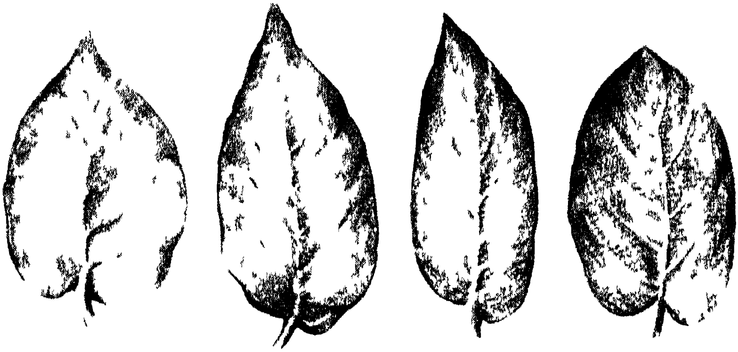
(*i*) *Stipule-like Growths.*—In the general description of the potato plant, it has been pointed out that two stipule-like growths (Fig. 14, E) occur at the bases of all normal leaves. With age these occasionally grow large and leaf-like, but in most varieties their size is typical. The upper surfaces of these growths are generally glabrous, hence varieties with hairy growths may be readily identified. Kerr's Pink and Gregor Cups are varieties which may be confused, particularly if the plants are affected with mosaic disease; reference to the stipule-like growths, however, leads to an easy separation of the two types, the growths in Kerr's Pink being large and glabrous, those in Gregor Cups being small and hairy.

LEAFLETS

The two types of primary leaflets are terminal and lateral, manifesting some of the same differences as the leaves, the varying characters being size and shape, colour and condition of surface, the set on the midrib, colour and length of petioles, condition of leaflet margin, joined leaflets, overlapping of leaflets and apparent thickness.

(*a*) *Size and Shape*

(i) *Terminal.*—Considerable differences appear in the shapes of terminal leaflets. In Herald and Harbinger, for example, the terminal is very large, while in Northern Star and Bobbie Burns it is small. An interesting feature of the



(a) (b) (c) (d)

FIG. 11.—Types of Leaflets

(a) Round and pointed
(b) Broad and tapering
(c) Narrow and tapering
(d) Broad and blunt

(a) (b)

FIG. 12.—Uneven and even Junctions of the Lobes and Leaflets next the Terminal. (a) Uneven; (b) even

leaflet is its base, which may be cordate (Fig. 11*a* and *d*), as in Red Letter and British Queen, or non-cordate (Fig. 11*b*), as in Kerr's Pink and Majestic. Terminals differ also in width; thus, King George may be easily distinguished from Majestic by its broader terminal alone, without regard to other characters.

(ii) *Laterals*.—Each variety has a typical lateral leaflet. In these descriptions the end pair of laterals, next the terminal, alone are considered. Length and width vary, so that many types appear. The leaflets of Champion and Arran Crest are long and narrow (Fig. 11*c*), those of Up-to-Date long and broad (Fig. 11*b*), those of Great Scot and Arran Chief broad but shorter, and those of Marquis of Bute and Lochar roundish (Fig. 11*a*). An essential shape feature is recognisable in the way the leaflets taper towards the tip. In some varieties, *e.g.* Sharpe's Victor and International Kidney, the tapering begins near the tip (Fig. 11*d*); in others it begins nearer the base. Most British varieties, however, have leaflets which begin to taper from about the middle of the long axis (Fig. 11*b*).

Differences may be seen also at the junction of the lamina with the petiole. Some varieties, *e.g.* Sharpe's Express, are markedly cordate at the bases of the leaflets, but in most this character is absent. A peculiarity of many types is found in the uneven junction of the two lamina lobes with the petiole: in many varieties, *e.g.* Ben Lomond, Baron and Up-to-Date, the upper lobe joins the petiole farther from the midrib than its neighbour (Fig. 12*a*); in many varieties the two lobes join the petiole at approximately the same place (Fig. 12*b*), this being typical of Arran Chief, Great Scot, Golden Wonder, Kerr's Pink and a number of other varieties; in some varieties, however, the character is not consistent and cannot, therefore, be used.

The leaflet tip is often valuable. In types such as Lochar, Dunbar Standard and Arran Crest it is pointed, whereas in Eclipse and Sharpe's Victor it is blunt.

A feature of great diagnostic value, although not often recognised as such, is the flatness of the leaflet surface. In most varieties there is a greater or lesser upwards folding of the two leaflet lobes—a folding which becomes less marked with age—hence the flat leaflets of varieties such as Arran Signet, Majestic, Arran Banner, Early Market and Redskin are characteristic.

(*b*) *Colour and Condition of Surface.*—Leaflets may be almost any shade of green, ranging from the light yellow-green of Early Market to the dark green of Gladstone. The colour is an extremely important feature, for although it can be altered by manuring it has always a relative value. Varieties may be classed as having leaflets of the following colours, viz.: (1) yellow-green, *e.g.* Fortyfold and Early Market; (2) grey-green, *e.g.* Ally, Dunbar Cavalier and Edzell Blue; (3) light green, *e.g.* Immune Ashleaf, Witchhill and Arran Signet; (4) medium green, *e.g.* Golden Wonder, Arran Consul; and (5) dark green, *e.g.* Gladstone, Di Vernon and Ben Lomond. Occasionally the younger leaflets are distinctively coloured: in Fortyfold, Craigs Snow-white, Lochar and Crimson Beauty, for instance, the younger leaflets are often much lighter than the remaining foliage; and in a few varieties, *e.g.* Redskin, the younger leaflets are often tinged purple. The surface of the leaflet may be matt or glossy, conditions determined largely by the prevalence, absence or condition of hairs. Ally, Early Market, Kerr's Pink and Golden Wonder are good examples of the first, and British Queen, Great Scot, King Edward and Ballydoon are typical of the second class. Another extremely useful character of the leaflet is to be found in surface smoothness or roughness. Some leaflets are corrugated, *i.e.* the tissue between the veins is raised above the level of the latter, giving the rough appearance. Arran Banner, International Kidney, the Rough-leaved Rogue, Conference and the Carrick Rogue are typical rough-leaved varieties. The occurrence of the yellow spotting of Aucuba Mosaic may be noted. In some varieties, *e.g.* Ninetyfold, practically every plant is spotted.

Another feature of the leaflet is the appearance of greyish-green "blotches." These are common in Arran Pilot and are found also in Arran Viking and Red Letter. According to Sheffield,[1] the "blotches" are due to necrosis of the epidermis, followed by cell division in the palisade tissue resulting in the formation of several layers of small, thin-walled, colourless cells. The proliferation may occur on the top only, or on both sides of the leaflets, and the new tissue partially masks the green plastids in the tissue nearer the centre of the leaflet. "Blotches" can usually be separated

[1] F. M. L. Sheffield, "The Blotches on the Leaves of Arran Pilot Potatoes," *Ann. App. Biology*, p. 29, 1942.

from Mosaic symptoms when the leaflet is held against the light: the "blotches" disappear while the Mosaiced leaflet appears mottled.

(*c*) *The Set on the Midrib of the Leaf.*—The position of the leaflet relative to the midrib of the leaf varies considerably; leaflets may be rigid or drooping according to the rigidity of the leaflet petiole. Arran Crest, British Queen, President, Kerr's Pink and many others have rigid leaflets (Fig. 13, A), whereas, for instance, in Royal Kidney and Harbinger the leaflets droop (Fig. 10*e*). Some varieties are characterised by drooping terminals, the laterals being more or less rigid. Such, for example, are Great Scot and Arran Victory. Another type of leaflet set is found when the leaflets rise first above the level of the midrib and then fall, a condition known as "arching" (Fig. 10*f*), and found in Crusader, Rocks and Beauty of Bute.

(*d*) *Colour and Length of Leaflet Petiole.*—The leaflet petiole may be either green or coloured. In some varieties colour is concentrated chiefly at the base of the petiole, but in others, *e.g.* Majestic and Arran Signet, and particularly in the younger leaflets, the colour may run well up the mid-vein of the leaflet. High colouring at the base of the leaflet petiole is associated with colour in the tuber cork. Petioles may be long or short; long, for instance, in Arran Banner, White City and Dunbar Rover, and short in Harbinger and Myatt's Ashleaf.

(*e*) *Condition of the Leaflet Margin.*—In most varieties the leaflet margin is straight, but in a few, *e.g.* Sharpe's Express, it is turned up slightly, presenting a cupped appearance. Fig. 10*c* illustrates a type of marginal waviness common in King Edward, Buchan Beauty, Mein's Early Round, Abundance and Arran Chief.

(*f*) *Joined Leaflets.*—The terminal leaflet is often joined with one or both of the nearest pair of lateral leaflets (Fig. 10*d*). This feature is varietal and is common in Ally, Herald, Ballydoon and King Edward. "Webbing," or the union of the petiole of one of the last pair of leaflets with the leaf midrib, is also a varietal character and is common in Early Pink Champion.

(*g*) *Overlapping of Leaflets.*—It has been previously noted that the overlapping of leaflets is a factor which produces close leaves. It frequently happens, however, that the overlapping is confined to the last pair of leaflets which project forward and overlap the terminal. This condition may appear even in open leaves and is common in many varieties, *e.g.* Up-to-Date,

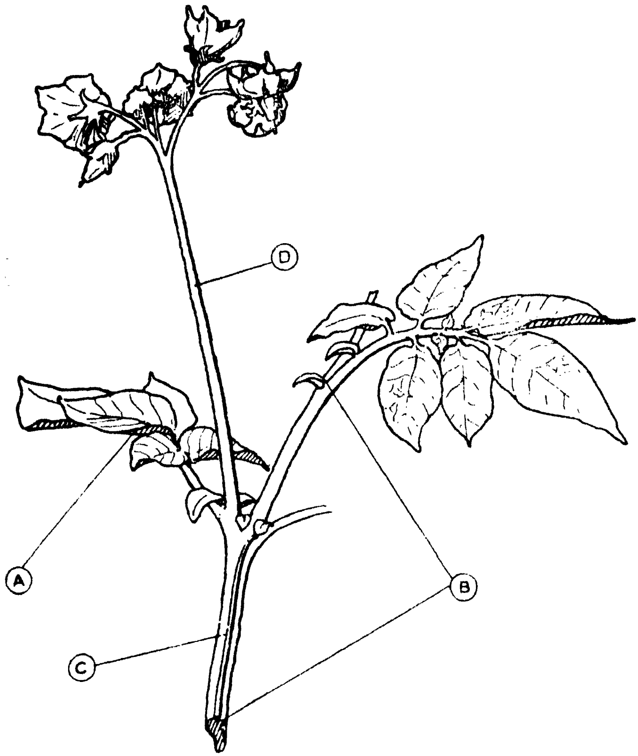


FIG. 13.—Shoot of a Variety showing Inflorescence Stalk (D) appearing to arise in the Axil of Leaf (A) and Stem (B); (C) Unwaved Wing. (In reality the Main Stem consists of (C) and (D).)

Magnificent, Puritan and Witchhill. The overlapping may be symmetrical or asymmetrical; in the latter instance one of the lateral leaflets projects more over the terminal than the other. Other varieties, *e.g.* Conference, are outstanding by reason of the fact that there is no overlapping whatever.

(*h*) *Apparent Thickness.*—Owing to a very slight downward curvature of the leaflet margins some leaflets appear thicker than others. Thus Ally, Arran Pilot and Evergood appear to have thick and Magnum Bonum, Great Scot and Herald thin leaflets.

SECONDARY LEAFLETS

The characters of the secondary leaflets not yet described are size, shape and set on midrib, and may be considered

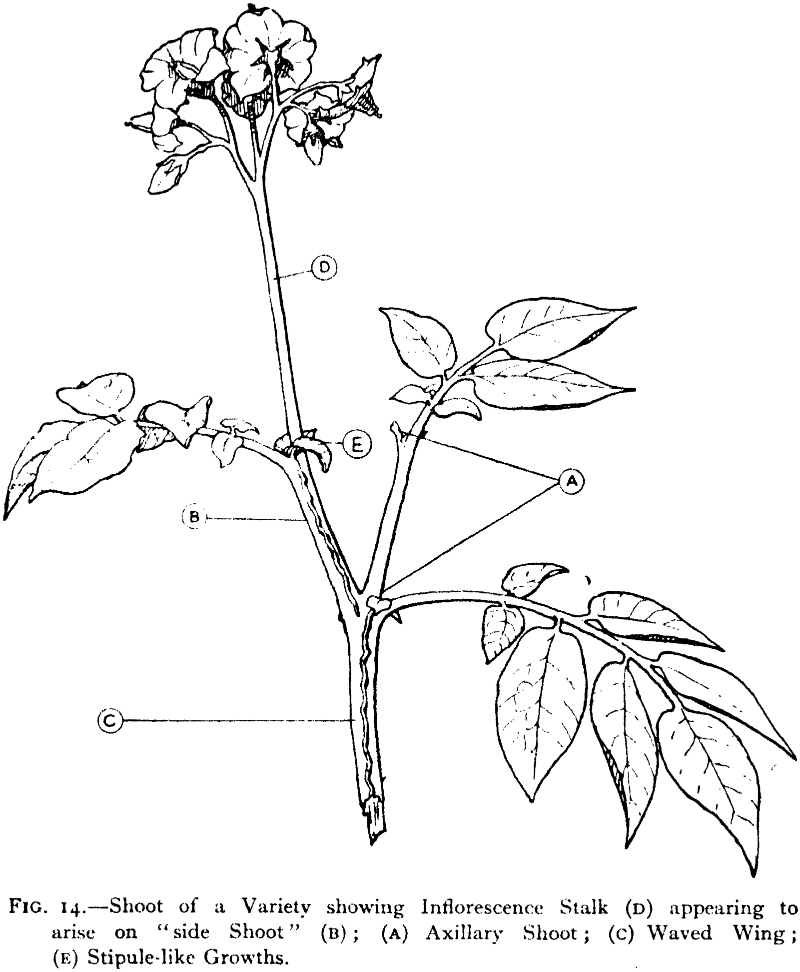


FIG. 14.—Shoot of a Variety showing Inflorescence Stalk (D) appearing to arise on "side Shoot" (B); (A) Axillary Shoot; (C) Waved Wing; (E) Stipule-like Growths.

(In reality (C), (B) and (D) constitute the Main Stem.)

together. The leaflets may be large or small, broad, narrow or rounded, pointed or blunt, projecting upwards or at the same level as the leaflets, or with straight or waved margins. All combinations occur and the typical secondaries for each variety are given in the varietal descriptions in Appendix II.

THE ORIGIN OF THE INFLORESCENCE STALK

The apparent origin of the inflorescence stalk is of importance in differentiating types. In varieties such as Duke of York, International Kidney and Eclipse, the stalk appears to arise in the axil of a leaf or rosette of leaves (Fig. 13); in others, *e.g.* Witchhill, Golden Wonder and President, it appears to be on a side shoot (Fig. 14). Many varieties show both types in approximately equal numbers. In Lord Tennyson Substitute, the Orkney Rogue and, occasionally, Eclipse, the stalk may arise from an internode and not be associated with a leaf.

CHAPTER IV

INTERVARIETAL DIFFERENCES IN THE POTATO

THE FLORAL PARTS

SINCE practically all ordinary potato plants produce floral parts, the absence of such is characteristic of wildings (see Chapter VI). The floral parts may develop normally and give rise to flowers and fruit, or may remain rudimentary and the buds fall without opening. Breeding and selection have resulted in the production of many varieties which flower only rarely and do not naturally produce fruit. Seedlings which do form berries in profusion are generally unsatisfactory in commercial qualities; hence they are seldom marketed.

Both morphological and physiological characters of the floral parts are useful in differentiating varieties.

A. MORPHOLOGICAL CHARACTERS

(*a*) *Peduncles and Pedicels* (Inflorescence and Flower Stalks) (Fig. 15).—Potato flowers occur in cymose inflorescence (Fig. 15). In some varieties, however, the main branches of the inflorescence are contracted and produce a simple umbel appearance (Fig. 16). This type is found in Immune Ashleaf, Arran Rose, Crusader and The Massie. Generally, the whole inflorescence is very conspicuous, but there exist varieties, *e.g.* Arran Pilot, in which the main stalk is so short that the flowers are often concealed by the foliage. The pedicel, or stalk on which the individual flower is borne, has on its upper half a corky abscission ring (Fig. 15 (6)). This ring marks the point from which the flower or fruit drops and is useful diagnostically; in most varieties it is colourless or just faintly coloured, but in some, *e.g.* Rector, Lord Tennyson, Adirondack, Buchan Beauty and Dean, it is very highly pigmented. This pigmentation is associated with colour in the tuber cork. The length of the pedicel above the abscission ring is also a varietal character. It may be long, as in Arran Banner, Bishop, Bobbie Burns and Cardinal, or short, as in Edzell Blue, Catriona and Myatt's Ashleaf. Indeed, one variety, Blackheart, exists which has practically no pedicel above the ring which, in this instance, nearly coincides with the base of the sepals. The peduncle and its branches vary in length. Frequently they are referred to as inflorescence and flower stalks, the latter being the pedicel. Intervarietal differences appear as regards colour on

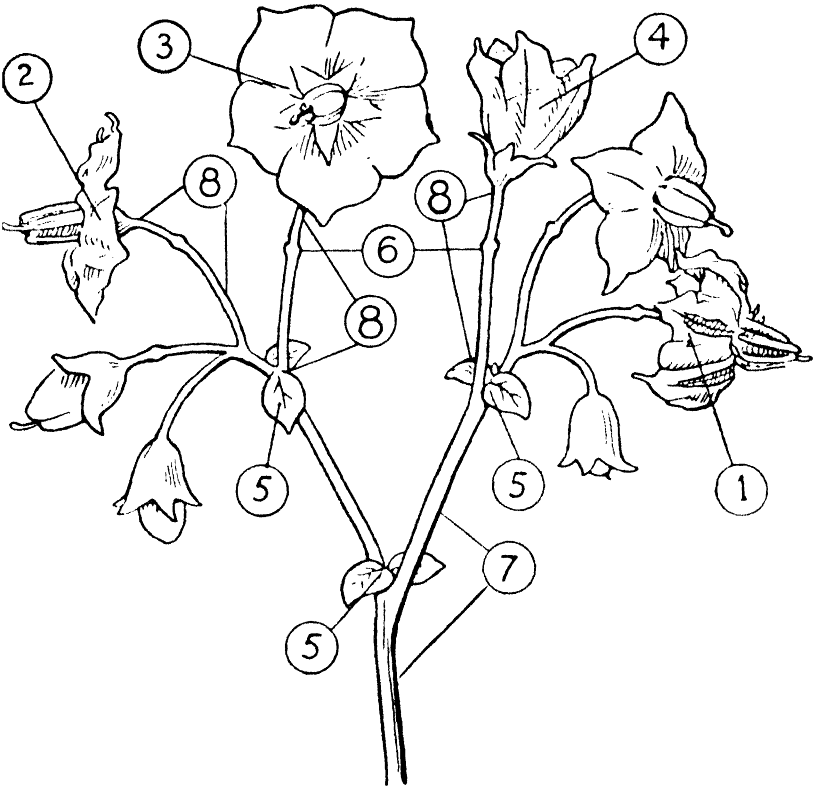


FIG. 15.—Typical Inflorescence of the Potato: (1) Immature Flower; (2) and (3) Mature Flowers; (4) Old Flower; (5) Leafy Bracts; (6) Abscission Ring; (7) Peduncle; and (8) Pedicel.

pedicels and peduncles, *e.g.* in Di Vernon and British Queen they are coloured, whereas in Arran Pilot and Doon Early they are green. The junctions of the inflorescence branches are frequently highly coloured. This occurs often in varieties the tubers of which have coloured cork, but not invariably so, as it is found in Pride of Bute. Indeed, in this latter variety the pigment penetrates right into the interior of the tissue.

Some varieties tend to form leafy bracts on the inflorescence stalks (Fig. 15 (5)), such being found regularly in Dominion, Edgecote Purple, Maud Meg and others, sometimes to a much more considerable extent than is shown. Often, owing to a proliferation of buds, the whole floral structure is malformed and confused, a characteristic especially common in Katie Glover and The Celt.

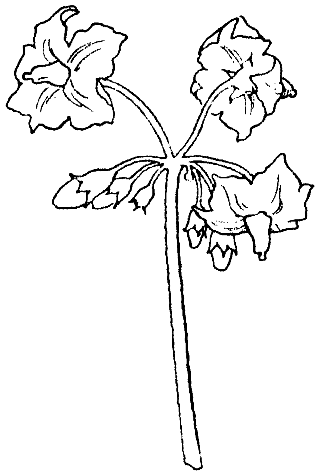


FIG. 16.—Contracted Cyme Type of Inflorescence

The density and condition of hairs on the inflorescence stalks are also varietal characters. Dunbar Standard, for instance, may be separated from Dunbar Archer by reason of its less outstanding hairs on the young inflorescence stalk.

(*b*) *The Bud.*—Bud characteristics of use diagnostically are shape, colour, manner of opening, pubescence and length of sepal tips. The last two will be treated as purely sepal characters.

Buds may be globular, *e.g.* those of Catriona, May Queen, Cardinal and Blackheart; more or less oval and blunt (Fig. 17*a*), *e.g.* those of Great Scot, Di Vernon or Doon Star; or pointed (Fig. 17*b*), *e.g.* those of Arran Banner, Arran Consul and Kerr's Pink. In most buds the sepal tips are directed forward towards the bud apex, but in some varieties, *e.g.* Arran Peak, Lochar and Arran Signet, sepal tips are generally reflexed.

(*a*) (*b*) (*c*)

FIG. 17.—Typical Buds.
(*a*) Oval and blunt; (*b*) pointed; and (*c*) pointed with long sepals.

Bud colour can be very helpful. Varieties such as Yam, Fortyfold, Magnificent, The Fife Rogue, The Dumfries Rogue and Arran Chief are outstanding in the possession of green buds. In others the bud is whole-coloured, very dark, for example, in Di Vernon, and lighter, say, in Arran Consul. Many varieties, *e.g.* Golden Wonder, Adirondack, Irish Queen and Magnum Bonum, have coloured buds with green bases, while the reverse condition characterises

Puritan, Witchhill and K. of K. Another feature of bud colour is conditioned by short sepals which do not completely enclose the unopened petals. In these circumstances very young white petals conduce to the exposure of a white tip in the bud, a characteristic feature of Gladstone and Arran Comrade.

Generally, the petals are the first structures to appear in the opening bud, but some varieties are distinctive in that the stamens and stigma protrude first. This phenomenon is found in the varieties Catriona, Rector and Arran Pilot.

(*c*) *The Calyx* (Sepals) (Fig. 18 (7)).—Normally, there are five sepals, united at the base, the tips remaining free. Irregularity in number has been noted in a few types, *e.g.* May Queen. The majority have short sepal tips, hence the long tips (Figs. 17*c*) of Witchhill, Arran Victory, Di Vernon and other varieties are useful for identification. All sepals are more or less pubescent and the frequency and condition of the hairs are often helpful; they may be infrequent and adpressed, as in Kepplestone Kidney, or, conversely, frequent and not adpressed, as in Arran Consul and Kerr's Pink Substitute. All calyx characters are visible on the bud and are thus of service for a long period during the growing season.

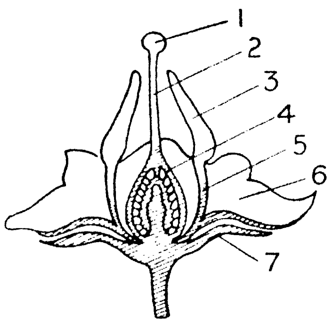


FIG. 18.—Floral Parts.

1, Stigma; 2, Style; 3, Anther; 4, Ovary; 5, Stamen filament; 6, Petals; and 7, Sepals.

(*d*) *Corolla* (Petals) (Fig. 18 (6)).—The typical flower has five united petals showing five tips. May Queen, Yam and other varieties are exceptions, and in them as many as ten tips have been counted. Double corollas are characteristic of a few types, *e.g.* Blackheart. The size of the flower, as measured at the broadest point of the petals, varies, and even on one plant different sizes are obtainable. Nevertheless, varieties may be divided into (*a*) those having small flowers, *e.g.* Edzell Blue, Champion and Arran Pilot, and (*b*) those with large flowers, *e.g.* British Queen, Bishop, Yam and Up-to-Date. Incompletely fused petals are found in some varieties, *e.g.* in Orion and Craigs Snow-white. The most important petal characteristic is colour and its distribution on the various parts. First, however, let us consider white flowers. These are classed as creamy white, milky white and greenish white, and flowers typical of each group are readily recognised. White flowers do not all react similarly when immersed in a solution of caustic potash; some, such as those of Abundance and Ballydoon, remain almost white; while others, those of Majestic and British Queen, for example, turn yellow-orange. In pigmented flowers, colour is located in the epidermis and is due to the presence of a red or purple cell sap, and, according to the proportions, the tint may be redder or bluer. As regards colour distribution the central ribs, or star, and the petal tips are generally colourless; but this is not an invariable characteristic, for the tips of Up-to-Date petals are coloured, and the stars of Dunbar Cavalier, Buchan Beauty, Peachbloom and some other coloured cork varieties are more highly pigmented than the remainder of the petals, especially in young flowers. The base of the corolla is usually white, but in certain coloured cork varieties, *e.g.* Rector and Dean, it is very highly coloured. Varieties are occasionally found in which the colour appears on the lower surface of the petals only. This feature is almost invariable in Arran Signet, is common in Arran Peak and Flourball, and occasional in Majestic. Although the normal colouring of flowers is a shade of purple, flowers which appear to be yellow have been found in a variant of Gladstone. Here, however, the whole flower is abnormal.

(*e*) *The Andrœcium* (Stamens) (Fig. 18 (3) and (5)).—Each stamen consists of an anther and a filament. The stamens are

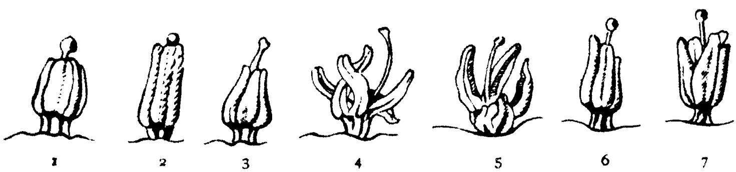


FIG. 19.—Stamens and Styles.

1, 2, and 3, Symmetrical columns of stamens. 7, Loose stamens.
4 and 5, Malformed stamens. 2, Short style.
6, Non-symmetrical column of stamens. 3, 6 and 7, Long styles.

normally arranged in a symmetrical column surrounding the pistil. Some varieties, however, *e.g.* Peachbloom, Irish Queen and Crusader, are characterised by loose but normal stamens (Fig. 19 (7)), while in others, *e.g.* Catriona, a non-symmetrical column is formed (Fig. 19 (6)).

Stamens differ in colour and in form: they may be pale yellow, yellow or orange, and as regards form, normal (Fig. 19 (1) or malformed (Fig. 19 (4) and (5)). Pale yellow anthers, always associated with male sterility, and frequently with malformation, are common in such varieties as King Edward, Ally and Arran Chief. Viable pollen is almost always found in orange anthers, while this feature varies in varieties the anthers of which are yellow and yellow-orange. Coloured cork varieties, *e.g.* Di Vernon and Catriona, have often purple on the inner surface of the stamen. Occasionally the outer surface is tinted red or purple, as, for instance, in Rector, in which the anthers are often red. The colour of the anthers is generally varietal, but exceptional plants occur in many varieties showing a departure from the normal.

The filaments are almost invariably white, and only in a few coloured cork varieties has colour been found on them.

The outside junction of anther and filament is often characteristic. In some varieties, *e.g.* Dunbar Cavalier and Arran Comrade, the base of the anther is straight and overlaps the apex of the filament; in others, *e.g.* Majestic and Edzell Blue, the apex of the filament has an inverted V-shape and joins the anther without the latter overlapping.

(*f*) *Gynæcium* (Stigma, Style and Ovary) (Fig. 18 (1), (2) and (4)).—(1) *The stigma* is usually bilobed, the lobes not being well marked. In some varieties, such as Abundance, however, the lobes are distinct. Multiple lobes are frequent in certain kinds, *e.g.* May Queen. The number of stigma lobes coincides with the number of chambers in the ovary. Generally, the stigma is green, but in at least one variety, Burnhead Rogue, it is often black.

(2) *The style* is usually erect and white. Varieties may be grouped in terms of style thickness. Examples of thick styles are found in Golden Wonder and Kerr's Pink, of thin styles in Dunbar Cavalier, Arran Peak and John Bull, and of intermediate styles in Arran Signet. Styles may be again classified by reference to their length. Thus some varieties, *e.g.* Bishop, Abundance and Arran Pilot, have long styles projecting well beyond the tops of the stamens (Fig. 19 (3)); others, including Dunbar Cavalier, British Queen and Myatt's Ashleaf, have short styles which project just beyond the anther tips (Fig. 19 (2)); others again, *e.g.* Kerr's Pink and

Arran Comrade, have intermediate styles (Fig. 19 (1)). Colour is found on the styles of some coloured cork varieties, *e.g.* Buchan Beauty. The lower third of the style has generally a large number of minute hairs, or papillæ, observable only with the aid of a lens. Some varieties, *e.g.* Epicure, Sunrise, John Bull and America, are outstanding by reason of their practically glabrous styles. Another interesting feature of the style is its junction with the ovary which is generally abrupt (Fig. 20 (2)), but in a few varieties is gradual (Fig. 20 (1)). To the latter type belongs Lord Rosebery.

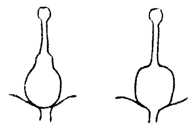


FIG. 20.—Female Parts of the Flower showing (1) gradual junction and (2) abrupt junction of style with ovary.

(3) While the ovary is normally two-celled, multilocular ovaries occur which are non-characteristic of any variety. Again, while the exterior of the ovary is usually white, colouring may be found on the exteriors of the ovaries of a few varieties, *e.g.* Exhibition Red Kidney. If the ovary be cut the interior is often found to be coloured, and this characteristic is definitely associated with colour in the tuber cortex. Kerr's Pink and Redskin have red ovary-interiors, while those of Edzell Blue and Arran Victory are purple. There are some varieties with coloured tubers in which no colour appears in the ovary-interior. Pride of Bute and Yam are outstanding examples, as their tubers are whole-coloured and the pigment is located in the cortex. Only a few parti-coloured varieties, *e.g.* Buchan Beauty, show the character. Lord Rosebery, a variety with whole-coloured tubers in which colour appears in the cork, has also a coloured ovary-interior. With this latter type of variety the association appears to hold only if, in addition to the cork, the cortex is also substantially coloured.

(*g*) *The Fruit.*—The fruit is normally round ; only one cultivated variety, the Holm Red of Orkney, is known to have the oval-shaped berry which characterises some of the wild species. Such berries have been found also in seedlings of the variety Gladstone. In present-day popular, fruit-bearing varieties the colour of the exterior of the berry is green, but in many of the older types and common rogues berries are found, the colour of which ranges from a light to a dark purple and may be present only to a slight degree or may cover the entire fruit surface. Its density and distribution are always typical of the variety.

Another feature of the fruit exterior is the appearance of white dots, generally most numerous on the two sides of the fruit facing the placentas. These occur in great frequency over the whole surfaces of the fruits of *S. demissum* and many species crosses, but in *S. tuberosum* they are much rarer and their appearance is usually restricted to the two sides already mentioned. In most varieties the dots are absent or, at most, have limited appearance; such varieties include Majestic, Arran Peak, Arran Signet, Doon Star, Ballydoon and Dunbar Cavalier. Only a few, *e.g.* Gladstone, Flourball and Peerless, show the white dots frequently. Other varieties, *e.g.* Reading Russet and Edgecote Purple, are, in this respect, intermediate.

The interior of the fruit, as of the ovary, may be either coloured or colourless. Colouring follows the same general lines as described for the ovaries and appears only in varieties with coloured tubers. The same exceptions occur whenever the varieties bear fruit.

If the calyx be removed from the fruit, normally a buff or yellow ring can be seen at the point of attachment; in many coloured cork varieties this ring is coloured, red in some and purple in others.

B. SOME PHYSIOLOGICAL CHARACTERS OF USE IN DIFFERENTIATING VARIETIES

Many physiological characters of the floral parts of the potato, although interesting, are of little use in discriminative work. Such characteristics include the downward bending of the inflorescence stalks soon after fertilisation has taken place, the influence of environment on flowering and the various phases through which flowers pass from the opening of the bud to full maturity.

Physiological characters which may occasionally be of service are:—

(*a*) *The Flower.*—Marked differences exist in flower sensitiveness to outside influences. Some flowers open early in the day and others only in full sunshine; in dry weather the time of opening and closing is relatively constant for any variety. Wet weather induces the closing of flowers, but a few varieties are insensitive to moisture. Many sorts bloom only for a short period, and others, of which Up-to-Date is a conspicuous example, bear flowers for a great part of the vegetative season.

Since most flowers have no scent, varieties such as Dunbar Cavalier, the flowers of which emit a pleasant odour, are distinctive.

The capacity of the flower to produce pollen is a definite varietal character. British Queen and Ballydoon, which may sometimes be confused, can be distinguished readily by this means, the latter variety having a considerable amount of pollen, while the former has practically none.

(*b*) *The Fruit.*—Berry formation is associated with the production of viable pollen and is, therefore, also a varietal character. Female sterility is uncommon; even varieties which flower but seldom, such as King Edward and Arran Chief, set fruit when fertile pollen is used. Environment influences fruit production more than flower production. In some seasons berries are rarely found, whereas in others berries are abundant and form even on varieties which flower only occasionally. Therefore, although fruit production is a varietal character in drawing conclusions, season and environment should also be taken into account.

As with flowers, the berries of some varieties, Myatt's Ashleaf, for example, are pleasantly scented, but most are scentless.

CHAPTER V

INTERVARIETAL DIFFERENCES IN THE POTATO

THE ROOT, TUBER, SPROUT, AND STOLON

THE root and stolon of the potato can be observed only during the growing season. Since also the characters of immature and growing tubers differ slightly from those of mature tubers, the study of the various characters will be facilitated by first discussing the differentiating points which are apparent only in summer.

A. CHARACTERS APPARENT ONLY DURING THE GROWING SEASON

ROOTS.—It has been noted that the roots are distributed mainly in the upper layers of the soil. Some varieties, nevertheless, are more deeply rooting, a feature which seems to be associated with the tall, upright foliage habit and, while of some economic significance, is of little value in separating types. Most varieties have white roots, hence the coloured roots of some coloured cork sorts, The Dean and Lord Tennyson, for example, are useful diagnostically.

As already noted, small roots may be found on tubers during the growing season arising in the depressions on each side of some basal tuber eyes. The appearance of these rootlets has not been found useful diagnostically, although, along with the depressions, they are more developed in deep- than in shallow-eyed varieties.

STOLONS.—These differ in frequency, length and colouring. Numerous stolons are associated with numerous and generally undersized tubers, and long stolons are objectionable commercially. Breeding and selection have, therefore, resulted in the elimination of these undesirable types. In some of the older varieties, *e.g.* Dominion and Templar, long stolons are found. Only in one recent introduction—Craigs Bounty—are long stolons found, these being inherited, it is presumed, from the wild species (*S. demissum*) used to secure Blight resistance. A much more useful characteristic of the stolon is its colour, which may be pink or purple. Most frequently, colouring is not pronounced and is obvious only at the lenticels, as, for example, in many varieties with white tubers and blue sprouts. Occasionally much of the stolon is coloured, as in the varieties Ben Cruachan and Doon Pearl.

THE IMMATURE TUBER.—Differences exist as regards the disposition of the tubers in the soil; generally, in early sorts tubers are formed near the surface; indeed, in some, *e.g.* Di Vernon and Ulster Monarch, the propensity to form tubers at soil level is a fault; in later types tubers are generally more deeply buried. This character is particularly noticeable in Golden Wonder, and has cultural significance in that the more deeply the tubers are buried, the less likelihood there is of serious damage by Blight, provided control measures for this disease are adopted. Some varieties tend to develop aerial tubers. This phenomenon, common in Edzell Blue, is frequently due to injury of the stem; hence its occurrence may be associated with weakness of some kind in the haulm.

It has been mentioned that the eyes of the tuber lie in the axils of scale leaves. During the growing season these scale leaves are visible and in some varieties are coloured, the colour corresponding to that of the sprout and forming a very useful diagnostic feature. The scale leaves of May Queen, Conquest and Blue Grey are blue, those of Fiftyfold are pink. The heel ends of growing tubers are also frequently coloured, although the colour often disappears at maturity. The same applies to the rose end. The heel ends of the immature tubers of Arran Chief, Champion and Abundance are blue, those of Epicure and Lymm Gray are pink, and King George and Rhoderick Dhu are characterised by the frequent appearance of colour on the rose ends of their immature tubers. Tubers exposed to light, as on the side of a drill, often develop colour. This character is noted in the variety descriptions in the Appendix (Appendix II).

B. CHARACTERS APPARENT DURING THE STORAGE SEASON

THE TUBER

Tuber characters persisting after maturity and useful diagnostically are: (1) shape, (2) colour and condition of skin, (3) position and depth of the eyes, (4) colour and consistency of the flesh, (5) type of second growth, and (6) chemical characters.

SHAPE.—Each variety has a typical tuber shape. Nutritional and soil conditions, however, may influence shape development as also may certain diseases and conditions, *e.g.* Spindle Tuber, Wildings and Stags. There is, in consequence, no great constancy of shape, and even on one plant different forms may appear. Nevertheless, some shapes, *e.g.* rounds and pear-shaped kidneys, are very constant. As regards other forms, an accurate conception of the varietal type can always be obtained by the study of a number of the larger tubers.

Except in spherical varieties, each tuber has normally an upper and a lower surface, the former always being more rounded than the latter and generally having more eyes. The true shape is apparent when the tuber lies on its lower surface. Thus viewed, the tuber outline may appear round or have a long axis. If round, the tuber is termed round, or round (flat) ; in the round (flat) or pebble tubers the body is not so thick as in rounds. If in the outline one axis is longer, the tuber is oval, oval (pointed) or pear-shaped, according as the largest diameter occurs at the middle, towards the heel end or towards the rose end respectively. In commerce, the term " kidney " is employed to describe all long tubers. Tubers may be thin, thick or of medium depth according to the thickness of the cross section. Very frequently the heel end is indented, a condition common in Champion, Rocks, Fortyfold, Gregor Cups, Epicure and many other varieties. Indented heel ends are never found in pear-shaped and long oval tubers, but occur commonly in round and oval (pointed) tubers. Fig. 21 illustrates the different shapes and, in the descriptions of varieties in the Appendix, the typical shape for each variety is noted.

COLOUR AND CONDITION OF THE SKIN.—Potato tubers may be whole-coloured, parti-coloured, white or russet.

(*a*) *Coloured Tubers*

The skin colour is fully developed only when the plant reaches maturity. The intensity of colour, however, depends to some extent on soil conditions and is generally most marked in sandy soils. Red and purple colouring is due to a pigment dissolved in the cell sap. The cells concerned are those of the cortex or the cork, or both of these tissues. Although both tissues are usually involved in coloured cork varieties, many

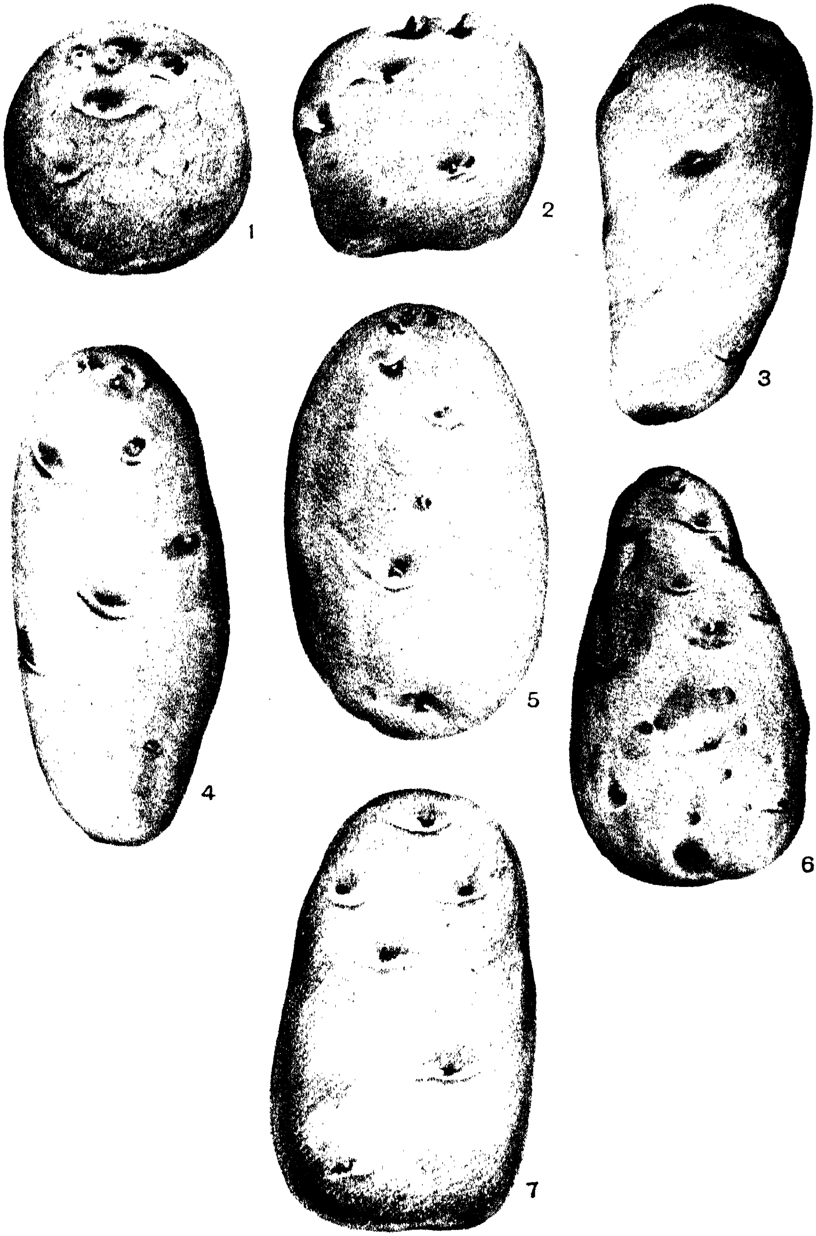


FIG. 21.—Tuber Shapes.

1. Round (flat) or pebble.
2. Round (spherical).
3. Pear-shaped
4. Long oval.
5. Short oval.
6. Oval (pointed).
7. Oval (slightly pointed).

varieties have pigment only in the cortex, hence it is possible to divide coloured tubers into two sharply defined groups according to whether pigment appears in the cork or not.

(i) *Coloured Cork Tubers*.—Colour in the cork has been noted in *S. andigenum* and other species as well as in *S. tuberosum*. Its appearance is associated with a number of coloured points in the foliage and flower (see Chapter VI). Such tubers may be whole- or parti-coloured. When the tuber is immature it is very easy to determine cork colouration, as the skin is then readily detached : in coloured cortex types this skin is light brown ; in coloured cork tubers it is red or purple. When the tubers are mature and the skin firm, microscopic section alone can determine the location of the pigment. Coloured cork tubers are always very much brighter than those with colour in the cortex ; this is because the light brown cork dulls the deeper-lying pigment in the latter types. Another interesting feature of coloured cork tubers is that their tuber eyes are very frequently more highly pigmented than the remainder of the surface.

The colour itself may range from light red, or pink, as in King Edward, to deep purple, as in Buchan Beauty. Sometimes it is not uniform, streaks of a darker shade intermingling with those which are lighter, and in some varieties, *e.g.* The Dean, both red and purple areas appear on the same tuber. As regards distribution, the whole surface may be affected, as in Lord Rosebery and Rector, or the colour may be restricted entirely to the eyes and lenticels, as in John Bull, or to the eyes and neighbouring parts, as in Di Vernon and Catriona. Occasionally the colour avoids the eyes, a feature of special significance in certain rogue varieties.

(ii) *Coloured Cortex Tubers*.—These show the same range of colour and colour distribution as the previous types. Kerr's Pink, Redskin, Arran Victory and Cardinal are whole-coloured ; Northern Star, Marquis of Bute and Lochar are coloured only at the eyes and lenticels ; and Tawny and Climax are parti-coloured, the coloured tissue generally occupying more space than the uncoloured.

(*b*) *White Tubers*

Most commercial varieties in this country have white skins. The term is rather misleading, as no variety has an absolutely white skin, and it is used commercially to include a wide range of light yellow shades. Varieties may be differentiated by the shade of yellow. Most yellow-fleshed varieties, especially those with high colour development, have yellow skins, *e.g.* Duke of York, Immune Ashleaf and Myatt's Ashleaf; in other sorts, the colour is slightly less yellow, as, for example, in Great Scot; but most have skins even paler than the Great Scot type.

A feature of considerable value in separating varieties is the faculty of certain white-skinned sorts to colour on exposure to light. The colour thus induced is always confined to the cortex and never appears in the cork; it may be red or purple, and cover the greater part of the tuber surface, as in Epicure and Arran Signet, or may be limited mainly to the tuber eyes, as in Duke of York. Again, in some varieties, it develops rapidly and in others slowly, warmth hastening the development. A note of such varieties, and the colour and distribution of colour developed, is given in the varietal descriptions in Appendix II.

All varieties become green when tubers are exposed to light. Some, however, green more rapidly than others, Arran Viking and Ulster Commerce, for instance, become green rapidly while Ulster Chieftain and Craigs Bounty do so less rapidly. If the skin of a greened tuber be scraped away, white dots may be seen in the green tissue exposed. These dots appear much more frequently in some varieties than in others; Eclipse and Sharpe's Express show them quite often.

(*c*) *Russet Tubers*

Several commercial varieties, *e.g.* Golden Wonder and Field-Marshal, have russet skins and, for this reason, are very readily identified. Some tubers, while not actually russet, have rough, netted skins, doubtless because of cork thickness. Such, for instance, are Ally, Arran Peak and Gregor Cups, the skins of which are quite distinct when compared with smooth-skinned varieties.

Position and Depth of the Eyes.—The eyes appear in greatest frequency at the rose end, where they cluster round the apical eye. In most varieties the apical eye and its cluster are situated at or near the apex of the tuber, but in some types the apical eye and its cluster are some distance from the point of the tuber, when they are said to lie on the shoulder. The remaining eyes are distributed spirally over the tuber surface, the internodes becoming longer towards the heel end. The basal internodes are usually longer in pear-shaped than in oval (pointed) tubers.

In some varieties, *e.g.* Epicure and British Queen, there is usually a distinct swelling below the eyes on the sides of the tuber. These swellings are termed raised eyebrows. The eyebrow itself is often helpful: in Abundance, for example, it is long, while in Arran Comrade it is short. The number of eyes also is a varietal character.

As regards depth, eyes may be classified as deep, medium or shallow; in the first group occur such varieties as Epicure, Champion, Rocks and Fortyfold; in the second, British Queen, Arran Victory and Kerr's Pink; and in the last, King Edward, Arran Signet and Duke of York.

COLOUR AND CONSISTENCY OF THE FLESH.—As with skin, flesh colour is fully developed only in the mature tuber. Immature tubers and second growths do not normally show the typical tone. Varieties are described as having yellow, pale yellow or white flesh. The diagnosis of these colours cannot be made in tubers which have become green. Typical yellow-fleshed tubers, *e.g.* those of Champion and Duke of York, can always be separated from those with white flesh. The varieties with pale yellow, or lemon, flesh can generally be separated from the other two types, but not invariably, since in them deeper yellows and whites sometimes appear.

The tuber flesh is sometimes coloured red or purple. The colour may be limited to the vascular tissue, as in Herd Laddie; but the non-vascular tissue may be affected, as in Cardinal, Crimson Beauty, the Blue President Rogue and, occasionally, the Dumfries Rogue.

Some varieties may be termed soft- and others hard-fleshed. Comparison, however, must be made with the mature tubers. Generally, earlies have soft and lates hard flesh, but exceptions occur. As examples of earlies, Puritan, Ninetyfold and May Queen have softer flesh than Duke of York, while amongst lates, Golden Wonder is outstanding by reason of its very hard flesh.

TYPES OF SECOND GROWTH.—Second growth occurs during the growing season generally when a dry spell is followed by rainfall and when plants, which have commenced to ripen, resume growth. In such circumstances the various varieties react differently. In some, particularly oval varieties, such as Ally, Red Fife and Majestic, large unsightly cracks (Fig. 22*a*) appear on the surface of the tubers. Absence of boron is stated to aggravate this type of injury, as also certain forms of virus diseases. Cracking, it should be noted, may occur at the act of digging or later and may not be a second growth symptom but due to over-turgidity, as when frost kills the foliage but allows root action to continue. In long tubers, *e.g.* those of Golden Wonder, Arran Pilot and Arran Cairn, there is often a prolongation of the rose end (Fig. 22*b*) ; the new growth thus formed has a smoother skin than the older tissue and often a constriction or waist separates it from the mother tuber. Other varieties are characterised by gemmation (Fig. 22*c*), which consists of protrusions of knob-like growths from the eyes, a feature common in certain long and oval (pointed) varieties, *e.g.* Ninetyfold, British Queen and Puritan ; here also the new growth has a smoother skin than the older tissue. The formation of a chain of tubers (Fig. 22*d*), separated by stolons, is also a second growth symptom and is common in some round varieties, *e.g.* Northern Star and Arran Chief. Generally, only two tubers are so linked, but occasionally there may be three. The secondary and tertiary tubers have smoother skins than the primary tuber. Hollow heart, or the appearance of lens-shaped hollows in the tuber pith, is also a second growth manifestation and is common in certain round and oval varieties, such as Great Scot, Arran Banner and Gladstone. Glassiness, or the disappearance of starch from the heel end, is common in dry seasons in long tubers such as those of Golden Wonder, Arran Pilot and Arran Cairn, and is probably conditioned by the absorption of starch by the apical end of the tuber when growth is resumed after drought. The condition is readily diagnosed in the cross-section of the tuber. Sometimes the heel end rots and collapses, particularly in storage, and the tuber appears as though cut by a knife.

According to Murphy,[1] prolongation, gemmation and chain-tuberisation form a series probably indicating a progressive decrease in the capacity for growth of the primary tuber, for, in the first, the whole rose end proliferates, in the

[1] Prof. P. A. Murphy, "Some Effects of Drought on Potato Tubers," *Empire Journal of Experimental Agriculture*, 1936.

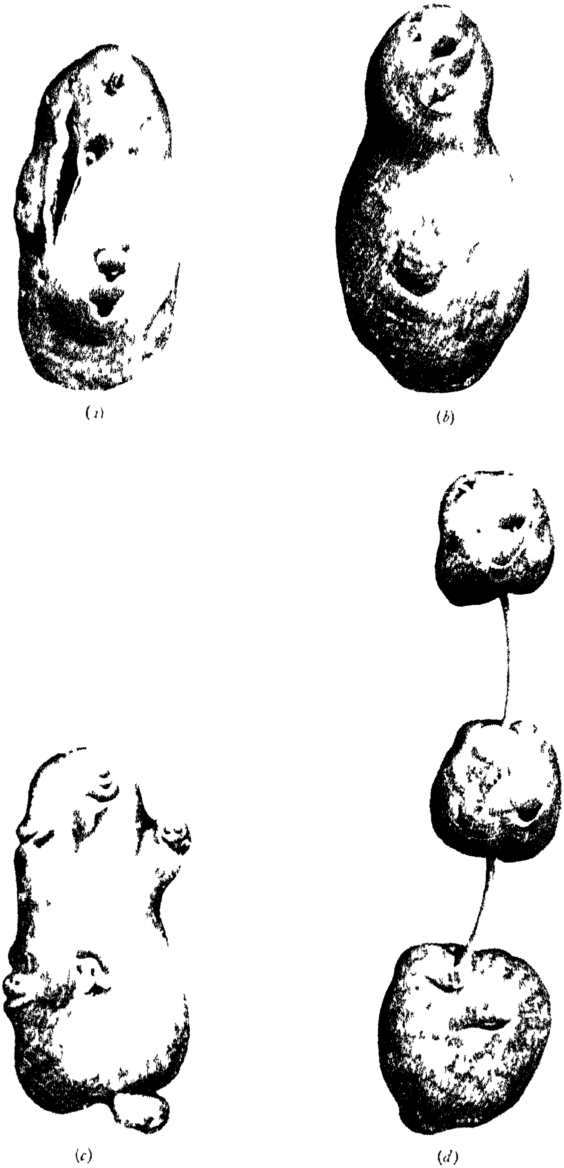


FIG. 22.—Types of Second Growth.

(a) Cracking; (b) Prolongation of rose end; (c) Gemmation; and (d) Chain tuberisation

second, the whole of an eye, and, in the third, a single bud from an eye. In some varieties, *e.g.* Arran Comrade, second growth has not been found, doubtless because of the inability of the plants to recover from prolonged drought.

When the normal flesh of the tuber is yellow, the flesh of the second growth tissue is of a lighter shade, if not actually white.

CHEMICAL CHARACTERS

Investigations into the chemical composition of tubers have been concerned primarily with starch, dry matter and nitrogen. These substances are valueless for varietal discrimination.

TABLE VI

The Alkali Test

1. Faintly Yellow.	2. Yellow.	3. Bright Yellow.
Arran Signet	Arran Pilot	Abundance
	Ballydoon	Ally
	British Queen	
	Catriona	
Eclipse	Duke of York	Arran Chief
		Arran Comrade
		Arran Consul
Edzell Blue	Di Vernon	Arran Victory
	Epicure	Great Scot
	Kerr's Pink	
Puritan	King Edward	Majestic
Witchhill	May Queen	Redskin
	Ninetyfold	
	Up-to-date	

Some of the rarer compounds in the potato are, however, useful for this purpose and tests have been devised to group varieties and separate types, the reactions of which differ widely.

THE ALKALI TEST.[1]—Almost universally distributed in the cell sap of plants are substances known as flavones. In bulk these are yellow, but they are present in such minute quantities in potato tubers as to be practically invisible. When treated with alkalies, however, a yellow colour develops, and since tubers differ in their flavone contents, there is a variation in the intensity of the colour. The technique of the test is simple: slices, about $\frac{1}{4}$ in. thick, are cut from the middle of the tuber, wounds and diseases being avoided, and, with the aid

[1] T. P. McIntosh, *Scottish Journal of Agriculture*, vol. xi, p. 304, 1928.

of forceps, immersed for a few seconds in a normal solution of caustic potash. Thereafter, they are laid out on an enamelled tray and the colour readings taken at the end of five minutes.

The results of some of the varieties tested are shown in Table VI. The varieties in column 1 can be separated from those of column 3 without difficulty.

THE TYROSINASE TEST.[1]—When a tuber is cut and the cut surface exposed for some time, a pink colouration often appears. Varieties differ in the amount of colour developed, that of Arran Peak, for instance, being much greater than that of King Edward. Colour is due to the oxidation of the substance tyrosine through the agency of the enzyme tyrosinase. Substances similar in chemical composition to tyrosine, *e.g.* *p*-cresol, are likewise affected by the tyrosinase and may be used for testing.

When a slice of tuber is treated with a *p*-cresol solution, an orange-red decomposition product is produced by the enzyme, and, under controlled conditions, the rate of formation of the colour is proportionate to the enzyme activity. The activity of the enzyme is typical for mature tubers of each variety. The following table indicates the separations possible by this test in the varieties so far investigated.

TABLE VII *

The Tyrosinase Test

A. *White Varieties.*

1. Eclipse can be distinguished from 4 (inclusive) downwards.
2. May Queen can be distinguished from 5 (inclusive) downwards.
3. Arran Banner can be distinguished from 8 (inclusive) downwards.
4. Great Scot can be distinguished from 9 (inclusive) downwards and from 1.
5. Royal Kidney can be distinguished from 10 (inclusive) downwards and from 2 (inclusive) upwards.
6. Witchhill can be distinguished from 10 (inclusive) downwards and from 2 (inclusive) upwards.
7. Arran Chief can be distinguished from 17 (inclusive) downwards and from 2 (inclusive) upwards.
8. Arran Comrade can be distinguished from 16 (inclusive) downwards and from 3 (inclusive) upwards.
9. Epicure can be distinguished from 19 (inclusive) downwards and from 5 (inclusive) upwards.
10. Arran Pilot can be distinguished from 19 (inclusive) downwards and from 6 (inclusive) upwards.
11. Ally can be distinguished from 19 (inclusive) downwards and from 6 (inclusive) upwards.

[1] T. P. McIntosh, *op. cit.*; I. M. Robertson, *Proc. Roy. Soc., Ed.*, vol. lii, p. 309, 1932; A. Lauder and I. M. Robertson, *Scot. Journ. Agric.*, vol. xiv, p. 47, 1931.

12. Majestic can be distinguished from 19 (inclusive) downwards and from 6 (inclusive) upwards.
13. Duke of York can be distinguished from 19 (inclusive) downwards and from 6 (inclusive) upwards.
14. Tinwald Perfection can be distinguished from 19 (inclusive) downwards and from 6 (inclusive) upwards.
15. Abundance can be distinguished from 19 (inclusive) downwards and from 6 (inclusive) upwards.
16. Immune Ashleaf can be distinguished only from 9 (inclusive) upwards.
17. Champion can be distinguished only from 9 (inclusive) upwards.
18. Golden Wonder can be distinguished only from 9 (inclusive) upwards.
19. Doon Star can be distinguished only from 13 (inclusive) upwards.
20. President can be distinguished only from 15 (inclusive) upwards.
21. Arran Peak can be distinguished only from 15 (inclusive) upwards.

B. *Pink Varieties.*

1. Kerr's Pink can be distinguished from 3 (inclusive) downwards.
2. Redskin can be distinguished from 5 (inclusive) downwards.
3. Rogue like Great Scot can be distinguished from 5 (inclusive) downwards and from 1.
4. Kerr's Pink Substitute can be distinguished from 5 (inclusive) downwards and from 1.
5. Gregor Cups can be distinguished from 6 (inclusive) downwards and from 4 (inclusive) upwards.
6. Sharpe's Pink Seedling can be distinguished only from 5 (inclusive) upwards.
7. Raeburn's Gregor Cups can be distinguished only from 5 (inclusive) upwards.

C. *Blue Varieties.*

Arran Victory can be distinguished from Edzell Blue.

D. *Parti-coloured Pink Varieties.*

1. King Edward can be distinguished from 2 (inclusive) downwards.
2. K. of K. can be distinguished from 3 (inclusive) downwards and from 1.
3. Dunbar Cavalier can be distinguished only from 2 (inclusive) upwards.
4. Gladstone can be distinguished only from 2 (inclusive) upwards.
5. Katie Glover can be distinguished only from 2 (inclusive) upwards.

E. *Parti-coloured Purple Varieties.*

Catriona can be distinguished from Di Vernon.

* The tests on which this table is based were made by Dr I. M. Robertson to whom the authors are indebted.

INDOPHENOL TEST.[1]—The potato, like many other vegetables, contains ascorbic acid and this may be tested by means of the oxidation-reduction indicator, 2 : 6 dichlorophenol-indophenol. Although the amount of ascorbic acid varies in the tubers of any variety according to the state of health and conditions of storage, it appears that the healthy tubers of some varieties can be separated invariably by means of the test. Thus, the following may be differentiated: (1)

[1] T. P. McIntosh, *Scot. Journ. Agric.*, vol. xviii. p. 173, 1935; A. M. Smith and W. Y. Paterson, "The Study of Variety and Virus Disease Infection in Tubers of *S. tuberosum* by the Ascorbic Acid Test," *The Biochemical Journal*, pp. 1992-9, 1937.

Arran Pilot from Sharpe's Express, (2) Majestic from Eclipse, (3) Dunbar Cavalier and Gladstone from King Edward and (5) Immune Ashleaf from Duke of York.

OTHER TESTS.—Phenosafranin may also be used in the separation of certain varieties. A few drops of a ½ per cent. aqueous solution of this reagent are added to a section of the tuber and the excess is washed off after fifteen minutes. An orange-red stain remains of the pectic substances present in the tuber. Arran Chief can thus be distinguished by its darker colour from Great Scot, which it closely resembles.

Much has been done on the Continent in differentiating varieties by means of ultra-violet ray fluorescence. Applied to British varieties, however, the test has so far yielded unimportant results. It appears, nevertheless, from the few results available that Golden Wonder and Arran Consul give characteristic fluorescences.

THE SPROUT [1]

The mature tuber of the common potato does not have a rest period in the true sense. Nevertheless, in Britain, until December or January, sprout growth is very slow indeed. In other species, *S. Rybinii* for example, sprouts develop very rapidly after lifting. It has been noted that tubers affected with Blight sprout very quickly and attempts have been made by various means to accelerate growth. The shortening of the rest period may be brought about in various ways, and general methods have been recommended for adoption in rapid sprout testing: first, the tubers may be subjected to a process of alternate warming and cooling, and for this purpose the following procedure is recommended by Snell,[2] viz., eight days at a temperature of 30°-32° C., eight days at 1°-2° C., and, finally, another eight days at 30°-32° C.; secondly, the tubers may be treated chemically, by dipping cut tubers in ethylene chlorhydrin (1 part to 50 parts of water), then storing them in a closed container, not more than twice the volume of the sample, for twenty-four hours and finally washing them with water, or, alternatively, by soaking similar tubers in a 3 per cent. solution of sodium thiocyanate for one hour and then washing

[1] For descriptions of the sprouts of varieties, see Appendix II.

[2] Dr K. Snell, *Die Lichtkeimprüfung zur Bestimmung der Sortenechtheit von Kartoffeln*, 1932.

them with water. Soaking the tubers in a 1 per cent. solution of thiourea for two hours has also been recommended as a satisfactory method. Another method has been described by Denny.[1] This involves the use of "Rindite" consisting of Ethylene Chlorohydrin 7 parts, Ethylene dichloride 3 parts, Carbon tetrachloride 1 part. Whole tubers are placed in a container and covered with cotton wool and cloth saturated with the mixture used in a concentration of 0·8 c.c. per kilogramme of tubers. The container should be sealed and kept at 72·5° F. for four days; thereafter the potatoes should be removed and kept at a temperature of from 68° to 86° F. for two days and then at room temperature. Sprouts emerge in from twelve to twenty days. Good sprouts, however, can always be obtained, without recourse to artificial means, long before the planting season.

Sprouts which develop in darkness lack chlorophyll and elongate considerably. Their tips never open and colour is seldom very pronounced. Nevertheless, varietal differences are evident in such sprouts: the tips of Majestic sprouts are always bent, while those of Up-to-Date are not bent to the same degree. In light, quite a different sprout is formed and colour is much more marked. It has been found that diffuse light is the most suitable for the best expression of sprout characters, and, in carrying out sprout tests, the following procedure, with or without the preparatory treatments discussed above, is recommended. The tubers should first be cut at the heel end to enable them to be set on a tray with the rose ends upwards; after they are set up, the tray should be placed in front of a window and covered with a sheet of newspaper. A temperature of about 50° F. is very suitable for the purpose. The characters of the sprouts, which subsequently develop, are remarkably constant and by means of them the identity of each tuber may be established. Aberrant sprouts occasionally appear on diseased or injured tubers of certain varieties, but these are readily identified and, for practical purposes, are unimportant. Thread-like sprouts, for instance, may arise from various causes: in certain varieties, Leaf Roll may be the cause; in many varieties the virus of Witches'

[1] F. E. Denny, *Synergistic Effects of three Chemicals in the Treatment of dormant Potato Tubers to hasten Germination.* Contrib. Boyce-Thomson Inst., 1945.

Broom is responsible; but the condition may be brought about by physical causes, *e.g.* chilling. In America,[1] such sprouts are sometimes attributed to hot weather when the tubers are being formed. The sprouts of genetical variations, *e.g.* certain wildings, are much thinner than the normal. In some years Bud Proliferation (Fig. 23), where the sprout growth simulates Wart Disease growths, appears. The cause of such proliferated sprouts is unknown but the evidence available suggests that storage conditions are of no importance and that the growths are conditioned during the growing season. Unless all eyes are affected, the tubers grow normally. Majestic seems to suffer from this trouble more than other varieties. Sprouts which develop in warm conditions and long daylight in spring are often atypical. This, however, is not the period when sprout tests are made. As conditions of light and humidity are difficult to standardise, it is recommended that on all occasions a few authentic tubers of the variety being tested should be included as a control.

The sprout itself consists of three parts, viz., the base (Fig. 24 (1) C), the middle part (Fig. 24 (1) B) and the tip (Fig. 24 (1) A). The base is equivalent to that part of the stem which in growth is underground. On it are found small rootlets and, in certain varieties, short stolons. Lenticels also are generally visible on the base. The middle part, which is equivalent to the above-ground stem, elongates considerably in darkness, but in light is usually short. The tip represents the growing point, enclosed by young leaves. Hairs and colour may be found on all three parts.

Observations on sprouts can be made at two periods. When the sprout is about 1 to 2 mm. long, differences in colour appear. It is true that the different shades of red and purple cannot be diagnosed at this point, but blue sprouts may readily be separated from those which are white or pink. Final observations can be made when the sprouts are 1 to 2 cm. in length, at which time differences appear in all of the following characters: shape of the individual parts, colour and distribution of colour, pubescence and the appearance of stolons. In addition to these, however, differences exist as regards the rapidity of development of sprouts.

[1] Circular 333. "Control Potato Diseases," University of Wisconsin, Madison, 1945.

FIG. 23.—Majestic tuber showing Bud Proliferation.

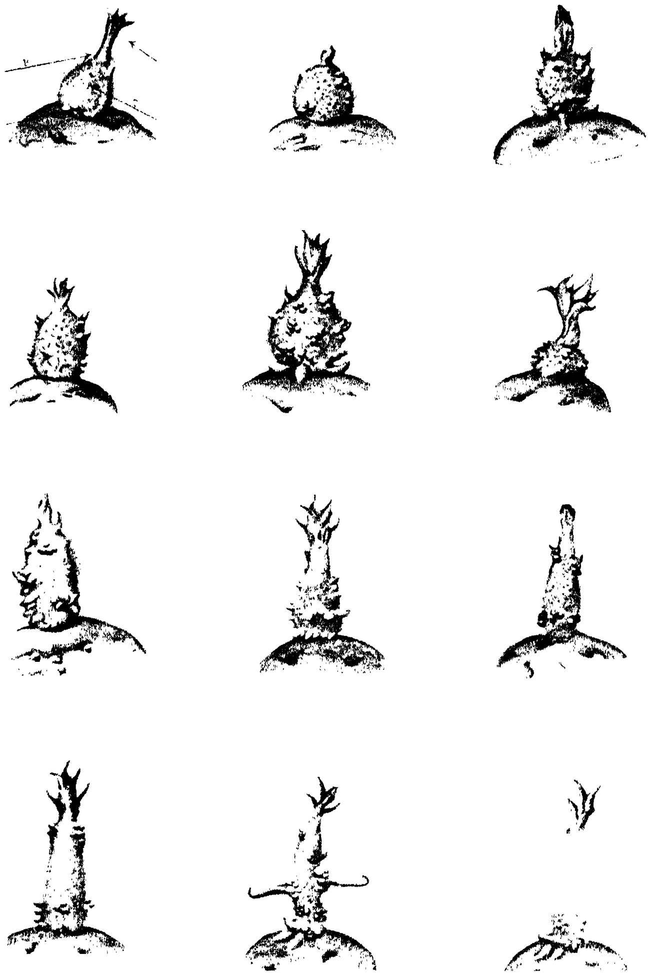


Fig. 24.—Sprout Parts and Variations in Sprout Characters (somewhat schematic).

1. A, Tip; B, Middle part; C, Base; and D, Rootlets.
2. Bulbous sprout with few rootlets and small closed tip; not hairy.
3. Bulbous sprout with more numerous rootlets and larger closed tip than 2; moderately hairy.
4. Cylindrical sprout with small unfolded tip; moderately hairy.
5. Bulbous sprout with numerous rootlets and large unfolded tip; moderately hairy; middle part conspicuous.
6. Sprout with small base, large middle part and large unfolded tip; hairy.
7. Cylindrical sprout with numerous rootlets and small closed tip; middle part short; very hairy.
8. Tapering sprout with fairly numerous rootlets, long middle part and large unfolded tip; not hairy.
9. Tapering sprout with long middle part and closed tip; rootlets coloured; hairy.
10. Tapering sprout with short middle part and large unfolded tip; very hairy.
11. Tapering sprout with long middle part, fairly numerous rootlets and unfolded tip; hairy; with stolons.
12. Tapering sprout with long middle part, fairly numerous rootlets and slightly unfolded tip; very hairy; with stolons.

A description of the sprouts of a number of common commercial varieties will be found in Appendix II, and below a note is given as to how the individual characters vary.

SHAPE.—In many varieties the base is bulbous; in others it is almost cylindrical; and, in others again, it tapers towards the middle part. The middle part may be relatively long or almost completely absent. The tip varies not only in size, so that some varieties have large and others small tips, but also in the condition of the leaflets, which may unfold or remain closed. The shape and size of the scale leaves on the base are also characteristic in some varieties.

COLOUR.—All sprouts have some colour, even though it be only very faint. The colour tones are not easy to describe for, although they may be pink or purple, the presence of green chlorophyll is a complication. Despite this, all sprouts may be grouped into two conventional classes, pink and blue. In some varieties there is very little colour and this is generally most obvious at the lenticels. In other varieties, particularly those of purple tubers, the colour is intense throughout the whole sprout. The scale leaves also vary in their colouring. The middle part, particularly in the young stages, is often light green. In blue sprouts the tip and base are always coloured, although the colour may disappear later from the tip. In pink sprouts the tip is sometimes only faintly coloured or green. Colour disappears more readily from the tips of pink than from those of blue sprouts. Colour, therefore, is generally more pronounced on the base than on the other parts of the sprout, although exceptions have been found.

THE HAIRS.—All sprouts have hairs. Great differences exist, however, as regards their frequency, condition and distribution. Some varieties are practically hairless and others are very hairy. The hairs may be long or short, outstanding or slightly adpressed. In general, the hairs on the base are the most important; nevertheless, those on the middle part may also be useful. Glandular hairs are found on all sprouts but these are not useful for diagnosis. It is to be noted that some variations, *e.g.* the Dahlia variation of Great Scot, have less hairy sprouts than the normal forms.

THE ROOTLETS.—These appear on the base. Varieties may be differentiated by frequency of rootlets. Normally, the rootlets are white, yet in some varieties, particularly those in which the tuber cork is coloured, they are pigmented.

THE LENTICELS.—The lenticels on the sprout base may be darkly coloured or of the same tone as the remaining tissue. In certain varieties the centre of the lenticel is conspicuously white, and in some varieties the lenticels are not raised much above the general level of the sprout epidermis.

STOLONS.—The sprouts of a few varieties are characterised by the appearance of short stolons.

RAPIDITY OF SPROUTING.—The rapidity of sprouting is a useful diagnostic character. Some varieties, *e.g.* Golden Wonder and Arran Consul, sprout only very slowly, while others, *e.g.* Craigs Defiance, Epicure and Arran Pilot, develop rapidly. It should be noted that variations sometimes differ from normals in sprout development. Bolters, for instance, usually sprout more slowly than the normal forms and, in addition, more of their tuber eyes sprout. This last characteristic is typical also of certain wilding types.

TESTING TUBERS FOR PURITY

We may now consider a method of examining a tuber sample for its purity.

The first essential being clean tubers, the sample should be carefully washed. After washing, the tubers should be examined for colour, those deviating from the type being regarded as impurities. Tubers showing substantial differences in shape and condition of the eyes must be treated with suspicion. These should be specially marked for further observation, although with experience some may be set aside as being definitely wrong. A fair section should then be cut from the heel end of each tuber and the flesh colour and flesh consistency determined, deviations from the normal being again set aside. If the variety be one in which the alkali reaction is very characteristic, as for example Eclipse, the heel portions of the tubers should be tested and those giving a markedly different reaction again set aside. The tubers should now be set up in the sprouting tray and exposed to full daylight for one to two weeks At the end of this period they should be examined for pigment development. The rapidity of greening, the type of colour development and the appearance of white dots under the skin should be noted. Deviations from the normal should again be isolated. The tubers at this stage can be covered with white paper and allowed to sprout, a true sample of the variety in question being included as a control. Until the student gathers confidence in his judgment he is best advised to sprout also those tubers which he has already eliminated by the foregoing tests.

The ordinary grower and merchant will generally be unable to carry out the more complicated chemical tests for purity, as these are practicable only under laboratory conditions.

CHAPTER VI

VARIATIONS AND CORRELATIONS

THERE occur from time to time in all potato varieties plants which differ from the normal type and which, in vegetative propagation, retain their distinctive characters. These are known as variations. In commerce, some of them although interesting may be disregarded but others which affect crop yields are of importance, and with these growers should in their own interest be familiar. Potato breeders are also concerned as it is always possible that a variation may excel the normal form in one or more of its commercial features.

When two or more characters, *e.g.* colour in the tuber cortex and colour in the interior of the flower ovary, are always, or practically always, associated, they are spoken of as correlated characters. Many such correlations have been found in the potato, and it has also been determined that other features, although not invariably associated, occur together with considerable frequency. When the characters involved have economic significance, they are important to the breeder; even when they have no economic significance they are often helpful in enabling varieties to be grouped and, indeed, in establishing their identity.

VARIATIONS

These include differences in form, colour, physiological and doubtless, chemical characters. The commonest are bolters, semi-bolters and wildings. Variations affecting the colour of tubers or flowers also appear quite often, but those involving other characters are less frequent.

BOLTERS (Fig. 25 (3)).—A bolter usually differs from the true varietal type in its greater height, stiffer foliage, smaller leaflets, later maturity, greater resistance to Blight, greater capacity for flower-bearing, higher pigmentation, more frequent and longer runners, coarser, fewer and sometimes longer tubers, slower sprouting and diminished apical dominance of sprouts. In some normally non-fruiting varieties, *e.g.* Ally, the bolter may bear berries. These differences are, however, not always

1. 2. 3.

FIG. 25.

1. Normal Foliage. 2. Wilding Foliage. 3. Bolter Foliage.

evident in younger plants and usually a bolter can be distinguished from the true form only when the stage of full growth is reached. Bolters mature from three to six weeks later than normal plants. Another type, intermediate in its characters between the bolter and normal, appears in some early varieties, *e.g.* Arran Pilot, Arran Signet, Duke of York, Di Vernon, Eclipse, Epicure and May Queen. This is known as a semi-bolter. Semi-bolters mature one to three weeks later than normal plants and their top rosettes of leaves have often small, stiff and folded leaflets as contrasted with the larger, flatter, less stiff and more glossy leaflets of normal plants. Unlike bolters, semi-bolters flower normally.

Bolters and semi-bolters, mainly by reason of later maturity, are commercially undesirable; the coarse tubers often produced by bolters are also not good marketable types. These variations are most frequent in early varieties, Ninetyfold being an exception; in some late sorts, *e.g.* Kerr's Pink, Dunbar Standard and Golden Wonder, they have never been observed. There appears to be little doubt that the "Giant Hills" of American literature refers to bolter types.

WILDINGS (Fig. 25 (2)).—The following points may be noted in regard to the manner in which a wilding differs from the normal type:—(1) In consequence of the production of a large number of thin stems, the plant presents a closer and more compact appearance; (2) associated with these numerous stems are numerous stolons, each bearing an undersized tuber; (3) the wilding leaf is shorter, the number of primary leaflets is smaller and the latter are rounder than normal; (4) there is a marked reduction in the number of secondary leaflets; (5) the floral parts are generally absent; (6) often it is slightly shorter than the normal plant; and (7) more of the tuber eyes sprout than is usual during storage, and the sprouts themselves are often thinner than the normal. Altogether, wildings give the impression of more primitive plants than those typical of the various varieties.

Several different forms of wildings are known, but essentially they all vary from typical plants in the above-mentioned particulars, some being more "wild" than others. In some forms the tuber is longer than normal and stolons may appear at leaf axils. All wilding forms are very constant when reproduced by tubers and none of them appears to differ in maturity or disease susceptibility from the normal type. The presence of wildings in a stock may seriously diminish the yield of ware tubers and, because they appear more in the seed than in the ware, they tend to increase, rather than to decrease, in crops. Wildings appear in practically all varieties and, unlike bolters, are as common in late as in early types. Wildings must not be mistaken for plants infected with the virus of Witches' Broom. Plants suffering from the latter disease generally show chlorotic areas at the leaflet margins and sometimes have normal as well as wilding-like shoots.

Another type of variation, known as the "Feathery Wilding," bears no relation to wildings. It is characterised by narrow leaflets in the apical foliage and it may flower quite freely. Its roots are more numerous and its tubers longer and more pointed than the normal and there is no apical dominance in its sprouts. Indeed it sprouts earlier than the normal tuber. Like the true wilding, it yields less than the normal and produces more seed-size tubers.

OTHER FOLIAGE AND CROPPING VARIATIONS.—Although they cannot be systematised, there are many other foliage variations. Some differ markedly from the normal forms and some approach so closely to the latter that they may be discriminated only if they are grown with abundance of room and not in drills with other plants. Names have been given to a number which can be readily identified. The organ most usually affected is the leaf, hence the names—dahlia-leaf variation, spinach-leaf variation, rasp-leaf variation, holly-leaf variation, ivy-leaf variation, docken-leaf variation, coarse-leaf variation and abnormally subdivided-leaf variation. Several of these types are found in a number of varieties while others are restricted to particular varieties: the Bindal variation, for instance, is found only in King Edward. Marginal variegation of the leaflets is characteristic of certain variations and fasciation is not uncommon. In the above-mentioned and other variations, characters other than those of the leaf may be affected; examples are found where the floral parts are reduced, *e.g.* docken-leaf variations, where the sprouts are glabrous, *e.g.* dahlia-leaf variation in Great Scot, and apical dominance in the sprouts is lost, *e.g.* in rasp-leaf and spinach-leaf variations.

Questions are often raised about the cropping of variations.

As a general rule, variants yield less than normals. Bolters, semi-bolters and some rare variations are exceptions, doubtless owing to their later maturity, and if they are allowed to reach full maturity they frequently out-yield normals. Lifted as early ware, however, when the foliage is green, normals almost invariably yield more than the two late variants. In Denmark [1] one type of bolter in the variety Bintje has been isolated which, when compared at full maturity with the normal, shows an increased yield of 39 per cent. Bald and Oldacre [2] give examples of variant clones of Up-to-Date and Brownwell that are consistently capable of outcropping other clones of similar maturity when grown under certain environmental conditions. It is possible, of course, that the poorer-yielding clones are retrogressive variants ; nevertheless, the point is of importance to the grower who is raising healthy stocks from individual, virus-tested plants. A further complication with clones is that they may react differently in different seasons so that one may crop well one year and another in a different year. More work requires to be done on this subject and it is only now, when virus-free potatoes are available, that investigations can be pursued free from complicating factors. In selecting individual plants as the basis for future stocks, the grower should retain only those clones which during their years of multiplying have given consistently high yields, other characters remaining the same : low-yielding clones must be discarded.

STAGS AND MOP-TOPS.—As these occur fairly frequently in certain seasons, a word about them will not be out of place. Their true nature is unknown and they may be pathological forms.

Stags resemble bolters : they are taller than the normal and, in addition, are characterised by delicate, sulphury tops and elongated tubers which sprout while the foliage is still growing. They are common in King Edward but occur also in other varieties. The condition does not seem to be transmitted by seed tubers.

In Mop-tops either the whole plant or only certain shoots may be affected. The salient features of affected shoots are : (1) a shortening of the internodes, leading to dwarfing and

[1] *Aktieselskabet de Danske Spritfabrikker*, 1950.

[2] J. G. Bald and C. E. W. Oldacre, "Testing and Maintenance of Potato Clones," *Emp. Journ. Exp. Agric.*, vol. xviii, no. 70, 1950.

crowding of the leaves, (2) a twisting of the leaflets which often show areas of darker and lighter green, and (3) the absence of flowers. When all shoots are affected, the plant is markedly dwarfed. The condition is found in Craigs Defiance, Dunbar Rover and Arran Pilot. Although occasionally transmission by seed occurs, frost is usually considered the main cause.

COLOUR VARIATIONS.—Variations in colour may occur in all parts of the plant where pigment appears. The parts most frequently affected are tubers, flowers and buds, but stems may also be involved. The variants are very constant in vegetative propagation, but occasionally reversion to the normal is found.

Variations in tuber colour occur fairly frequently and have been observed in the following amongst other varieties, viz. :—

White varieties:

- (*a*) Duke of York—White to purple (coloured cork).
- (*b*) Duke of York—White to pink (coloured cortex).
- (*c*) Great Scot, Up-to-Date, Arran Comrade, Langworthy—White to russet.

Coloured cork varieties:

- (*a*) Catriona and Di Vernon—Parti-coloured purple to whole coloured and to almost white.
- (*b*) Fortyfold—Parti-coloured purple to white.
- (*c*) King Edward—
  - Parti-coloured red to almost whole coloured.
  - Parti-coloured red to parti-coloured red, colour avoiding eyes.
  - Parti-coloured red to almost white.
  - Parti-coloured red to parti-coloured purple.
  - Parti-coloured red to parti-coloured red and purple.
  - Parti-coloured red and purple to almost whole coloured.
- (*d*) Gladstone—Parti-coloured red to almost whole coloured and to white.
  - Parti-coloured red to parti-coloured red, colour avoiding eyes.
- (*e*) Katie Glover—Parti-coloured red to almost white.

Coloured cortex varieties:

- (*f*) Arran Victory—
  - Blue-purple to parti-coloured.
  - Blue-purple to parti-coloured with coloured flesh.
  - Blue-purple to red-purple with blue-purple eyes.
  - Blue-purple to almost white.
- (*g*) Kerr's Pink—
  - Pink to parti-coloured blue-purple.
  - Pink to parti-coloured pink.
- (*h*) Northern Star—Parti-coloured pink to whole-coloured blue.
- (*i*) Redskin—Pink to blue-purple.

The variants found in the coloured cork group of varieties appear to be less stable than those of the coloured cortex group. Variations in tuber colour do not always affect sprout colour.

Changes in flower colour are equally frequent. Those which have been observed, however, concern mostly the loss of pigment rather than its gain. Thus, white-flowered variants have been isolated from the following varieties which normally bear coloured flowers, viz., Arran Cairn, Golden Wonder, President, Sharpe's Express, Glenshee and Up-to-Date. The appearance of a "yellow flower" variation in the variety Gladstone has already been noted.

The flower bud, which is rather a conspicuous character, may also vary. Thus, an alteration from coloured to green has been found in Kerr's Pink, Gladstone and rogue varieties. Stems may be affected and green-stemmed variants of several varieties, including Kerr's Pink, are now known.

VARIATIONS PRODUCED ARTIFICIALLY.—While the above-described variations occur naturally, it is possible by artificial means to bring about changes in some varieties which, in vegetative propagation, remain constant. In 1923 one of the writers attempted to ascertain if from the deeper layers of the tuber tissue variant forms could be produced, and for this purpose the eyes of the tuber were excised and growth from the deeper layers induced. All varieties selected for trial produced normal plants. Later in U.S.S.R., Asseyeva,[1] adopting the same methods, recovered the normal forms from mutants. Repetition of the work in this country with certain "sports" led to results similar to those of Asseyeva. It has been found, in addition, that treatment of the sprouts, *i.e.* the removal of the sprout buds, is as effective as treatment of tubers. In Britain three types of varieties have now been investigated, viz., (1) those, such as Golden Wonder, purple Duke of York, blue Northern Star, Arran Victory variations and certain foliage variations which have "sported" from normal forms; (2) parti-coloured, coloured cork varieties, such as King Edward, Di Vernon and Gladstone; and (3) coloured cortex varieties, such as Edzell Blue, Arran Victory and Kerr's Pink which have not sported. As regards the first

[1] T. Asseyeva, "Bud Mutations in the Potato," *Bulletin of Applied Botany, of Genetics and Plant Breeding*, vol. xxvii, No. 4, 1931.

group, the method leads often to the recovery of the normal forms although it has not been successful with all variants. Various results have been obtained by applying the technique to members of the second group. In some the colour of the tuber is intensified and distributed over more of the surface, while in others it is reduced to isolated and very small speckles, as contrasted with the very much larger colour splashes found in the original forms. Sometimes there is a more general effect. Thus, in Gladstone, one of the variants differs from the normal in several respects: intensity and distribution of colour are very greatly reduced and appear as very faint spotting at the eyes, or the tubers may be entirely white; the flower bud changes from coloured to green; and there is less colour on the stems. In addition to these colour changes, this Gladstone variant is characterised by a certain stiffness of the foliage, by a curious lantern-like appearance of the petals prior to opening, as if they had some difficulty in separating at their tips, and by an apparent reduction in the rapidity of vegetative growth. In another Gladstone variant, leaflets are flatter and stiffer and the tubers longer than in the normal form. A King Edward variation with purple instead of pink colouring on its tubers and a typical bolter have also been produced by this technique.

As regards the third group, few successes have as yet been reported. This, however, may be due to the fact that little work has been done; one of the authors has, however, obtained Kerr's Pink variants by the application of the same technique.

Asseyeva has described other changes brought about by eye-excision. A certain group of Russian varieties has whole-coloured tubers with eyes darker than the remaining tissue. It is presumed that in the tubers of these varieties the colour is located in the cork. On treatment these produce "spectacled" tubers in which the eyes are colourless and the remaining surface coloured. Somewhat similar variations have been obtained in this country from the varieties Gladstone and King Edward. In these the colour avoids the eyes but does not cover the whole of the remaining surface. By the same methods Asseyeva has recovered the typical forms from variants showing abnormal leaves and, very occasionally, from certain "wilding" types. The recovery of normal from wilding and bolter plants has not been obtained in this country by this technique and it seems certain that Asseyeva's terminology is incorrect here.

Fasciation has been induced by removing the buds from sprouts, this being in harmony with Blodgett's and Nielson's [1] suggestion that this condition appears to be due to some genetic disturbance and not to virus infection.

It will be seen from the above that the changes affect both physiological and morphological characters.

THE NATURE OF VARIATIONS.—Plants in a pathological state often assume abnormal forms and, if the diseases be transmitted by the seed tubers, the abnormalities will naturally appear from season to season so long as the plants survive. Virus diseases of the potato are so transmitted; hence, before considering other causes, the possibilities of some "variations" being due to virus infection must be examined. Grafting experiments with bolters and true wildings have shown that these conditions are apparently not due to anything of an infectious nature. Davidson [2] suggests that the term wildings should be dropped, as such plants are really infected with the virus which causes Witches' Broom. His illustration (Fig. 26), however, does not depict a true wilding. It is possible by grafting to transmit the virus of Witches' Broom but it is impossible to transmit the wilding condition. Unfortunately, a few of the other foliage abnormalities have not been so tested, and it is just possible that they may not be true variants but diseased forms. The variety King Edward has a great many variations, but in the present state of our knowledge it is impossible to attribute these to mutations in the paracrinkle virus with which every plant of this variety is infected.

Somatic variations are attributable to changes in those structures of the cell which maintain the identity of the type; such changes, for instance, may occur as qualitative and quantitative alterations in the chromosomes of the nucleus or in the sorting out of plastids. Chromosomes are regarded as the important organs of heredity and every chromosome, and indeed every part of every chromosome, is assumed to have a specific function or specific functions. In sexual reproduction

[1] E. C. Blodgett and L. W. Nielson, *Phytopathology*, vol. xxxvii, no. 8, 1947.

[2] W. D. Davidson, B.A., B.Sc., N.D.A., *Potato Growing for Seed Purposes*, Department of Agriculture, Eire, 1938.

there is always a sorting out and redistribution of chromosomes which do not occur in the vegetative growth, such as is being discussed, in which the chromosomes suffer merely equational division. Nevertheless, changes in the chromosome numbers and constitution do occasionally occur in somatic tissue, due to abnormal behaviour, and, depending on the position of the affected cell, or cells, the plant tissue will be either wholly or partially affected by the change. In the latter instance the mutated and unmutated tissue may assume different positions, such as the one enclosing the other (periclinal chimæras), the two running parallel to one another and occupying different proportions of the cross-section (sectorial chimæras), or both forming a mosaic patchwork. The cause of the changes in the chromosomes and the nature of these changes are unknown. It appears, however, that certain points (genes) on the chromosomes are more unstable than others, and to this instability is attributed certain variations in plants which appear in regular and constant proportions in different varieties. In the potato, colour is due in the first place to chlorophyll which is green, and, in the second, to soluble anthocyanin pigments which produce a range of colours from pale pink to deep purple. The green of the chlorophyll and the yellow and orange colours of plants are located in protoplasmic bodies known as plastids. There is, however, no evidence that the anthocyanin pigments of the potato, occurring in solution in the cell sap, are derived from the activity of plastids, hence changes in colour cannot at present be attributed to variations in the distribution of these bodies.

No matter how the changes are brought about, the variations produced differ in type. Asseyeva states that by far the great majority show the character of periclinal chimæras, *i.e.* the modifications embrace only one or two of the outer layers of cells. As previously stated, it is possible to recover the normal forms from these by eye-excision. The fact, however, that this treatment does not lead to the recovery of normals from all variants means that many are not periclinal in nature. According to Asseyeva, the mutational changes may affect the "epidermis" or "subepidermis." Epidermal variations cannot affect the germ cells, but subepidermal variations usually do. Thus the character of the two different types may be demonstrated genetically. Only in subepidermal variations is stem colour altered. Whereas some of the types of variations found

FIG. 26.

Right—Normal President. *Left*—President affected with Witches' Broom. Note the resemblance of Witches' Broom to the Wilding condition and the chlorotic leaflet margins in the former. (NOTE.—The name Witches' Broom has long been used in Scotland to describe a virus disease which may not be identical with the Witches' Broom of American literature, *cf.* Chapter XXVI.)

FIG. 27.

Leaves showing some Leaf Forms found in certain Variations: 1. Normal. 2. Abnormally subdivided leaf. 3. Rasp-leaf variation. 4. Ivy-leaf variation. 5. Docken-leaf variation.

in Russia have not been observed in this country, there seems to be little doubt that many potato mutants behave as if they were periclinal in structure. In this country, the following have been found to be periclinal chimæras: Golden Wonder, Sefton Wonder, Field Marshal, purple Duke of York, blue Northern Star, broad-leaf variation in King Edward, dahlia-leaf variation in Great Scot, abnormally subdivided leaf variations, coarse grey-leaf variation in Kerr's Pink, raised epidermis in Kerr's Pink and Redskin, lead-green variation in Arran Pilot and all Arran Victory variations mentioned on page 78; on the other hand the following have been tested and so far have not been found to be periclinal in nature: bolters, semi-bolters, wildings, feathery wildings, rasp-leaf, spinach-leaf, docken-leaf and the Bindal variation in King Edward.

Salaman,[1] although accepting Asseyeva's thesis broadly, differs from her in considering that the mutated and unmutated cells usually form a mosaic patchwork and are not relegated into specific layers. Such a patchwork might explain the occurrence of certain variations where, occasionally, normal and abnormal shoots appear on the same plants. Salaman supports his theory by citing evidence to the effect that in certain mutant forms colourless and colour-producing cells exist in the very depths of the tuber tissue. On the other hand, the relative constancy of most colour variations is not consistent with the theory of a mosaic structure. The fact that differently coloured variations may be obtained from the deeper tissues of one tuber is no evidence that a Mosaic structure exists, rather it points to some irregularities occurring when cells are dividing; such irregularities can be expected in calluses from which the new plants arise.

The explanation of the variations produced in certain coloured cork varieties by the eye-excision technique may not follow the same lines as those described above. The colour pattern of these varieties is a definitely inherited character and they cannot be regarded as periclinal chimæras or as plants which have mutated in any way. Moreover, Asseyeva has found that the genetical behaviour of the variant forms produced in these varieties by eye-excision is inconsistent with the periclinal theory. Until the true solution is found, such

[1] Dr R. N. Salaman, "Somatic Mutations in the Potato," *Report and Proceedings of the Ninth Horticultural Congress*, 1930.

varieties may be considered as structural chimæras behaving in the same way as periclinal chimæras. These variations have not been studied cytologically, but it is possible that, by the treatment of the tubers, they may arise in some varieties through irregularities in nuclear behaviour, such as might be expected to happen in polyploid varieties of hybrid origin. In these latter the balance of the chromosomes of the two sets originally present might be changed by irregularities of divisions. Whatever the explanation, it is easy to comprehend how, in these varieties, variations can arise in nature: injury to the tuber eyes might induce growth from the deeper-lying tissue. It has been noted already that many variations which show the same characteristic differences from the normal plant occur in many varieties and, whatever their origin may be, it appears as if the same causes operate to bring them into being. Such, for example, are bolters, semi-bolters, wildings, feathery wildings, ivy-leaf, docken-leaf, coarse-leaf, rasp-leaf, spinach-leaf and abnormally subdivided-leaf variations.

One of the authors has produced bolters in much greater frequency than normal by inducing tubers to develop on top cuttings dibbled into the ground, and, as has already been noted, a bolter has been developed from a half-tuber planted after all the eyes were excised, the other half being a control. Both of these point to some irregularity in cell division. Carson and Howard [1] consider bolter Gladstones differ from normals in being genetically "wilder" and that this is an inherited character. Thomas [2] suggests that the bolter condition may be due to the production of a chromosome fragment found by him in the cell nuclei of bolters. Carson and Howard apparently do not accept this explanation and attribute the bolter condition to changes in genes, *i.e.* points in the chromosomes. Revell [3] found that normals, selfed, gave a significantly lower proportion of "bolters" than bolters, selfed, or crosses between bolters and normals and that there was very little difference between bolters, selfed, and crosses between bolters and normals. As a result of preliminary work, Driver and Hawks [4] suggest

[1] G. P. Carson and W. H. Howard, *Nature*, 30th December 1944.

[2] P. T. Thomas, "Bolters in Potatoes," *Nature*, 24th February 1945.

[3] *Annual Report*, 1946. John Innes Horticultural Institution.

[4] C. M. Driver and J. G. Hawkes, *Imp. Bur. of Plant Breeding and Genetics* (Cambridge, 1943).

that the bolter condition is due to a genetical alteration of some nature converting a long-day plant to a short-day one. Under short days, the bolter grows normally, but shows various "wild" characters under long days. Further work by Hawkes [1] has convinced him that the bolter is a reversion to the more ancestral type of short-day adapted potato such as is found under cultivation in the S. American Andes and from which our own domestic potatoes have probably arisen. The results obtained by him show that the bolter, when grown under short days, is indistinguishable in most of its features from the normal, thus lending weight to the hypothesis that the change from normal to bolter is due to a mutation of one or more relatively unstable genes controlling response to day-length.

Bolters may arise direct from normal plants as also may semi-bolters. The origin of bolters from semi-bolters has, however, never been demonstrated. Occasionally one bolter shoot only arises from a tuber derived from a normal plant. When this happens, the bolter shoot gives bolter and the normal shoot normal tubers.

Marginal variegation is a phenomenon probably similar to that occurring in other plants. Normally, the outer layer of the growing point gives rise to the single outer layer (epidermis) of the mature tissues. Similarly, the second layer of the growing point gives rise to the second layer of the mature plant. While this is true for most organs of the mature plant, the leaf is exceptional. In most leaves the whole thickness of the leaf at the margin to a width varying with the species is derived from the first and second layers of the growing point, so that the whole margin of the leaf, though it may be many cells in thickness, is derived from the first and second layers of the growing point exclusively and will, consequently, partake of the characters of these, forming a conspicuous mass of colourless tissue, if they happen to lack the capacity to form chlorophyll.

INCREASE OF VARIATIONS IN STOCKS.—It is not known with certainty how all variations arise or what conditions predispose plants to vary in the field. As, however, variants normally retain their forms and characteristics when multiplied by seed tubers, they present a serious problem to the grower.

[1] J. G. Hawkes, "The Photoperiodic Reactions of Potato Bolters," *Emp. Journ. Exp. Agric.*, vol. xv, 1947.

There exist few experimental data indicating how frequently new variations arise in varietal stocks. The prevalence of variations in any stock does not necessarily mean that new forms are continually arising in the latter, rather it is usually a symptom of inadequate roguing and of the multiplication of existing variations within the stock. Observations on new varieties and stocks thoroughly rogued for abnormal types suggest, however, that in sorts which do not "bolt" very frequently one bolter may arise in about 15,000 plants each year. Semi-bolters in earlies appear to arise with greater frequency. In Arran Pilot the annual increase of semi-bolters seems to be about 0·3 per cent. Wildings and feathery wildings originate slightly less frequently than bolters, and foliage variations, such as those with coarse, abnormally simplified or abnormally subdivided leaves, arise rarely. Colour variations differ considerably: some tuber changes occur fairly frequently, while flower changes are rare. Varieties differ in the number of new variations which arise, and certainly early varieties are much more prone than maincrops to mutate.

Once variations have originated in any stock, certain factors and practices restrict while others accelerate their multiplication. The use of chats as seed considerably increases the number of wildings, feathery wildings and all other variants characterised by the production of small tubers. The multiplication of variations in any stock is promoted by anything which renders their detection difficult or which leads to their producing more seed than normal plants. So far as bolters and semi-bolters are concerned, the burning down of the foliage has both effects, while, as regards all variations, recognition and consequent elimination are made difficult, and often impossible, by bad furrowing-up, the use of uneven size of seed and the beating down of foliage by wind and rain.

CORRELATIONS

The association of several characters in the potato is quite common; indeed, it is difficult to find varieties in which correlated features do not appear. The most conspicuous are colour associations, but morphological, physiological and chemical characters may also be involved. A few of the more obvious associations, *e.g.* numerous stolons and small tubers,

FIG. 28.

"Stag" tubers. Note elongated form and premature sprouting

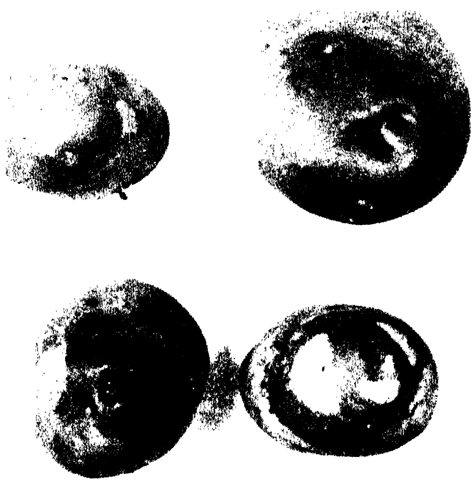


FIG. 29.

Variations in tuber colour arising after excision of eyes and growth from callus tissue (Variety—King Edward)

Top (*right*)—Normal.
Top (*left*)—Variation without colour.
Bottom (*right*)—Colour avoiding eyes.
Bottom (*left*)—Purple variation.

are not discussed. In these, as also possibly in some of the others mentioned, the characters in question may not be correlated in the true sense, but are rather of the nature of manifestations of cause and effect.

COLOUR ASSOCIATIONS.—Most of these concern the association between tuber colour and the appearance of pigment at various other points on the plant. It is, therefore, important that the tuber types involved should be defined. They are :—

Type I.—Coloured cork, entire tuber highly coloured red or purple, the eyes being deeper in tone than the remaining tuber surface.

Type II.—Coloured cork ; parti-coloured pink.

Type III.—Coloured cork ; parti-coloured purple.

Type IV.—Colour absent from cork but present in cortex ; whole-coloured, red or purple.

The various correlations found are set out in Table VIII.

MORPHOLOGICAL AND PHYSIOLOGICAL ASSOCIATIONS.—The most obvious associations of this kind are those existing between type of foliage and maturity : the low-growing and weak-stemmed varieties are nearly all early in maturing, whereas the tall and robust-stemmed sorts are late. Male sterility is also associated with maturity, being a marked feature of earlies. A weak alkali reaction of the tuber flesh is also associated with early maturity. In British varieties certain foliage characters are very frequently found together with distinct tuber types. For instance, when the eyes appear on the shoulder of the tuber, the foliage habit is usually upright ; and when the habit is spreading and the basal foliage dense, the associated tubers are generally long. Deep eyes and indented heel ends are found often in round but seldom in oval and kidney tubers. The coloured cork group of varieties is often characterised by the appearance of small stigmas and thin styles. There is also an association between the tuber shape and the shape of the sprout base : long tubers have generally thin, and never bulbous, sprouts, whereas thick and bulbous sprouts are typical of round tubers. The connection between very hairy and almost glabrous sprouts on the one hand, and hairy and comparatively hairless stems on the other, has already been indicated. Varieties with matted,

TABLE VIII

Colour Correlations

Characters	Associated Characters	Degree of Correlation
Type I Tuber	Coloured flower Coloured absciss ring Highly coloured leaf axils Highly coloured inner axil of petioles Coloured sprout rootlets Coloured centres of sprout lenticels	Apparently absolute
	Highly coloured junctions of inflorescence branches Coloured base of corolla Coloured base of berry	Very frequent
Type II Tuber	Coloured centres of sprout lenticels	Apparently absolute
	Coloured flower Coloured absciss ring Coloured sprout rootlets	Very frequent
	Coloured leaf axils Coloured inner axils of petioles	Frequent
Type III Tuber	Coloured flower Coloured centres of sprout lenticels	Apparently absolute
	Highly coloured leaf axils Highly coloured absciss ring Coloured sprout rootlets	Very frequent
	Highly coloured junctions of inflorescence branches Highly coloured inner axils of petioles Highly coloured base of corolla	Frequent
Type IV Tuber (*a*) Purple (*b*) Red	Purple ovary interior Red ovary-interior	Almost absolute
(*a*) and (*b*)	Coloured stems Coloured midribs of leaves	Very frequent
Faintly coloured Sprout	Flower white	Apparently absolute
Blue Sprouts	Flower white or blue-purple	Absolute
Pink Sprouts	Flower white or red-purple	Absolute
Red or Purple on Anthers or Filaments	Coloured tuber cork	Apparently absolute
Coloured Roots	Coloured tuber cork	Apparently absolute
Coloured Star of Flower	Coloured tuber cork	Frequent

fibrous roots are invariably poor croppers and are discarded by breeders without testing.

ASSOCIATIONS CONNECTED WITH DISEASE. Susceptibility to certain diseases is associated with maturity. Thus, early varieties are generally more subject to Dry-rot than are lates. All very slow-growing varieties appear to succumb rapidly to Leaf Roll. Why this should be so is not clear, but it is suggested that at the time aphides are most active in spreading infection, such varieties are at a stage of growth when the virus is most readily accepted. Resistance to Common Scab appears to be related to the character of the lenticels and surrounding tissue. Varieties which are top-necrotic to the less serious viruses, *e.g.* " X," " A," " B " and " C ," appear to be susceptible to virus " Y," although the information on this point is insufficient to enable a positive assertion to be made. In addition, the top-necrotic reactions to viruses " A " and " X " seem to be closely linked. Other associations undoubtedly exist, but in this field little work has yet been done.

CHAPTER VII

MAINTENANCE OF PURE STOCKS OF VARIETIES OF THE POTATO AND THE ROGUING OF FIELD CROPS

DETAILED descriptions of the varying characters of potatoes have been discussed in the preceding chapters. Let us now consider their application to field work.

PRECAUTIONARY MEASURES.—Effective roguing is sufficient to maintain the purity of any particular stock, provided the conditions of growth are such that danger of admixture in the field is eliminated. To avoid such danger, certain precautions must be taken.

The purchase of pure "seed" from certified crops, is for most growers the starting-point in raising true stocks. Adequate steps must always be taken, however, to prevent the introduction of impurities into such seed when brought to the farm. The mixing of stocks is nearly always due to carelessness in the handling of crops or mismanagement of rotations. Groundkeepers are a frequent source of contamination. Care must be taken, therefore, to ensure that these are either eliminated from the soil or reduced to a minimum. Wherever a short rotation is practised, the field, or portion of the field, should always be planted with the same variety. The use of farmyard manure from animals fed with unboiled potatoes must be avoided on potato land. One effective way of reducing the danger from groundkeepers is to feed pigs on the land after the removal of the crop and even later in the rotation. The best method, however, is to have long intervals between potato crops. Pure stocks frequently become mixed owing to inadequate separation of varieties in the field; where more than one variety is grown, the stocks should be separated by at least two drills free of potatoes. Headrigs should never be planted with a variety different from that grown in the field, otherwise serious mixing may occur through tubers from the inner drill of the headrig becoming mixed with the main crop at lifting. It is desirable also to pit each variety on the land on which it grew or on land not intended for potatoes in the near future. Again, different varieties should not be put into the same pit, separated only by straw. This applies with equal force to different stocks of the same variety. Finally, harrowings should always be pitted separately.

As regards bolters, semi-bolters and variations generally, certain precautions must also be taken. Bolters and semi-bolters are apparent only when the stage of full growth is reached, and many will not be noticed if the haulms are destroyed at the time of maximum seed production. The grower of seed should, therefore, periodically allow part of his stocks, particularly of early varieties, to reach full growth, so that bolter roguing is possible. Wildings and all varieties producing small tubers increase rapidly when chats are planted, hence the latter should not be used in seed production.

Roguing for Purity: Procedure

The foregoing precautions having been taken, the grower must apply his mind to the question of eliminating impurities and variants from his stocks.

The first opportunities of roguing occur at dressing time and when seed is boxed. It is then possible to identify obvious impurities by reference to substantial differences in tubers and sprouts. After the seed is planted little can be done until the plants are well grown. The crop is at the best stage for roguing when flowering begins, but it is possible to rogue prior to this and often advisable to do so later. Early roguing has the advantage that the tubers, being small, are not difficult to remove or carry from the field. It should, however, be remembered that, as impurities differ in their maturity dates, they are not all at their most conspicuous stages at the same time, hence the necessity for repeated examinations of crops.

The conditions under which roguing is undertaken are important, as the efficiency of the work may be impaired by inattention to certain details. Strong sunlight makes the identification of plants difficult and it is better to avoid bright days. When roguing must be carried out in such circumstances, it should be limited to bolters and semi-bolters, which are generally obvious, or to fields the drills of which run at right-angles to the direction of the sun. Rain also affects the leaf appearance and is apt to cause confusion, hence roguing in wet weather is best avoided. Dull weather undoubtedly provides the best conditions. Everything must be done to facilitate the task of the roguer, for although the work is not physically exhausting, the eye readily tires and plants may be missed. Physical exertion accentuates this tiredness, hence in the organisation of roguing it is best to limit the roguer's duties to the marking of rogues and variants with canes or in some other manner such as laying the shaws across the drills, and for the actual lifting to be done by followers. Indeed, from all points of view, it is best to proceed thus, for this not only prevents the roguer from becoming tired, but also enables the best advantage to be taken of dull weather. The marked plants can be lifted when the weather conditions for roguing are unsuitable. Roguing must never be hurried and not more than two drills should be examined at one time by one person. Lastly, very great pains must be taken to ensure that all rogue tubers are removed from the soil.

The problems presented by different varieties must necessarily vary. Although certain rogues, *e.g.* Yam and the Rogue like Great Scot, are peculiar to the stocks of certain varieties, no systematic scheme of roguing for any particular variety can be formulated ; tubers of the ordinary commercial varieties are continually becoming mixed, and the grower must not approach his crop with preconceived ideas as to what he should look for or find. Before roguing begins, it is essential to confirm the identity of the crop itself, reference being made to the descriptions in the Appendix, if necessary. The points which, either singly or in combination, are of greatest service in the detection of rogues are enumerated in Chapter III, and the characteristics of bolters, semi-bolters, wildings and other variations are described in Chapter VI. The roguer should remove or mark all plants which in any character differ substantially from the variety under consideration. Plants with coloured flowers must be removed from crops the flowers of which are white. Tall plants in low-growing varieties, bushy plants in open and upright varieties, dark green plants in varieties with light green foliage, plants with green buds in varieties the buds of which are coloured, and so on, must be similarly treated. When the differences between rogue and crop plants are not pronounced, only practice can help, but whenever suspicions arise, the root of the doubtful plant should be examined for such features as shape, colour of skin, flesh and scale leaves of tubers and stolon characters. Differences in maturity are frequently helpful. When an early rogue occurs in a late crop, or *vice versa*, it is often easy to rogue when the haulm of the earlier variety is dying down. In this way it is possible to eliminate all late rogues, bolters and semi-bolters from early varieties.

Computing the Purity of a Growing Crop

In computing the percentage purity of any growing crop, the first step to be taken is to ascertain how many paces are necessary to include 100 plants. After this is done, such distances should be inspected at various points selected over the entire field, two drills, *i.e.* 200 plants, being taken in each count. The total number of rogues found, divided by twice the number of counts taken, will give the percentage purity. The number of counts to be taken will naturally depend much on the size of the field, but in large fields, exceeding 10 acres, two counts per acre at least should be made ; in smaller fields the number of counts per acre can be higher.

While inspecting a field for purity, the observer must always pay special attention to the probable sites of old pits, where groundkeepers may be common.

Roguing for Virus Diseases

Although this type of roguing is similar to purity roguing, there are some special considerations which the grower must bear in mind. Most virus diseases are infectious and infection may be spread during the current season. Every effort must, therefore, be made to eliminate diseased plants as quickly as possible and to avoid planting healthy stocks near unhealthy ones. The neighbours of diseased plants, particularly where Leaf Roll and Severe Mosaic are concerned, are likely to become infected and should in consequence be removed as though they themselves were obviously diseased. One of the most troublesome of potato viruses is virus " X " which is responsible for most of the Mild Mosaics. Unlike the viruses of Leaf Roll and Severe Mosaic which are spread by greenfly, virus X is spread mainly by foliage contact. It is possible also that roguers may carry this virus on their clothing and spread it in the field, although this has not been proved. For safety, however, roguers should not move from diseased into healthy stocks. Groundkeepers are a serious menace and pains should be taken to avoid this danger. In removing diseased plants, not only should all the tubers be taken but also all the foliage, the best plan being to put the complete plants into sacks and take them some considerable distance from the crop.

The symptoms of the various virus diseases are described in Chapter XXVI.

As with purity roguing, dull weather provides the best working conditions: the milder mosaics are not easily recognised in strong sunlight. The procedure should be as previously described, the roguer taking not more than two drills at a time. Leaf Roll can be identified often only by the condition of the basal leaves. Should any difficulty arise in identifying this disease, it is an excellent plan to have the crop rogued twice at each roguing period—once for Mosaic, impurities and variations, all of which may be recognised by the foliage tops, and once for Leaf Roll when the basal foliage alone is examined.

Environment, particularly temperature, has an important influence on the symptoms of Mild Mosaic which in hot weather often disappear. Thus it may happen that a crop which seems to have been satisfactorily rogued may still contain many virus-infected plants the progeny of which may show Mosaic in the ensuing year. Seed growers who wish the higher grades of certificates should discard such stocks. From all points of view, in particular for the maintenance of stocks in a sound condition for many years, the development of crops from individual virus-tested plants propagated in families and repeatedly tested is the best method. The purchase of certified virus-tested seed and the best derivatives of such seed, it is hoped, will do much to eliminate the excessive labour frequently employed in roguing, to say nothing of the exasperation encountered in endeavouring to deal with the vagaries of Mild Mosaic. Because of the danger of spreading virus " X " to such stocks by implements and other such means, cultivation should always begin in them and proceed to the lower grades and not *vice versa*. It was established at East Craigs in 1952 that virus "X" can be transmitted by workers while roguing.

CHAPTER VIII

POTATO BREEDING

THE search for new and improved varieties of the potato has been in progress for approximately 200 years. During that time innumerable varieties have been raised and brought into cultivation, some to attain popularity and an important place in agricultural economy, but many to disappear after a short sojourn by reason of some inherent weakness which commercial cultivation revealed. The successful types represented important improvements over their predecessors and reflected great credit on the ability and enthusiasm of breeders who had little better parental material to work upon than the derivatives of a few specimens of potato which had been introduced by chance into this country. The situation is now substantially altered. Not only are commercial varieties from many different countries of the world at hand, but an extensive collection of indigenous Mexican and South American potatoes, both cultivated and wild, is maintained at Cambridge for the benefit of breeders. The potential value of this array of species and varieties can hardly be estimated, but there is no doubt that it will provide the means of adding new qualities of various kinds to our commercial sorts, especially in the realm of disease resistance. The annual losses incurred through the ravages of diseases and pests are so heavy that problems of inherent resistance to them must necessarily occupy a leading place in any breeding programme.

ECONOMIC CHARACTERS.—The characters which determine the economic value of varieties are so numerous and sometimes intangible that the compilation of a comprehensive detailed list is hardly possible. It may, however, be of advantage here to list in general terms the more important features aimed at in present-day potato breeding, on the understanding that a range of maturity types possessing nearly all the following qualities is required to suit a wide range of environmental conditions.

1. High yield.
2. Attractive tuber shape.
3. Good colour, texture and flavour of tuber flesh.

4. Uniform medium-sized tubers.
5. Good keeping quality.
6. Good grouping of tubers in drill.
7. Good foliage to suppress weeds.
8. Immunity from Wart disease.
9. Immunity from Blight.
10. Immunity or field-immunity from Mosaic viruses.
11. Resistance to Leaf-Roll.
12. Resistance to Scab.
13. Resistance to Dry-Rot and other storage diseases.
14. Resistance to Eelworm.
15. Resistance to minor diseases, *e.g.* Black Leg, Skin Spot.
16. Resistance to climatic extremes.

Such a list, if compiled for the continent of Europe, would include resistance to the Colorado beetle. Since this pest has so far failed to establish itself in Britain the problem does not appear to be of immediate urgency. The characteristics mentioned are the more obvious ones, but the time will no doubt come when more consideration will have to be devoted to nutritional factors such as higher contents of starch, protein and vitamins.

FLOWERING AND FRUITING.—The production of flowers and the setting of fruit in a commercial crop are unnecessary and constitute a waste of plant food materials, but from the breeder's point of view both flowers and fruit are essential. Commercial potato varieties differ widely in their inherent ability to flower and set seed and it is a significant fact that the so-called "potato plums" are seldom seen on the vast majority of our commercial varieties. Flowering and fruiting are also influenced by climatic conditions. A moderate temperature and relatively high humidity tend to encourage fruitfulness while high or low temperature and low humidity discourage it. Success or failure in hybridisation may therefore be dependent upon weather conditions during the flowering season.

Potato varieties which do set seed are normally self-fertilised but natural cross-fertilisation may at times occur. In commercial crops where varietal purity and pollen sterility are common, the conditions are unfavourable for cross-fertilisation, but even so it has been estimated by Bukasov (1937) that, on the average, about 3 per cent. cross-pollination by insects takes place.

Flowering and fruiting, according to Bartholdi (1942) have a depressing effect on yield of tubers. In one particular variety flower production was found to cause a loss in tuber yield of 10 per cent. while fruit production reduced the crop by a further 14 per cent. These results indicate that selection for higher yields would tend to eliminate the profuse-flowering and heavy-fruiting types. The lack of fertility in commercial varieties lends support to this view.

Since desirable commercial types are often shy-flowering, the breeder has frequently great difficulty in effecting hybridisation. The mating of such varieties is particularly desirable since they tend to throw a high proportion of shy-flowering seedlings from which to select potential economic types. Several methods of encouraging the production of flowers by artificial means may be adopted, *e.g.* by removing the tubers from the growing plant as they are formed or by ligaturing the stem when the buds are developing. Probably the most effective method, however, is to graft a young shoot of the shy-flowering variety on some other plant such as tomato. The flowers which will eventually be produced may then be used for crossing purposes.

STERILITY AND INCOMPATIBILITY.—The comparative infrequency of fruit formation in commercial varieties is due primarily to male sterility. Two kinds of male sterility are encountered, viz., genotypic, which is directly due to the genetic constitution of the plant, and phenotypic, which is caused by environmental influences. The former is a feature of triploid and pentaploid hybrids.

Female sterility in cultivated potatoes is extremely rare. The shy-flowering types can, as a rule, be induced to set seed if suitable pollen is available. But a certain amount of ovule abortion is of common occurrence and Arnason (1943) found it in all varieties examined, reaching 100 per cent. in one particular case.

The crossing of pollen-sterile with pollen-fertile varieties gives progenies which invariably show segregations of sterile and fertile pollen types. Segregations also occur in most progenies obtained by selfing or intercrossing pollen-fertile varieties, but 100 per cent. fertility may be found in certain cases. Krantz *et al.* (1939) found that, in a large number of progenies obtained by self-fertilisation, flowers were produced in 47·8 per cent. of the seedlings, and that 60·9 per cent. of the flowering plants set fruit. They suggested that segregations may be explained by assuming the presence of a tetrasomic gene, which, when present in the pollen in homozygous condition, is lethal and in heterozygous condition is partly lethal.

In the native American species pollen sterility is, on the whole, less common than in commercial varieties. A serious handicap to their utilisation in breeding experiments, however, is the incidence of incompatibility which is particularly pronounced amongst the diploids. Some of them are self-incompatible yet cross-fertile, while others can be induced to set seed only by interclonal pollination. It is probable that many of the wild diploid species which are regarded as sterile could be induced to set seed if more than one clone were available. The effect of environment on fertility is also important. Kameraz (1940) and Perlova (1940) have shown that good seed may be obtained from certain species when grown in the Pamirs, although these species had previously been regarded as sterile. Examples of the complexity of fertility relationships in potatoes have been recorded by many authors and these have been summarised by Hawkes (1945). In an examination of physiological incompatibility in crossing tests with species of potato, Pal and Pushkarnath (1944) established 20 intra-sterile but interfertile groups each possessing a different pair of the eleven sterility factors, S^1, S^2, etc., which, operating in various combinations, controlled self- and cross-incompatibility.

TECHNIQUE OF SEED PRODUCTION.—Since the production of viable pollen may vary from season to season and the possibility of cross-pollination cannot be ruled out, precautionary measures should be taken to prevent contamination of crosses or selfs for experimental purposes. Accordingly, flowers to be self-fertilised should be enclosed in pollen-proof bags before the buds have opened and, apart from removal for hand-pollination, they should remain until the flowers have withered.

In the case of crossing, a flower truss on the plant to be used as female parent should be selected and trimmed to leave three or four good buds. These buds should be emasculated by carefully removing the anthers, and then protected by enclosing in a pollen-proof bag. Two or three days later, when the buds have opened and are ready for pollination, the bag should be removed and the pollen, taken from the anthers of the selected male parent, applied to the receptive stigmas. On completion of pollination, a small tag label bearing details of the cross should be tied to the flower stalk and the whole enclosed in the pollen-proof bag. No further attention is required, apart from guarding against storm damage, until berries have set. In order to prevent loss of berries, a small muslin bag may be fitted in which the berries can remain until fully developed. They should then be stored under dry conditions for a month or more.

Normally, the seed can be extracted at any convenient time during winter. An effective method is to cut the berries in quarters, place them in water in a shallow vessel such as a Petri dish, and scrape out the seeds. After removing the pulp, the seeds can be washed and then placed on filter paper to dry. Seeds are usually stored in small paper envelopes, and under average conditions will remain viable for ten or more years.

EFFECT OF SELFING.—The self-fertilisation of potato varieties through successive generations tends to result in loss of vigour and reduction of yield. Krantz and Hutchins (1929) found that the effect of inbreeding through several generations was a relatively large decrease in crop yield in the first and second generations and smaller decreases in subsequent generations. According to Guern (1940), seedlings of the first selfed-generation yielded 20-40 per cent. below the asexually propagated parents. Nevertheless, many commercial varieties have been produced by self-fertilisation, *e.g.* Early Rose, Paterson's Victoria and Arran Chief, and on that account, limited inbreeding cannot be condemned in practical potato breeding. The loss in yield of successive selfed generations must depend to a large extent upon the particular plant or plants selected as parents and the effect of high- or low- yielding selections in early generations may be apparent in each generation thereafter.

The decline in cropping capacity by continued inbreeding is usually accompanied by an increase in the proportion of weak, abnormal, or hereditary degenerate plants which fail to flower. These plants can have no further effect on the course of inbreeding and hence yields which may be obtained in later generations will tend to be greater than the theoretical average and will deviate accordingly from the calculated rates of reduction through inbreeding.

For practical purposes, inbreeding to obtain greater homozygosity of desirable characters is probably of little value beyond the second or third generation, but even so, greater progress would probably be made by crossing individuals similarly constituted in respect of the characters desired. Such crosses, while providing the necessary genes, would obviate, at least partially, the reduction in heterosis. The value of inbreeding in potatoes may therefore be limited to the purpose of procuring new combinations of characters from F_1 selections and of duplicating the genes controlling individual characters.

EFFECT OF CROSSING.—Most potato varieties are extremely heterozygous, *i.e.* mixed in constitution, and may already have attained the limit of effective heterosis within the species. Repeated crossing therefore, while maintaining hybrid vigour at a high level, is unlikely to result in a significant increase in heterosis. On the other hand, it is possible that some varieties are too heterozygous in constitution and would benefit by limited inbreeding.

The crossing of inbred lines of potatoes, unlike maize, generally fails to restore the lost heterosis. The low-yielding capacity may be partly due to the greater flower and fruit production usually present in crosses of inbred lines, but fertility cannot account entirely for the absence of high-yielding selections. The intercrossing of commercial varieties and inbred lines, on the other hand, frequently produces high-yielding selections.

The effect of crossing, however, is very variable and is dependent upon the hereditary constitutions of the parent plants involved. Some varieties combine more effectively than others ; their characteristics blend to greater advantage, and this combining ability may be ascertained by following a system of diallel crossing. When the potentialities of a series of varieties have been established, further breeding can be limited to the most promising combinations.

The introduction of wild species into economic breeding programmes must necessarily entail hybridisation. In these cases the primary object is to combine some particular virtue or virtues of the wild species with the commercial qualities of standard varieties. Hybridisation must be followed by a system of repeated back-crossing to economic types in order to bring together all the characters which are desired and to eliminate those derived from the wild species which are unsuitable for agricultural purposes. Experiments of this nature are usually of long duration.

INTERSPECIFIC HYBRIDISATION.—As already indicated, the inter-relationships of the 220 or more species of potato so far described forms a complex pattern. Some are closely related and intercross readily while others are so far apart systematically that direct hybridisation cannot be effected. The potato family forms a polyploid series of five groups with somatic chromosome numbers of 24, 36, 48, 60 and 72. Wild species are represented in each of these groups but in the case of cultivated species no hexaploid types have been found. A knowledge of the chromosome numbers may be helpful in planning hybridisations but chromosome numbers alone may be misleading and the systematic position of the particular species must be taken into consideration. European and North American commercial varieties are tetraploids ($4x = 48$), a complement of chromosomes which appears to be economically more efficient than any other. The doubling of chromosome numbers by the use of colchicine has, in certain cases, proved advantageous as a preliminary to hybridisation but, on the whole, the results of colchicine treatment of potatoes has been disappointing as an aid to practical breeding.

INHERITANCE OF CHARACTERS.—The genetical basis of inheritance in potatoes has long been the subject of controversy The basic chromosome number has been regarded by several investigators as 6 (*e.g.* Choudhuri, 1944) on the evidence of secondary association in species with 24 somatic chromosomes. Since no plant with fewer than 24 somatic chromosomes has been found, however, the basic number is now widely accepted as 12 and commercial varieties are therefore regarded as tetraploid ($4x = 48$).

Earlier work on the inheritance of characters was invariably explained on the assumption that potatoes are functional diploids but Lunden (1937) and Cadman (1942) from the evidence of segregations of different characters, declared that domestic potatoes are autotetraploids. In a cytological examination of cultivated varieties, wild species and interspecific hybrids, Thomas (1945) concluded that the cultivated potato is an allotetraploid hybrid between related species whose chromosomes are structurally similar.

Many of the important commercial characters of potatoes are quantitatively inherited and are therefore unpopular as subjects for genetic analyses. As a result little detailed information is available regarding the inheritance of characters such as size, shape, yield, keeping quality and cooking quality of tubers, maturity, resistance to some diseases and resistance to climatic extremes.

In the case of yield, the nature of inheritance is complex and depends not only on inherent cropping capacity, but also on photoperiodic reaction. It has been shown by Bukasov (1937), Driver and Hawkes (1943) and van der Plank (1946 and 1947) that some types may be genetically high yielders ; yet on account of adverse photoperiodic effect, their actual yield may be very low. Good croppers under the short-day conditions of the tropics may be poor croppers in Britain where summer daylight conditions are relatively long. On the other hand, few European varieties yield an economic crop in the tropics, since they have been bred and selected specially to suit long-day conditions. In general, the cropping capacity of British varieties is good but it could be greatly improved by breeding, and particularly by the production of types adapted to local conditions. Further, there are indications that some of the South American species, *e.g.* *S. andigenum*, possess high-yielding properties which could be introduced with advantage into commercial types.

The character which has received most attention by geneticists in the past is tuber colour, due to the presence of anthocyanin pigments. Coloured varieties may be placed in two main groups, reddish-purple and bluish-purple, within each of which wide differences in intensity and distribution of pigment are found. The pigment is located in the cortex of most coloured varieties and is seen through a thin non-pigmented layer, the periderm ; but in some varieties, *e.g.* King Edward VII the colour is concentrated mainly in the periderm.

Many attempts have been made to explain the inheritance of tuber colour and various factorial hypotheses have been suggested. A comparison of the earlier contributions, which were based on disomic inheritance, shows the lack of agreement in detail and illustrates the genetic complexity of the character (Black, 1933). In general terms, however, the production of reddish-purple pigment is dependent upon the presence of two complementary factors D and R, and blue-purple pigment upon the presence of a third factor P. Each of these factors is incapable of producing colour independently. All authors agree that further factors are necessary to account for differences in location, distribution and intensity of pigment. Among the factors which they suggested are an additional basic, an additional red-producing, an additional blue-producing, a diluting, a restricting, an inhibiting, an intensifying, and an eye-colour factor.

In a more extensive study of the inheritance of anthocyanin pigment in different parts of the plant, Lunden (1937) employed seven factors operating in autotetraploid fashion. Certain deviations from typical autotetraploid ratios which were observed, were attributed to double reduction at chromosome division.

For practical purposes, a study of the inheritance of many of the quantitative characters in potatoes would probably help very little in the improvement of varieties since the available parental material is extensive and is already highly developed. On the other hand, the mode of inheritance of newer and comparatively undeveloped characters such as resistance to Blight and virus diseases is of utmost importance and genetical investigations are now largely concerned with these characters.

RESISTANCE TO BLIGHT.—All known South American potatoes are in some degree susceptible to attack by the Blight fungus, *Phytophthora infestans*, but resistance to the disease is present in certain wild species indigenous to Mexico. The most promising of the latter, *S. demissum*, has been widely used in breeding experiments. *S. demissum* is a true wild form and is hexaploid in constitution. It crosses readily with several other wild species and with commercial varieties, and its Blight-resistant qualities, due to the hypersensitive nature of its protoplasm are inherited in Mendelian fashion. Resistance behaves as a dominant character and, as a result, resistant seedlings are readily obtained; but unfortunately several generations of breeding are necessary to eliminate the many undesirable characters also introduced by *S. demissum*.

The work is further complicated by the instability of the fungus and its tendency to produce new specialised biotypes. Reddick and Mills (1938) succeeded in increasing the host range of Blight by culture on certain resistant plants. In Britain, several new strains of the fungus have been isolated which are capable of attacking certain seedlings known to be resistant to the common strain of the disease. These new strains, all of which have a greater infective power than the common strain, are physiologically different from each other and may be distinguished by the reactions which they induce on a special test series of seedlings bred from *S. demissum*.

The exact origin of these new strains is not clear, but the available evidence indicates that they arise mainly by mutation and that such mutant forms are frequently produced. The number of new forms which may ultimately be identified will probably be large and will depend upon the range of suitable test plants available. More important, however, is the degree of specialisation which may ultimately be reached by the fungus. If, by progressive mutation, it can eventually attack the wild species, at present regarded as immune, then the best protection possible in commercial varieties will not be immunity but merely a degree of resistance. But the answer to this question is unknown. It is apparent, however, that the seedlings upon which biotypes of the disease have developed represent comparatively low levels on the scale of resistance and that the fungus has a formidable task to penetrate the defences of the Mexican species.

Resistance to Blight is physiological in nature and is therefore based upon a balance of physiological conditions within the plant. According to Müller (1941) resistance genes do not produce an " all or none " reaction but function only as accelerators of the defence reaction of which both susceptible and resistant genotypes are capable. In susceptible varieties the reaction is therefore too slow while in hypersensitives it is sufficiently rapid to prevent the establishment of the disease.

In genetical terms, the inheritance of resistance to the various strains of Blight is controlled by at least four independent major genes each of which confers resistance, *i.e.* hypersensitivity, to a particular group of biotypes (Black, 1943, 1945, 1949 and 1950). Each of these genes behaves as a simple dominant and segregations of resistant and susceptible seedlings have been found to conform with Mendelian expectations. Systematic breeding has resulted in the production of high yielding types which are resistant to all known strains of the disease and some of these appear to have good prospects of competing with established varieties as economic plants.

RESISTANCE TO MOSAIC.—Potato varieties may be divided into four main groups on the basis of their reactions to the several viruses and virus strains which cause Mosaic in commercial crops. These are :—

(1) True resisters, *i.e.* resistant to infection.
(2) Carriers, *i.e.* tolerant after infection.
(3) Susceptibles, *i.e.* visibly affected.
(4) Hypersensitives, *i.e.* intolerant.

True resistance may be found in commercial varieties but is seldom present in a high degree. One instance of true immunity from virus " X " has been found in a non-commercial seedling in the U.S.A. but no commercial variety is known to be so constituted. Apparently true immunity is difficult to attain and parental material is extremely limited.

Commercial varieties giving a hypersensitive reaction to viruses " A " and " X " however are already available, *e.g.* Epicure, King Edward and Craigs Defiance. Such varieties are known as " field-immune " since their intolerance protects them from systemic infection under field conditions. For practical purposes, this protection is equivalent to true immunity.

The inheritance of field-immunity from viruses " A " and " X " has been shown by Cadman (1942) and Cockerham (1943) to be relatively simple. Field-immunity from several strains of virus " X " occurs in the presence of a single dominant gene Nx. This gene, however, is ineffective against certain aberrant strains of the virus. One of these strains, Xb, has been investigated and has proved to be under control by a gene designated Nb (Cockerham, 1945).

Field-immunity from virus " A " is determined by a gene Na which is closely linked to Nx. The linkage of Na to Nx observed in several commercial varieties is convenient for the production of new seedlings possessing field-immunity from both viruses.

The problem of virus " Y " is more difficult to solve since no commercial variety is either immune or field-immune from it. Virus " C," which is a strain of " Y," has been found to be controlled by a gene Nc present in many commercial varieties but no gene equally effective against virus " Y " has yet been found. Cockerham (1943) has shown that certain clones of several wild species exhibit necrotic reactions to virus " Y " and that these may provide the basic structure of field immunity.

Seedlings reacting in hypersensitive manner to virus " Y " have been found in progenies bred from commercial varieties in Australia (Hutton, 1945, 1946). The proportion of hypersensitive segregates in progenies was very small, suggesting that the character is inherited as a recessive. The intercrossing of hypersensitive seedlings yielded 10 to 30 per cent. hypersensitive offspring. Thus it is apparent that field immunity from virus " Y " can be obtained and that suitable varieties so constituted will in due course be produced.

Although virus control through field-immunity is of great commercial value, it must be recognised that a potential disadvantage may lie in the inherent variability of individual viruses. It is possible that field-immune varieties may exercise a selective effect in favour of aberrant strains to which they may be susceptible. However, there is no indication of any widespread dissemination of aberrant strains within existing field-immune varieties, some of which have been in cultivation for approximately half a century.

RESISTANCE TO LEAF ROLL.—No form of immunity from Leaf Roll virus is at present known but a high degree of resistance is found in several varieties, *e.g.* Shamrock, Southesk and Imperia. It was suggested by Cockerham (1943, 1945) on the evidence of the comparative behaviour of named varieties and of seedling progenies in diallel series, and from the segregations observed in individual families, that resistance is a heritable character and is controlled by several factors. The aggregation of these factors results in increased resistance and they may entirely prevent infection if highly concentrated.

BREEDING METHODS.—The methods employed in potato breeding are determined largely by a number of characteristics of economic varieties to which reference has already been made. The main feature is that potatoes are propagated vegetatively and it is therefore possible to multiply a selected segregate without affecting heterosis or altering its genetic constitution. Breeding is also greatly facilitated by the comparative simplicity of the technique of selfing and crossing and by the fact that practically all varieties are heterozygous in constitution, giving wide segregations in both selfed and crossed progenies. The nature of the inheritance of pollen sterility is convenient for the production of male sterile types which are preferable for commercial purposes on account of their greater cropping potential. The loss in yielding capacity following inbreeding provides a sound reason for the greater use of hybridisation as the more promising method of varietal improvement.

In view of the above facts, the chances of success would be greatest in a progeny obtained by crossing two plants, a pollen-sterile shy-flowering type and a fertile plant, which between them possess the maximum concentration of the qualities necessary in an economic variety. When the desired seedling has been selected it may be multiplied vegetatively forthwith. But the ideal cross cannot yet be made because no two known varieties possess all the required characters. Potato breeding is still concerned with the introduction of new qualities and with the combination in one variety of a greater number of desirable characters than already exists. In some cases such as the introduction of Blight-resistance, many undesirable characters of the wild species also appear and these must be eliminated by appropriate selection in subsequent generations. The method of breeding consists of hybridisation followed by back-crossing to commercial varieties in order to build up productivity, accumulate as many desirable qualities as possible, and eliminate the unwanted characteristics of the wild species. During these operations the resistance genes tend to become dispersed. The final phase therefore consists of inter-crossing selected plants from highly bred lines in order to recombine the genes and so regain as far as possible the resistance of the original wild species.

Raising of Seedlings.—Potato seedlings may be successfully grown without the aid of artificial heat provided exposure to frost can be avoided. Under these circumstances the seeds should be sown in seed pans or boxes as early in April as weather permits and should be protected in cold frames. The soil should be a good compost mixture. After five or six weeks, when the seedlings are about 1 in. high they should be transplanted into boxes at a spacing of about 3 in. Towards the end of June they will be strong enough to be transplanted into open ground where they may be spaced 36 in. apart in 28-in. drills. The wide spacing is necessary to avoid the intermixing of tubers from neighbouring plants. Thereafter the seedlings may be earthed up as necessary and allowed to grow to maturity. The plants must be harvested separately since each is likely to be a distinct variety.

TABLE IX

Seedling Year.	Quantity Grown.	Basis of Selection apart from Morphological Characters.
1st	1 plant	Reaction to Blight, tuber diseases
2nd	4 plants	Reaction to Blight strains, tuber diseases, virus diseases, yield
3rd	30 plants	Reaction to Wart disease, reaction to virus X, tuber diseases, virus diseases, yield, cooking quality
4th	180 plants	1st-year official trials (60 tuber sample)
5th	1/12th acre	2nd-year official trials (300-tuber sample)
6th	½ acre	3rd-year official trials (1006-tuber sample)
7th	3 acres	...

Much better results are obtained, however, when seedlings are raised in a heated greenhouse. The seeds may be sown a month earlier without the risk of frost damage and the resulting plants may be hardened off and planted in the open before the end of May. The longer growing season results in stronger plants, many of which will yield crops of tubers comparable in size and weight with the produce of plants in an average commercial crop.

SELECTION AND MULTIPLICATION OF SEEDLINGS.—As a general guide to the routine methods of selection and multiplication of seedlings, a scheme is presented in Table IX. It is not necessarily complete and is subject to alteration, according to circumstances; but it has proved a satisfactory basis for handling large numbers of seedlings under average conditions of growth. It gives an indication of the minimum time required for initial selection and subsequent participation in official trials, in accordance with present regulations. Frequently an extra year is required for initial selection, especially when growing conditions are below normal.

The rate of multiplication may appear slow but it is inadvisable to increase the quantities much beyond the needs of the following season since selections are liable to be discarded at any stage in the course of examination and trial. On the basis of this scheme, a period of seven years is required to raise a new variety and place it on the market in suitable quantity.

Selection in the first year is limited to characters which can conveniently be assessed at that stage. If seedlings are bred for resistance to Blight the susceptible plants may be eliminated a few weeks after germination by submitting the progenies to intensive infection with the disease. Otherwise selections may be made on the basis of morphological characters such as attractiveness of haulm, length of stolons, shape and colour of tubers and freedom from tuber diseases. Very little reliance can be placed on yield at the single plant stage but the relation between size and number of the tubers may be a useful criterion. If the tubers are numerous and small they should be discarded, but if few and large they may be worth continuing. On the average it is possible to discard about 80 per cent. of the seedlings in the first year.

In the second year a more accurate impression of the morphological characters of the seedlings can be obtained but yields are liable to be misleading on account of the unavoidable variation in size of the setts planted, and should therefore not be over-rated. Otherwise, selection can be based on tuber diseases such as Scab, on the appearance of virus diseases caused by infection the previous year, and on the reaction to specialised strains of Blight. Probably about 5 per cent. of the original seedlings raised will survive the second year's tests.

In the third year selections may be tested for resistance to Wart disease and reaction to virus "X." Yield trials of a limited nature may be carried out and observations made on the incidence of diseases. The tubers may also be examined for cooking quality. At the end of the third year a reasonably accurate impression of the probable value of most of the selections should be formed; but in some cases it will be desirable, on account of environmental influences or other factors, to repeat some of the tests listed for third-year seedlings before submitting selections for official trials.

The main purposes of official trials are, first, to provide an independent estimate of the economic potentialities of promising seedlings for the benefit of everybody concerned, and, secondly, to prevent the marketing of Wart-susceptible or synonymous varieties and to discourage the introduction of mediocre types. It is generally appreciated, however, that no series of trials can be conclusive; the final verdict must rest with the commercial grower.

In the course of official trials the first consideration of the breeder should be the multiplication of healthy stocks of the seedlings involved. For that purpose it is advisable to build up in isolation, from specially tested plants, at least one virus-free stock which will assure in later years a supply of reliable seed tubers.

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CHAPTER IX

THE CULTIVATION OF THE POTATO

THE chief aim in the cultivation of the potato crop is the production of the maximum number of ware-sized tubers for human consumption, although there is, of course, a large area, particularly in the north, in which the main pre-occupation of the grower is to produce tubers of about two ounces in weight, suitable for the ware growers to plant as seed-setts. Some modification in the details of cultivation is advisable when the crop is grown mainly for seed, but the general principles remain the same for whatever purpose the crop is cultivated.

Potatoes can be profitably grown on almost any soil except very heavy clays or wet undrained land. Nevertheless, the best crops are obtained on medium loams, containing ample organic matter, which are therefore not liable to suffer from drought even in a dry season. Such soils are easy to cultivate and the crop is able to make steady growth during the whole of the growing season. The soil in many of the chief potato growing districts is of this nature, but often, of course, the soils are not of this ideal type, and it is the job of the farmer to try, by means of cultivation and manuring, so to alter the texture and fertility of his soil as to approximate as nearly as possible to the best types.

Different views are held as to the effect of various types of soil on the cooking quality of potatoes. (For cooking quality the reader should consult Chapter XIII.) Doubtless, to some extent, this divergence of views represents differences of "taste," but it is generally accepted that the best quality (however one defines the word) is to be found in potatoes grown on suitable soils in districts where the rainfall is low, such as the Dunbar district of East Lothian. According to the Ministry of Food, the most suitable soils for the production of high quality in tubers are limestone, silt or warp, such as are to be found in Lincoln and neighbouring counties. These types of soil are placed in the highest soil class on which market prices are based. Second place is taken by red soil, followed by "skirtland" soil, all others being regarded as producing lower quality tubers which therefore command only a lower price. Peaty soils usually give good yields, but the quality of the tubers is of the poorest. It must be noted, however, that climate as well as soil affects quality.

Although "quality" has an important bearing on the popularity of varieties, and hence on the producer of the crop, other factors also have a place. Shape of tuber and the depth of "eyes," colour of tuber flesh or even of tuber skin, as well as the possibility of resteaming cooked potatoes, all help to determine the variety selected for use in the various ways in which tubers are prepared for human consumption.

In England potatoes are grown mainly for ware, although in some districts seed-sized tubers are kept for planting the following year. Maincrop varieties form the bulk of the acreage and at the present time Majestic is most largely grown, King Edward VII which used to be the favourite comes next. These are grown mainly in Lincoln, York and Cambridge, followed by Norfolk, Nottingham, Essex and Durham. Arran Peak has increased during recent years chiefly in York and Lincoln. Gladstone and Arran Banner are grown to a fair extent, the former in Lincoln, Essex and York and the latter in Lancashire, Durham and York, while the acreage of Redskin is increasing in the northern counties.

In Scotland, Kerr's Pink is still by far the most popular variety for ware, the largest acreage being in the North-East. Redskin has increased during recent years especially in Fife and Angus. The acreage of Golden Wonder has decreased greatly during the last few years but it is tending to rise again. It is most largely grown in Fife and Aberdeen. All these are also grown for ware in the counties round Glasgow.

For seed many varieties are grown (see Table X) chiefly in Angus, Perth and Fife.

In Northern Ireland no variety is so popular for ware as Arran Victory but the acreage of Kerr's Pink is increasing. For seed, Arran Banner and Arran Peak are largely grown while there are smaller acreages of Arran Consul and Gladstone. The new variety Stormont Dawn is finding favour.

There are comparatively few second-early varieties grown in Britain, the most common being Great Scot followed by Dunbar Rover in England and British Queen in Scotland and Northern Ireland. Small acreages of Royal Kidney and Catriona are grown for seed.

Early varieties for ware are most extensively grown in Lincoln, Cheshire, Cornwall, Lancashire, Norfolk, York, Kent and Pembroke with smaller acreages in Essex, Cambridge, Bedford and Shropshire. Arran Pilot is most extensively grown; during the last few years, however, Home Guard has increased greatly while the new variety Ulster Chieftain is fairly largely grown. There are decreased acreages of the former favourites, Epicure, Eclipse, Duke of York, Ninetyfold, Sharpe's Express and May Queen.

Certain districts, especially in coastal areas where the soil is light and high temperatures are attained in the early part of the year, are particularly suitable for the production of ware for the earliest market when high prices are obtainable. Although in such areas the crop is lifted exceptionally early, so that an average yield is no more than 4 or 5 tons per acre, the tubers command very high prices, which, however, fall very rapidly as the supply increases. Exceptionally early districts include the Scilly Isles, Isle of Wight, the Tamar Valley and the south coastal area of England, Pembroke in Wales and Wigtown and Ayrshire in Scotland. In these Scottish areas the chief variety grown is Epicure, which is comparatively tolerant to eelworm and recovers very quickly after frost. Small quantities of Duke of York are grown in several early districts, more particularly for those who wish good quality tubers.

In Northern Ireland Ballydoon is the favourite early variety.

The following table gives the acreages of the different varieties of potatoes grown in Scotland in 1920, 1930, 1940 and 1950. They indicate the relative popularity in Great Britain of the varieties in those years. Acreages for the country as a whole will be found in Table XXXVI.

Soil Fertility.—The inherent fertility of the soil is governed largely by the presence of adequate amounts of humus. Every effort should be made to maintain fertility by applications of dung, or by ploughing in grasses and clovers, or special crops grown for this purpose.

The cheapest means of maintaining fertility is to allow the field to lie in grass for a year or two. When well and evenly grazed by mixed stock there should be a good turf of deep-rooting grasses and clovers, and these, when ploughed under, are ideal for potato growing. It must, however, be ploughed

TABLE X

	1920 (acres).	1930 (acres).	1940 (acres.)	1950 (acres).
Early Potatoes				
Arran Pilot	...	...	3,926	7,994
Duke of York	825	1,794	1,225	1,923
Eclipse	1,462	948	1,806	1,401
Epicure	9,878	7,703	9,030	15,206
Home Guard	...	...	...	7,107
May Queen	163	127	180	93
Ninetyfold	125	209	630	126
Sharpe's Express	623	1,712	936	1,153
Second Early Potatoes				
Ally	2,270	339	117	0
Arran Comrade	5,225	331	195	0
British Queen	7,610	3,518	1,781	1,277
Catriona	...	163	159	246
Dunbar Rover	...	...	352	600
Edzell Blue	870	278	165	0
Great Scot	16,989	10,059	7,315	5,374
King George V	5,540	200	114	0
Royal Kidney	390	252	317	397
Maincrop Potatoes				
Abundance	3,666	665	254	0
Arran Banner	...	678	2,831	5,446
Arran Chief	29,188	3,035	950	1,210
Arran Consul	...	617	841	806
Arran Peak	...	...	262	3,077
Arran Victory	950	284	273	457
Champion	2,979	526	130	0
Craigs Defiance	...	...	...	611
Doon Star	...	...	6,437	1,432
Dunbar Standard	...	...	380	575
Evergood	1,731	6	0	0
Field Marshal	...	434	418	0
Gladstone	...	...	2,452	5,903
Golden Wonder	4,155	7,986	7,874	4,713
Kerr's Pink	4,451	39,097	37,777	44,232
King Edward	13,286	15,346	10,059	9,300
Langworthy	2,328	239	98	0
Lochar	1,487	31	0	0
Majestic	3,184	5,657	16,854	36,794
Northern Star	698	27	0	0
President	2,485	96	14	0
Red King Edward	...	...	1,047	1,709
Redskin	...	...	6,675	16,286
Tinwald Perfection	4,764	145	11	0
Up-to-date	6,726	1,195	634	1,863

early in order to be benefited by the winter frost and allow the turf to rot. The turf of old grass is much more difficult to break down and rot than that of younger grass. In some potato growing districts two-year-old grass is ploughed, while in others the organic matter is maintained by sowing a seeds mixture containing a large proportion of Red Clover, the first cut of which is made into hay, while the aftermath is ploughed under as green manure. Special crops may be grown for ploughing in as green manure in order to maintain the supply of organic matter. These are usually catch crops, the most common of which are rye and Italian ryegrass, or rape and Italian ryegrass, or rye and tares (vetches), which are sown after an early crop has been removed.

THE PLACE OF THE POTATO IN THE ROTATION.—Potatoes are chiefly grown (*a*) after a grain crop, usually oats, (*b*) after lea, and (*c*) after potatoes.

(*a*) *After Oats.*—This is the most common method, the oat crop having been taken after the lea was ploughed up. In this case the land is usually in good condition for potatoes as part of the turf will be left, especially if a good seeds mixture containing wild white clover had been ploughed in.

When grown after oats, potatoes usually take the place of part of the turnip break, one of the chief functions of the potato being to act as a cleaning crop. For this purpose, if the land is at all overgrown with weeds, it is well to select a maincrop or late variety with strong vigorous haulms, particularly if little labour is available, for such varieties are ideal for smothering weeds. When the land is clean the less robust earlier varieties may safely be planted.

It is useful in many cases when potatoes are taken after oats to sow, say, 15 or 20 lb. of Perennial Ryegrass, either alone, or with 3 to 4 lb. of Red Clover, along with the grain crop. If grazing is scarce, the resulting crop may be eaten by stock in early winter; but it is better for the ensuing potato crop to allow the grass and clover to grow after the grain harvest and then to plough them under in readiness for the potato planting.

(*b*) *After Lea.*—During recent years farmers who have had great difficulty in getting their oat crop to stand after lea containing much wild white clover, have substituted potatoes for the grain crop—a practice which is to be recommended.

If the pasture had been down for three or four years it should have a thick uniform covering of wild white clover. The potato crop therefore will be much later in maturing due to excess nitrogen supplied late in the season by wild white. This nitrogen induces haulm production rather than tuber formation especially with late varieties. Unless suitable precautions are taken a full crop would therefore rarely be got as the haulms are always liable to be destroyed by frost or Blight long before they are ripe.

In order to ensure a good crop arrangements should be made to secure early ripening. This can be done by planting well-sprouted seed of comparatively early varieties early in the season.

(*c*) *After Potatoes.*—Two or more potato crops are sometimes taken in succession, more particularly so in early-potato-growing districts where suitable soil and other conditions are limited ; indeed, in some fields potatoes have been successively grown for thirty, forty or more years. In such cases of continuous potato-cropping, the plants are liberally treated and the soil fertility is maintained by sowing such catch crops as rape or Italian ryegrass, or a mixture of both. These are usually sown and harrowed in, without ploughing, as soon as the potato crop is lifted. Whilst the fertility problem is thus solved, risks are nevertheless being taken by continuous potato growing on the same land, for there is no better way of encouraging pests, such as eelworms or diseases of the potato, than by not following a rotation of crops.

Cultivation before Planting

Soil Preparation.—The potato is a fairly deep-rooted plant, so that if the best results are to be obtained the cultivation must also be deep and thorough. However, it is usually not necessary, as is often advised, to plough to a depth of from 15 to 18 in., for much of the best potato-growing land is well under 12 in. in depth. In comparatively shallow soil there is a risk of bringing subsoil to the surface, but care will naturally be taken to reduce this risk to a minimum ; the little which does reach the surface will thus be insufficient to affect the crop adversely, and by becoming weathered during winter will help gradually to increase the depth of the soil. Generally speaking, potato land should be ploughed to a depth of about 9 in. and the bottom soil stirred to facilitate root development. In districts where the soil is heavy, subsoiling may be practised either by the use of a special subsoiling plough or by following one plough with another. This should be carried out in autumn or early winter and the surface soil left in a rough condition so as to benefit by winter frosts.

(*a*) *After Lea.*—It is advisable to plough the lea as early as possible, always taking the oldest and toughest fields first. The whole operation aims at turning the turf completely over and encouraging the rapid decay of the plant remains. A skim coulter should therefore always be attached to the plough to ensure that the surface turf is well covered, without being too deeply buried. When there is a large proportion of bent grass, the surface turf will be tough ; it should therefore be well disced beforehand so as to cut it up as much as possible and thus facilitate rotting. On the other hand, three- or four-year-old grass with a good proportion of wild white clover will have a tender turf and will break up readily when ploughed without preliminary discing.

(*b*) *After a Grain Crop.*—The chief difficulty when ploughing stubble for potatoes is to destroy the many objectionable weed grasses, such as couch, creeping Yorkshire fog or bent grasses, which may be present. This may be done by a preliminary shallow ploughing or by tearing up the surface with a spring-tine harrow. The stubble should then be harrowed in the ordinary way and the weeds, as far as possible, collected and destroyed. The process may be repeated and, finally, the soil should be ploughed deeply, again using a skim coulter.

(*c*) *After Potatoes.*—Following potatoes the land should be reasonably clean for ploughing and the preliminary cleaning can therefore be dispensed with. Under such conditions it is often the custom to apply dung on the surface and plough it in, although some prefer to wait until spring and apply the dung in the drills. Both methods have their advantages, but on the whole it has been found that applying dung in the drills will usually give the heavier yield of tubers, planting being carried out at the same time as the manuring. Spring, however, is a busy season, and when there is a large area to plant, the application of dung may delay planting to such an extent that part of the crop may suffer in yield. For this reason part at least of the dung should be put on in autumn.

The dung should be laid out in heaps of the same size at a uniform distance apart, usually 5 yards by 5 yards, the field being marked off beforehand by shallow furrows. As soon as possible after it is carried on to the field the dung should be spread uniformly and ploughed under, so as to avoid loss of valuable manurial ingredients, more particularly nitrogen. Dung is unnecessary after lea containing wild white clover as there is already sufficient humus and nitrogen for potatoes; hence it can be used to better advantage for other crops. In coastal districts dung is often replaced by seaweed. This is a valuable manure and contains more potash than does dung; it is usually applied in autumn in the same way as dung.

DISTANCE OF PLANTING.—The width of drill and the distance apart of the seed-setts in the drill vary with the kind of soil, the variety of potato and the use to which the crop is to be put, *i.e.* whether the tubers are destined mainly for the ware or the seed market. In any case it is advisable, on poor soils, to ensure wide spacing of the plants either by increasing the width of the drills or of the intervals between the seed setts in the drill.

For ware production, the object is to get a crop of fairly even-sized tubers with as few small ones as possible. Early varieties are usually grown in 24-in. drills and the setts are placed 9 or 10 in. apart; but in some districts where exceptionally early lifting is carried out, the drills may be as narrow as 22 in. Second early varieties are most frequently grown in drills of 26 in. with setts 12 to 14 in. apart in the drill, and maincrops in 27- to 29-in. drills with the setts spaced 16 to 24 in. apart.

In order to test these points many trials were carried out at Craibstone when tubers were planted in drills of different widths and at different distances apart in the drill. In one trial Arran Pilot was planted in 24- and 26-in. drills, the tubers being 12 in. apart in both cases. The results were 6 tons 6 cwt. ware and 8 tons 12 cwt. seed from the 24-in. drills, and 7 tons 15 cwt. ware and 7 tons 10 cwt. seed from the 26-in drills. A similar trial was carried out with Majestic planted in 26- and 29-in. drills. The yields were 6 tons 6 cwt. ware and 7 tons 2 cwt. seed from the 26-in. drills and 6 tons

12 cwt. ware, and 5 tons 13 cwt. seed from the 29-in. drills. In both of these trials, as in most others, there was more seed and less ware from the narrow drills than from the wider.

Among trials when seed was planted at different distances apart in the drill was one where Golden Wonder was planted at 12, 18 and 24 in., the size of the seed being the same throughout. Where the seed was planted wide the plants were much stronger and more vigorous, while the leaves were much larger. The yields per acre obtained were :—

	Ware over 2¼ in. T.C.	Seed 1¼-2¼ in. T.C.	Chats under 1¼ in. T.C.	Total. T.C.
12 in.	2·19	5·12	1·9	10·0
18 in.	4·1	4·7	1·3	9·11
24 in.	4·15	3·10	0·8	9·1

In another trial small tubers (1-1¼ in.) of Duke of York were planted at 6, 9 and 12 in. apart. The yields per acre were 4 tons 8 cwt., 5 tons 7 cwt. and 5 tons 10 cwt. respectively of ware ; 8 tons 8 cwt., 7 tons 5 cwt. and 5 tons 18 cwt. of seed size and 24, 17 and 16 cwt. chats from the different distances.

Both these trials show that although the total yield is somewhat less the largest amount of ware is got when the tubers are planted wide, whereas the largest amount of seed-sized tuber is got with close planting. However that may be, the varietal habit of tuber-growth must be taken into account. The seed-setts of varieties such as Arran Banner and Great Scot, which tend to produce large and often hollow-hearted tubers, should be spaced comparatively closely in the drill, while varieties such as King Edward or Doon Star, which normally produce much smaller tubers, should be given every encouragement to grow by wider spacing of the setts.

When grown for seed, where the object is to produce a large number of medium-sized tubers, the drills are usually made an inch or two narrower and the seed-setts spaced an inch or so closer in the drill. Very often in the seed-growing areas small ware (2¼ to 2½ in.) and " thirds " are planted as seed-setts, in which case the former are usually spaced about 12 in. apart and the thirds about 6 to 8 in. apart in the drill.

DEPTH OF PLANTING.—The depth at which the setts are planted will depend on the size of the tubers and on the kind of soil ; too deep planting, however, increases the difficulty of lifting the crop. Large setts require to be planted 4 to 5 in. deep, while 3 or 4 in. will suffice for "thirds" and 4 in. for setts of ordinary seed-size. It is well to plant setts an inch or so deeper on light sandy soil than on heavier types.

When farmyard manure is applied in the drills, the latter must be sufficiently deep to hold the manure and at the same time ensure that the tubers are planted at the proper depth. It is a common practice to make the drills somewhat deeper than appears necessary and then to drag a wooden beam over six or seven drills at a time ; this fills the bottom with loose soil and so ensures a nice bed for the seed-setts. Artificial manures may be applied either on the flat before ridging or in the drills ; trials with both early and late varieties indicate that there is practically no difference in yield of tubers, whichever method is followed, except in the case of small setts which do better when the manures are applied in the drill.

TIME OF PLANTING.—The time of planting depends on the district, season, variety of potato and the purpose for which the crop is grown. A start is usually made with early varieties, in early districts, as soon as conditions will allow in January or February. At the other extreme, in some late areas (especially on the stiffer classes of soil in a late season) planting is often delayed until the latter part of May or, occasionally, even until June.

When potatoes are grown for ware, the ordinary farm practice is to start with the planting of early and second early varieties, as these are sold off the farm as soon as they are lifted. It is therefore important to give such crops the maximum time possible in which to ripen the tubers for the sake of quantity and quality of the crop, both of which suffer when the plants are prematurely lifted. It is good practice to follow on with late maturing varieties as these require a long growing season and, unless they are sprouted and planted early, they rarely reach maturity before the haulms are destroyed by Blight or frost. The early maincrop varieties, requiring a period of growth intermediate in length between the early and late kinds, are usually the last to be planted.

It has been suggested that seasonal factors have to be taken into account in determining the optimum time for planting. The way in which these factors influence the yield is, however, still not fully understood. In trials carried out over a number of years, for instance, in which tubers were planted on different dates, it has been found, in some years, that tubers planted as late as the middle of May gave as heavy a yield as those planted earlier in the season. There appeared to be a connection between the yield and the soil conditions at planting time, rather than between yield and calendar date, a relatively small crop being lifted when the soil was in a raw condition and the soil temperature was less than 40° F. at or after the time of planting. The general result of the trials, however, indicate that in most seasons early planting is an advantage and confirms the usual farm experience that from the middle to the end of April is the most suitable planting time for maincrop varieties. A great disadvantage of late planting is that the quality of the tubers so produced is poor.

An interesting feature brought out by the above-mentioned trials was that, when planting was late, the haulms were very much taller than those developed from early planted seed, no doubt owing to more rapid growth induced by the higher soil temperature. They were, however, very much weaker and broke down readily under high winds and heavy rain; the haulms of the early planted seed, being shorter and sturdier, stood up well. Further, the trials did not fully confirm the common belief that more seed-sized tubers are obtained when planting is carried out late in the season. The actual amount of seed-sized tubers varied very little in the crops planted at different planting dates, but with late planting there were fewer large tubers and more "thirds" or "chats."

PLANTING ORGANISATION.—Careful organisation is necessary when planting to ensure that all the operations proceed smoothly. Sufficient drills should always be set up and, if required, dunged and dressed with artificial fertilisers, to enable planting to continue without hindrance. It is not always profitable to plant the maximum possible area unless the work is done carefully. This usually entails efficient supervision, and it is the foreman's business to see that careful instructions are given and carried out. These instructions should ensure (1) that a plentiful supply of seed, in boxes or bags, is readily available as planting proceeds, (2) that the correct spacing of the tubers in the drill is adhered to, (3) that special care is taken, when planting sprouted tubers, to avoid breaking off the sprouts, and (4) that the ends of the drills are planted to the same length; irregular ends not only do not look well but result in much ground being wasted.

Finally, the covering of the setts should be completed close behind the planting. This is particularly important when freshly-cut setts are planted on a bright sunny day. The cut surface dries quickly and this may induce tuber-rotting, the reason for which is discussed in Chapter XIV. If, for any reason, the covering of the setts has lagged behind, and it is not possible to close the drills before work ceases for the day, alternate ridges may be split so that the tubers are covered with soil, the ridges being completed later.

Details of field work and planting machines will be found in Chapter XI.

LATER CULTIVATION.—At one time it was customary to expend a considerable amount of time and labour on the cultivation of the potato crop, but recent trials have shown that, in many cases, much of it can be omitted without reducing the yield. Nevertheless, the conditions under which the crop may have to be grown vary so much that trials carried out by the grower himself provide the only safe guide as to what operations may be dispensed with.

The chief objects of the cultivation are to keep the land clean by preventing the growth of weeds and to provide loose soil for earthing up. In most cases it will be advisable to go over the drills with a saddleback harrow in good time, not only to give the young shoots early access to light, but also to kill any new growth of weeds; weeds are much more easily killed when they are small than when they are full grown. If there is any immediate risk of frost, however, the operation should be postponed until the danger is past. When the young plants are well through the ground the drills may be shimmed in order to destroy weeds and loosen the soil around the haulms. An effective way of doing this is by means of spring-tined cultivators adjusted to run three tines in each row. Before the final earthing up it may be necessary to hand-hoe in order to ensure the destruction of weeds around the bases of the haulms. Undoubtedly earthing up is often done far too late.

DESTROYING THE HAULMS.—Nowadays, the haulms of most of the crops of potatoes grown for seed are either cut or burned down when they are quite green. There are two objects in view, (1) to get a larger proportion of seed-size tubers, and (2) to prevent, if possible, the tubers taking Blight. Growers often complain that they have a high proportion of large tubers in their crops. This is possibly due to the fact that they had planted comparatively small tubers too wide apart in the drill and given an excessive dressing of fertilisers, more particularly nitrogen.

To get the maximum amount of seed-size tubers comparatively large setts should be planted fairly close in the drill and only a moderate dressing of fertilisers should be given.

Several trials were carried out at Craibstone where, at the same time (1) part of the crop was lifted when it was considered that there was the largest proportion of seed-size tubers; (2) the haulms were (*a*) cut, (*b*) burned down with sulphuric acid and (*c*) destroyed with sulphate of copper, and (3) on another part the crop was allowed to ripen naturally. An examination of the results showed that (1) there was a smaller crop of both ware and seed-size tubers when the crop was lifted early, (2) the crop continued to grow after the haulms were cut or sprayed and the yield increased, (3) there was comparatively little difference between the yields from cutting or spraying, (4) none of the treatments materially increased the amount of seed-size tubers, (5) there was the largest amount of ware and the smallest amount of chats when the crop was allowed to ripen.

When crops are sprayed, lifting should not begin for two or three weeks in order that the skin of the tubers may become tough and firm.

Information about harvesting will be found in Chapter XI.

Whatever the method of lifting, the work must be well organised so that it may proceed expeditiously. There should be sufficient gatherers on both sides to keep the digger going, each being allotted a definite length of drill. This length or "stretch" should not be too great or the gatherers may tire and become discouraged. They should have sufficient time to go over their stretch a second time to pick up stray tubers which, if not gathered at the time, may be covered.

The tubers may be collected into baskets or, if intended for seed, into boxes, care being taken to free the tubers as far as possible from adhering soil. The baskets may either be emptied at once into a cart, or the full baskets carted away and emptied directly into the pit or store; the latter is the better way since there is less likelihood of damage to the tubers.

When a field is finished, it is essential to go over it with a spring-toothed harrow in order to bring up any buried tubers, these being gathered at once. However well this is done, other tubers are often to be seen on the surface after heavy rain; these also should be collected before there is any risk of frost. Harrowings should be kept separate from the main store of potatoes as many may be damaged and storage rots thus encouraged.

STORAGE.—The crop may be stored (1) outside, in what are called in different parts of the country, pits, pies, graves, hogs or clamps, (2) inside, in sheds, and (3) in boxes.

(1) Certain precautions must be taken in making this outside store. In the first place the foundation must be firm, level and dry, and sited higher than the surrounding ground so that water will drain away after continuous rain; it is an advantage if the pit can be made near a road. The pit can be made anything from 3 to 8 ft. wide at the base, with the tubers built up to form sides as high and steep as possible; the narrow sizes are most suitable when potatoes are pitted in a wet condition. In some cases a frame the size and shape of the pit is first set up. This has a wide opening at the top into which the tubers, carted from the field in baskets, are emptied. When filled, the frame is moved along to other sections in succession until the whole length of the pit is completed. This method saves a considerable amount of work in trimming the sides of the pit and reduces tuber-damage to a minimum.

When the sides are trimmed, they are covered with a good uniform layer of straight wheat or rye straw at least 6 to 8 in. deep and placed lengthways from bottom to top; straw is also put over the top and bent down on both sides to keep out rain. A thin covering of soil is usually put on to keep the straw in place, although sometimes heaps of soil or divots are placed at intervals for the same purpose. In order to provide for ventilation, drain pipes or small bundles of straw are placed at intervals along the top or, more usually, the ridge is left uncovered for some time. Unless some such precaution is taken, a rise of temperature may occur, and this may have a detrimental effect on the tubers. Although the loss in a pit due to overheating may be substantial, the effect of chilling is very much more serious. Before frost occurs, therefore, earth must be put on the pit to a depth of 10 to 12 in. or more, depending on the severity to be expected in the winter conditions. The pit should not be regarded as completed until some means have been provided to drain water away after heavy rains; failure to do this may cause serious loss through water seeping into the pit.

(2) *In Sheds.*—During recent years there has been an increase in the use of sheds for storing potatoes, particularly for the seed market, and in many cases existing buildings have been modified for this purpose. This method not only reduces the risk of tuber-damage but also effects a considerable saving in labour. In addition, the tubers can be riddled in comfort at any time during wet or stormy weather, a factor of importance in securing good well-graded samples of tubers.

The potatoes are carted directly into the shed and built up to a depth of about 4 ft. for early varieties and up to 6 ft. or even more for later varieties if the tubers are dry and free from Blight. A good method of emptying the container on the heap is to have a movable erection about 20 to 30 ft. long which can be adjusted to any height and on which there is a travelling belt about 2 ft. wide. By its use the tubers are conveyed to any part of the heap. There is, therefore, no need to use a graip and so there is much less injury.

In order to provide for ventilation, bunches of wheat or rye straw are sometimes set on their ends and placed at intervals throughout the heap, the whole then being covered with straw to a depth of fully 1 foot to help to maintain an even temperature in the heap. If the building is not frost-proof, braziers or Valor perfection paraffin heaters can be used to warm the store during frosty weather.

A few years ago when oat straw was very plentiful a new method of storing potatoes was tried in Scotland. The straw was baled and outside sheds were constructed with it. The width of these sheds varied from about 14 to 16 ft. and the potatoes were built up in them to a depth of 4 or 5 ft. at the sides and 6 to 7 ft. at the centre. Once the potatoes were in position bunched wheat straw to a depth of 12 in. was put over the top as a covering and left for a few weeks to enable evaporation to proceed. Thereafter the straw covering was removed and a fresh supply sufficient to keep out frost added. Special tarpaulin covers were placed on the top of the straw to keep the latter in position and to prevent the entry of rain. When the precaution was taken to ensure that there were no openings to allow frost or rain to penetrate the method was quite successful.

(3) *In Boxes.*—Where the soft varieties of early potatoes are grown for seed, it is advisable to gather them directly into boxes and store them until they are ready for riddling. When so stored the tubers have the best chance of the skin becoming firm and tough, so that tuber-damage is minimised and, with it, the risk of the spread of disease from any tubers which may be affected. Nevertheless, the presence of diseased tubers is always a source of danger, and it is well to examine the boxes periodically and remove any tubers showing signs of rotting. If light is admitted to the shed the outside tubers become green, which is not objectionable in tubers to be used for seed, but makes them unfit for consumption. Hence it is advisable to exclude all light until the larger tubers have been riddled out.

DRESSING.—There are several methods of grading the tubers.

(1) *By Hand.*—This has already been described in the case of the first-lifted early varieties which are graded in the field at lifting time. In some cases, however, the soft-fleshed, thin-skinned early varieties such as Ninetyfold, May Queen, etc., which are stored in boxes, are also graded by hand. The boxes are placed on a bench at a convenient height and the workers soon become expert at sorting out the different sizes; riddles kept near at hand serve to test any doubtful tubers.

(2) *By Hand Riddles.*—The smaller growers usually grade the crop by shaking the tubers over a hand riddle of known mesh. The size of ware is regulated by the Ministry of Food with the object of maintaining a continuous supply. Ordinarily the Ministry prohibits the sale of tubers for ware which pass

through a riddle of 1½-in. mesh, but if the supply so obtained is insufficient to meet the demand the riddle may be reduced to 1¼-in. mesh. The smaller tubers, which are usually sold for stock-feeding, are put over a ¾ or 1-in. riddle (often called an " earth " riddle) to remove any soil.

A description of graders will be found in Chapter XI.

DESPATCHING.—Great care must always be taken when despatching potatoes especially for seed and the bags should be carefully handled. Many seed tubers especially of the thin-skinned, soft varieties are often damaged and rendered useless by careless handling. Workmen should not tramp on the bags when building them and they should not throw bags about or drop them several feet into railway wagons. Wagons and vans should always have a good layer of straw on the floor and round the sides as a precaution against frost; the wagons, in addition, must always be properly sheeted.

CHAPTER X

MANURING OF THE POTATO CROP

EVEN though a good stock of seed is planted, the maximum yield cannot be expected unless the soil is in good condition, drained, well-cultivated and thoroughly manured. On most farms all crops are grown as part of a rotation which will vary according to the district, and the manuring has usually to be considered as a whole rather than from the point of view of any particular crop in the rotation.

ORGANIC MANURES.—The potato is a gross feeder and responds to generous manuring. While satisfactory crops may be obtained by the use of fertilisers only, bulky organic manures (and more particularly farmyard manure) are necessary in order to help to maintain the fertility of the soil. The function of bulky organic manure is to replenish the soil humus, which is essential not only from the standpoint of plant food, but also because of its beneficial influence on the texture of heavy soils and the water-holding capacity of light soils.

Since it is produced on the farm, farmyard manure is the most commonly used of these organic manures and, except under certain conditions, may be regarded as the foundation of the manures to be applied during the rotation. The chief exception to its use for the potato crop is when the latter is grown after lea with a good proportion of wild white clover. Many trials have shown that the full benefit is not obtained from farmyard manure when it is applied after breaking up good lea grass, better results being achieved under such conditions when the dung is applied later in the rotation, and hence nearer the time when grass and clover seeds are again to be sown. Where there is little wild white clover, however, and the grasses lack vigour, a dressing of dung will be beneficial, if spread on the pasture several weeks before ploughing so that first the grasses and then the potatoes may derive benefit.

Farmyard manure varies somewhat in composition but is always rather badly balanced, being deficient more particularly in phosphates. There is a fair proportion of nitrogen and also of potash, though these constituents are often reduced to an unnecessary extent by wrong methods of storage. The quantity to apply will, of course, depend on what is available, but a usual dressing is about 12 tons per acre, supplemented by fertilisers. If dung is scarce it is better to give a small uniform dressing to the whole area than to leave a portion without dung. On the other hand, except in special cases, such as in growing earlies, it is inadvisable to apply quantities much larger than 12 or 15 tons per acre, for the extra yield obtained is not commensurate with the increased cost of production in addition to which the quality of the tubers may be adversely affected. The methods of application of dung are discussed in Chapter IX.

In coastal districts seaweed, and in certain areas in England, shoddy or other forms of bulky organic manures sometimes replace all or part of the farmyard manure which would otherwise be applied. Seaweed, like farmyard manure, varies a good deal in composition ; but in comparison with the latter, seaweed usually contains more potash, only about one-quarter the amount of phosphates and fully one-half the nitrogen present in the same weight of dung. Further, seaweed contains a good deal of common salt which has a detrimental effect on the quality of potatoes. For this reason the seaweed should be applied sometime beforehand so that the salt may be washed out of the soil.

FERTILISERS.—A considerable number of experiments with fertilisers are carried out annually in different parts of the country and, although results vary according to district, certain general principles have been determined. For example, no application of fertilisers, however generous will make up for inadequate cultivation or will compensate for deficiencies of any kind ; nor will large quantities of fertilisers make a naturally poor soil fertile. Indeed, the best soils often respond more to heavier dressings than do poorer soils.

Again, although each of the chief ingredients of fertilisers (nitrogen, phosphate and potash) has its own specific influence on plant growth, the magnitude of the effect will vary according to the kind of soil, the supply of moisture and other local factors, while the maximum result cannot be obtained from any one of these ingredients unless a sufficient amount of each of the others is also present. That is to say, the mixture must be balanced—it must contain nitrogen, phosphate and potash in proper proportions to suit the conditions under which the crop is to be grown.

NITROGEN.—Nitrogen is of primary importance to the potato crop. This element is usually deficient in soils except those of a peaty nature and in fenland and after lea with wild white clover. When present in sufficient quantity and with adequate amounts of phosphates and potash, the haulms are dark green in colour, tall and vigorous, and there is an increase both in the number and size of the leaves. As starch, the chief constituent of the tubers, is formed in the leaves, both the number and size of the tubers are consequently increased when the maximum foliage canopy is produced. Further, unless the plants are destroyed early by Blight or frost, nitrogen prolongs the growing season, and this also results in an increased yield.

When insufficient nitrogen is available the plants are more or less stunted, the leaves are small and of a light green colour which later becomes yellowish green, and the period of growth is reduced ; the result is a small crop of small tubers. On the other hand, when nitrogen is used in excess, and especially with insufficient phosphates and potash, there is usually a luxuriant growth of very dark green foliage, tending to be soft and easily broken down by wind and rain, while the yield of tubers is less than one would expect from the appearance of the foliage. With late varieties the effect is very pronounced.

Almost all trials have shown that sulphate of ammonia is the best form in which to apply nitrogen for the potato crop, both from the point of view of quantity as well as quality of tubers produced. Nitrate of soda, however, is sometimes applied to early potatoes in some districts of England, where it is considered that this form of nitrogen leads to early maturation of the crop.

It is often said that fertilisers, and nitrogen in particular, adversely affect the cooking quality of the tubers. This is only true, however, when nitrogen is used to excess, or when a badly balanced mixture is used, the effect being particularly marked with late-planted and (in the case of late varieties) unsprouted tubers. Early varieties appear to be specially susceptible to this harmful effect of excess nitrogen, and the all too common inferior quality of "earlies" is doubtless due in large measure to the heavy nitrogenous dressings they receive. Later maturing varieties vary in the effect of excess nitrogen on the quality of the tubers; thus "good quality" kinds, such as Golden Wonder, are less adversely affected than "poor quality" varieties like Majestic.

POTASH.—Potash is also of prime importance for the potato crop. Its use tends to produce sturdy plants with leaves of a thick, firm texture. One of the functions of potash is the promotion of starch formation, but it has never been clearly established whether the action of potash is direct or only indirect. The crop matures later so that the yield is increased, particularly of ware tubers. It has its maximum effect upon yield, however, when there are adequate amounts of the other necessary ingredients present, more particularly nitrogen.

Potash is usually most necessary on light sandy or peaty soils, while on clay soils it sometimes has comparatively little effect. The potash requirement of maincrop varieties is greater than in the case of earlies, but with all varieties its effect appears to be greatest in seasons in which there is a lack of sunshine. When a soil is deficient in potash the potato plants are retarded in growth, the internodes being shortened so that a compact, bush-like habit results. The leaves at first are unusually dark green in colour, but later become stippled with minute brown spots which give a characteristic bronzed appearance to the foliage. The surface of the leaves is frequently corrugated and the tips and margins tend to curl downward. The tops die down prematurely and the yield is reduced. The quality of the tubers is also poor and there is a tendency for them to blacken readily when boiled (see Chapter XIII).

In pre-war days potash was supplied in the form of sulphate, muriate, potash salts and kainit. Both kainit and potash salts were impure forms and consisted of muriate of potash together with varying quantities of other salts such as magnesium sulphate and sodium chloride. The manurial value of these various forms of potash is assessed by the percentage of potassium oxide (K_2O) present. Nowadays, there is no kainit which contained only 13 to 14 per cent. K_2O. Potash salts or potash manure are at present sold in one grade only, containing 40 per cent. K_2O. Muriate of potash is the common form and there are two grades containing 50 and 60 per cent.

K_2O respectively. Only a small amount of sulphate of potash was available during the war and post-war years; it is, however, now more abundant and it contains 48 per cent. K_2O.

When the sulphate is used the potato foliage is often lighter in colour than with other forms of potash but, generally speaking, on light soils and in a dry season there is little difference between the muriate and sulphate of potash in the yield or the cooking quality of the tubers produced. On heavy soils, however, and especially in wet seasons, the sulphate is usually superior to the muriate in both these respects, a superiority which becomes more marked when large dressings of potash are used. Almost always, potash salts produce smaller crops than either the muriate or sulphate and, in addition, the tubers are much poorer in quality. This reduction in quality is usually ascribed to the presence of sodium chloride (common salt) in low grade potash salts.

PHOSPHATES.—Although phosphates are usually considered the least essential of the three main ingredients of artificials for potatoes, they are still of considerable importance, more particularly on the heavier soils or those of a peaty nature. Phosphates encourage root development in the early stages of the growth of the plant and hasten maturation. This latter fact, however, calls for a word of caution, for although the very soluble superphosphate has been repeatedly shown to be the best form in which to apply phosphates, its very solubility may induce too early ripening on light sandy soils liable to dry out quickly in dry seasons. Where the soil is deficient in phosphates the plants are slower in development and are much smaller, the leaves assuming a dull green appearance. Ripening is considerably delayed and the yield is less both in number and size of tubers; the cooking quality of the tubers suffers also. When phosphates are used in excess the crop may show a potash deficiency even although potash is supplied. As in the case of potash, the only reliable means of determining the amount of phosphates to apply is by the chemical analysis of and experience with the soil; thus, soils with a high humus content (or on which a heavy dressing of dung is applied) require more phosphates than would otherwise be necessary to give a well-balanced artificial manure.

Quantity of Fertilisers to Use.—The amount of fertilisers that may profitably be used will depend on (1) the condition of the soil and (2) the previous crop and manuring; the probable market prices of ware and seed tubers must also be taken into account. When prices are low, it is often hardly worth while to apply the maximum quantity of fertilisers since the increased yield may not compensate for the extra cost of manuring; with a high market price, on the other hand, a small increase in yield may be worth striving for.

It will be clear from what has been said that the application of fertilisers deserves careful consideration. The considerable difference in the amounts used in various parts of the country is, no doubt, often a reflection of local experience modified by scientific advice, but too often it is evident from the appearance of the crop that "rule of thumb" methods have been the only ones employed. The general principles of manuring described below should therefore not be too rigidly adhered to, but should be modified where necessary in the light of what has been said in the previous paragraphs.

When second early or maincrop potatoes are taken after oats, and dung is applied, a suitable mixture for average medium soils in fair condition would be:—

1 to 1½	cwt.	sulphate of ammonia	per acre.
3 ,, 4	,,	superphosphate	
1	,,	sulphate or muriate of potash	

If no dung is applied, these quantities may be increased by about one-half.

In some of the large potato-growing areas in England such as Lincoln and Yorkshire where the crop is usually grown after grain, very large quantities of fertilisers are used. Quite a common dressing is 15 cwt. per acre of a mixture containing 6 per cent. N, 7 per cent. P_2O_5 and 10 per cent. K_2O. This is approximately equivalent to:—

4½	cwt.	sulphate of ammonia	per acre.
6	,,	superphosphate	
3	,,	muriate of potash	

After lea, with abundance of wild white clover, no dung will be necessary, and only a small amount of nitrogen is required in order to help to start growth before the nitrogen from the turf becomes available. A suitable mixture would be :—

½ to ¾	cwt.	sulphate of ammonia	per acre.
3 ,, 4	,,	superphosphate	
1 ,, 1½	,,	sulphate or muriate of potash	

If little wild white clover is present the same mixture may be used, supplemented by dung and a little extra nitrogen.

Generally speaking, on light soils more nitrogen and potash and less superphosphate should be used. When a large amount of superphosphate is used on such light soils and especially when the season is dry the plants ripen prematurely. The result is that the tubers are small and the yield low. On heavier clay soils more nitrogen and superphosphate should be applied and the potash reduced.

When potatoes are grown after potatoes, the soil is usually in a somewhat impoverished condition and much more manure must be used. If dung is applied, a suitable mixture for average conditions would be :—

1½ to 2	cwt.	sulphate of ammonia	per acre.
3 ,, 4	,,	superphosphate	
1½	,,	sulphate or muriate of potash	

If no dung is used then these quantities should be increased by about one-half.

Early ware crops, which are usually grown on early and lighter classes of soil, are always liberally manured, not only to increase the yields but also to hasten the development of the crop. Very often 12 or more cwts. per acre are applied in addition to dung or seaweed. A common mixture is :—

3 to 4	cwt.	sulphate of ammonia	per acre.
5 ,, 6	,,	superphosphate	
1 ,, 2	,,	sulphate or muriate of potash	

Such high quantities of sulphate of ammonia, however, adversely affect cooking quality.

If a mixture has to be made up beforehand, it is as well to add a small quantity of steamed bone flour, or other dry material, in order that it may keep well and be in good condition for sowing. When no dung is used the evidence indicates that phosphates may be increased by about one-third, potash and nitrogen by about one-half.

Complete concentrated mixtures of artificial fertilisers are available on the market, and trials have shown that they give results quite as good as and sometimes better than home-mixed fertilisers of similar composition. In the nature of things, however, these ready-made mixtures cannot allow for differences in soil or farm management, so that at the cost of some inconvenience there are sound reasons for mixing to be done on the farm in order to get the most suitable mixture. In this case, care should be taken that the mixing is done thoroughly. Only small lots, say 10 cwt., should be mixed at any one time, and the heap must be turned over several times. It is advisable to add a little steamed bone flour or other dry material, as already mentioned, to avoid lumpiness and ensure ease of sowing. The heap should be kept over-night before bagging and, if necessary, should be riddled.

METHOD OF SOWING.—Artificial fertilisers are sown either on the flat before drilling or in the drills, the results of trials of the two methods being somewhat conflicting. Very often there is little difference in the yields obtained, especially when fairly large and well-sprouted setts are used, but small setts appear to do better when the manure is sown directly into the drills. Possibly the reason for this is that the larger setts, having a good store of food in the tubers, are independent of the artificial fertiliser during the first period of growth and so, when sprouted, the roots are very soon in contact with sufficient plant food in the soil, whereas the small setts have not this initial advantage and must rely on the fertilisers near at hand to get an early start. Whatever method is followed care must be taken to sow the fertilisers uniformly. One often sees drills in fields that have not got their fair share while others have got too much. The manure distributor should be over-hauled and put in good order before use.

In recent years much attention, more particularly in America, has been paid to what is called "placement" of artificial fertilisers. These investigations have been made by placing the fertilisers in layers at different distances along the sides of the drill, above and below the tubers. A review of the literature indicates that there are some variations in the results, probably due to variations in the conditions of the experiments. The best results were, however, obtained when the fertilisers were placed in layers 2 in. from each side of the tubers and at a slightly lower level. Trials in this country are not sufficiently far advanced to show if similar results would be obtained here ; one difficulty still to be overcome if the method is to be a success is the provision of suitable machinery to sow the fertilisers at the required places.

LIME.—Potatoes tolerate acid conditions and even appear to thrive best on acid soils, so an application of lime may sometimes reduce the yield whilst at the same time increasing the risk of "scab." The effect of lime in increasing the intensity of scab appears to be greatest under dry conditions, that is on a dry soil in a dry season. Thus in 1947 there was an extremely dry period in June, July and August and scab was much more widespread than it usually is in ordinary seasons. Part of a field at Craibstone was limed in 1946 and potatoes were planted in 1947. On the limed part almost every tuber was affected with scab whereas on the unlimed part the tubers were quite clean. It would be well to get the soil tested beforehand as occasionally, under very acid soil conditions, such as on a peaty soil or on newly reclaimed land, an application of lime has been found to be beneficial to the potato crop.

Nevertheless, other crops in the rotation are usually improved by liming so that the total profit from the rotation is increased. Lime, therefore, must have its place in manuring, but its place should be after the potato crop has been taken, so that during the necessary cultivation for the remaining crops the lime becomes well mixed with the soil before the field is again cropped with potatoes. The most convenient form in which to apply lime is as ground limestone ; but, whatever form is used, much depends on its being spread uniformly. When lime is placed in heaps and spread by hand, the distribution is usually far from uniform : much the best plan is to use a good manure distributor.

CHAPTER XI

POTATO MACHINERY

RIDGING PLOUGHS.—Land required for potatoes is worked to a deep loose tilth in the spring before being drawn into ridges for planting by hand or by some mechanical planters. After planting, the ridges are split back so that new ridges are formed over the potatoes. The ridges are made by an implement which carries one, two, three and, occasionally, four double-mouldboard-ploughs or ridging bodies. An ordinary single-furrow mouldboard plough is sometimes used for drawing ridges and covering-in potatoes. The ridger is equipped with an adjustable marker which is set so that the ridges are a uniform distance apart. The one- and two-row implements are usually horse-drawn and the three- and four-row ones are tractor-drawn. The tractor multiple-row ridger may have large diameter land wheels, in which case it is merely towed behind the tractor, or, as is more usual, it is a general purpose toolbar, mounted on the tractor, to which the ridging bodies are attached. There are three types of tractor-mounted toolbar—rear, underslung and forward, depending on whether the toolbar is carried on the rear of the tractor so that it cannot move laterally or only to a limited extent independently of the tractor, or placed beneath the sump of the tractor between the front and rear wheels or placed on the front of the tractor forward of the front wheels. Almost any tractor, wheeled or tracklaying, can be equipped with a rear or forward toolbar, but a wheeled tractor with a high clearance beneath the sump is necessary to accommodate the underslung type. Toolbars are usually equipped with a pair of depth regulating wheels or skids, but on wheelless toolbars other methods of depth control are adopted. These include a hydraulic mechanism on the tractor, an adjustable stop on the power lift which allows the toolbar to fall to a predetermined depth relative to the wheels of the tractor, and a series of springs which can be adjusted to take more or less of the weight of the toolbar and thus control penetration. Most toolbars do not have any lateral movement independent of the tractor, but where this is possible the toolbar is kept steady by a special fin or keel.

The rear toolbar is usually better than the forward or underslung types for setting up ridges because the furrow bottoms are not trodden down by the tractor wheels. When drawing ridges the toolbar carries a marker which makes a mark on the ground along which the front wheel of the tractor is driven on the next bout up the field. If the marker is correctly set, the " join " between successive bouts is accurate and it is impossible to distinguish it from the other rows. It is not always easy to drive the single front wheel of a tricycle-type tractor down a mark, and to overcome this difficulty a pair of sighting markers is fitted to the front of the tractor where they are clearly visible to the operator. When setting the true markers the sighting markers are treated as front wheels and in work are driven above the marks made by the true markers. If the ridging bodies are directly behind the front and rear wheels, markers can be dispensed with if the wheels and ridging body on one side of the tractor are run down the outside furrow made on the previous bout.

For covering-in the forward toolbar is the easiest to handle, especially if it is fitted with diabolo-shaped rollers to run on the ridges being split, because all the tractor wheels, being behind the covering-in bodies, run in furrows. With the rear and underslung toolbars some or all of the tractor wheels have to be kept on top of ridges. This is often a difficult operation especially if the ridges are pointed or if the work is on a sideland.

The ridger sometimes carries a fertiliser distributor which places the fertiliser in the bottoms of the furrows. There may also be small lengths of chain trailing along the sides of the ridges to pull a small amount of soil into the furrows so that the potatoes are not put into direct contact with a large quantity of fertiliser. The fertiliser may also be applied with an ordinary distributor to the land before or after ridging. If applied after ridging the fertiliser may be spread over the whole of the ridges or it may be directed by means of baffles placed on the base of the distributor into the furrow bottoms.

To assist hand planting, a " dibbing " machine may be run in the furrows prior to planting to mark the positions that the potatoes are to occupy. A dibber is usually a three-row machine consisting of three large diameter wheels mounted on an axle and carrying on their circumference a number of projections which make shallow depressions in the furrow bottom. The projections are uniformly spaced round the circumference of the wheels, and the spacing distance is varied by increasing or decreasing the number of projections on the wheels. A continental method of planting potatoes, which, so far, has only been tried experimentally in Great Britain, uses special dibbling tools and very small covering-in bodies attached to horse-drawn or tractor-mounted toolbars. Each dibbling tool consists of a centre boss carrying a series of spade-like projections and is mounted so that as it is pulled along the ground the projections scoop out pockets of soil and leave shallow depressions into which the potatoes are dropped by hand. The spacing distance is determined by the amount the spade-like projections stand out from the centre boss. The covering-in bodies are small with shallow mouldboards which are designed to put only a small amount of loose friable soil over the potatoes.

PLANTERS.—The function of a potato-planting machine is to place potatoes singly in furrows at predetermined regular intervals. In the simplest machine, where the potatoes are dropped into the furrow by hand, the spacing is dependent on the efficiency of the feeder, although there may be a mechanical device, worked off a land wheel, to indicate when the potatoes should be dropped. Usually the spacing is done mechanically, either by simple hand-fed or by relatively more complicated, fully-automatic devices. The commonest type of hand-fed mechanism is a series of cups on an endless belt driven from the land wheels. The cups carry the potatoes down a chute and release them near the furrow bottom. Another type takes the form of a wheel with a channel-section rim. Transverse partitions divide the rim into a number of equal-sized compartments into each of which the feeder puts a potato. The wheels may be of very large diameter and revolve through being in contact with the ground, or they may be small wheels mounted on an axle and driven from the land wheels. A third type of mechanism is a wheel revolving in a horizontal plane on a platform which carries the mouth of a chute leading down to the furrow. The potatoes, placed between the spokes of the wheel as it revolves, fall down the chute. In one make of planter the flat spacing cups are hinged on radial projections from a horizontal turn-table. As the cups pass round in front of the feeder they are held horizontal, but when they reach a point immediately behind the furrow opener, they swing down and drop the potatoes into the furrow. Very few "misses" or "doubles" should occur with hand-fed machines, unless the forward speed is so great that the feeders are unable to handle the potatoes quickly enough. The maximum sustained rate at which a feeder can handle potatoes singly is about 120 per minute, and therefore the highest forward speed of a hand-fed planter having one feeder per row is 2 m.p.h. with 18-in. spacing and 1½ m.p.h. with 13-14-in. spacing. Most wheeled tractors are unable to exert a steady pull at such low speeds and because of this many hand-fed planters have two feeders per row.

The efficiency of fully automatic planters depends on the type of mechanism employed, the quality of the seed (*i.e.* the evenness in size) and the shape of the seed (*i.e.* variety). There are two main types of fully automatic feeding mechanisms. One consists of cups on an endless chain which passes up through the potatoes in a hopper. This works well with closely graded round seed, but if the seed is very variable in size, the cups pick up the small seed first, often two setts at once, from a full hopper, and when only large potatoes are left, fail to pick up setts. This results in a high proportion of "misses" and "doubles." "Misses" can be prevented by having a small hand-fed mechanism which automatically drops a potato into an empty cup, but no mechanical method has been devised for correcting "doubles." An extra man is sometimes put on the machine to fill empty cups and separate "doubles." Both of these methods require additional hand labour; but unless the seed is very uneven, one man can look after a 2-row planter working at a higher forward speed than is possible with a hand-fed machine. A second type of fully automatic spacing mechanism consists of a series of radial arms with spikes which pick up the potatoes from a subsidiary hopper below the main hopper. The potatoes are stripped from the spikes and fall down into the furrow. "Misses" and "doubles" are frequent with uneven seed, but with even seed the numbers are small.

Spacing mechanisms can be adjusted to give spacing distances suitable for all farm requirements, usually by altering the speed of the mechanism relative to the forward speed of the machine. The actual spacing of the setts is wider than the theoretical spacing distance with those machines on which the spacing mechanism is driven from the land wheels because of wheel slip which may amount to as much as 20 per cent.; but with those mechanisms driven from the tractor p.t.o. the actual spacing distance will be less than the theoretical because of tractor wheel slip. The discrepancies may be appreciable, but they are not important because the machine can be set for a theoretical spacing which because of wheel slip will give approximately the desired spacing in the field. Several factors affect the evenness of spacing. If the height above the furrow bottom at which the potatoes are released is considerable, the time the potatoes take to fall to the ground may vary sufficiently to give erratic spacing. The potatoes may not leave the spacing mechanism at regular intervals. On most planters, small potatoes leave the cups more quickly than large ones because release is usually effected by the edge of the cup moving away from the lower end of a chute. Therefore uneven seed will tend to be spaced erratically. With the planting mechanism consisting of cups hinged on radial projections of a turn-table, the cups drop at regular intervals and large potatoes are released just as quickly as small ones. The shape of the furrow bottom also affects the spacing. A narrow V-shaped furrow traps the potatoes as soon as they reach the ground, but a wide-based furrow allows them to roll. Although there is an optimum spacing distance for seed of a given size, it is doubtful whether, with present-day commercial seed, extremely accurate spacing is essential; and it is probable that at least some planters reach a sufficiently high standard.

Tractor toolbars are being used on an increasing scale for the inter-row cultivation of potatoes, and, for this to be successful, accurate planting, giving even row widths, is essential. Such accuracy is not always possible with machines working "on the flat" because "crabbing" takes place, in spite of various devices such as elongated furrow openers, deep skid rings on the land wheels, and a ridging plough running in the outside furrow of the previous bout. These devices help on reasonably flat land, but they are not entirely successful on sloping ground especially if the planter is used across the slope. Uneven "joins" between successive bouts of one- and two-row planters, often prevent satisfactory work with a three-row toolbar. "Crabbing" with a three-row machine is not so serious because the toolbar can always follow the machine and never straddle the "joins," but uneven "joins" spoil the appearance of the work and may interfere with the final moulding-up of the crop. For work on previously-ridged land, one- and two-row planters are just as successful as a three-row, because the accuracy with which the ridges are set up determines whether the row width is constant or variable. Machines for ridged land plant either in the furrows or in the ridges. If farmyard manure is applied after ridging, the planter must plant on top of the farmyard manure lying in the furrows. Most planters are equipped with pairs of discs, or ridging ploughs to cover-in the potatoes.

Many American planters have fertiliser distributors and the means of securing accurate placement of the fertiliser relative to the potatoes. This procedure results, in America, in the more efficient utilisation of the fertiliser compared with broadcasting the fertiliser over the whole of the ground. Sowing the fertiliser with the planting machine also saves an operation, but against this saving must be set the reduced working speed resulting from the extra time spent on the headland handling the fertiliser; the additional cost of the distributor; the "crabbing" that often results from the heavy drive to the distributor; and the shorter "life" of the planter due to the corrosive action of the fertiliser.

INTER-ROW CULTIVATIONS.—After planting but before the potatoes appear through the ground the ridges are alternately harrowed down and set up again to improve the tilth and to kill weeds. The harrowing is done with either saddleback or chain harrows or worn spike-tooth harrows. The inter-row cultivations of grubbing and hoeing continue after the plants are through the ground until the crop has grown to the stage where further cultivations would do damage. The final operation consists of earthing up the crop. On small acreages, the inter-row cultivations are nearly always done with horses but, for large acreages, tractor toolbars, with the appropriate cultivating bodies attached, are used. Of the three types of toolbar, the rear is the most suitable for this work because with it the tractor wheels do not run on the freshly cultivated soil.

Just prior to earthing-up or at a later stage the crop may be sprayed or dusted as a precaution against Blight, and this may be repeated if conditions favour the development of the disease. Sprayers may be horse- or tractor-drawn or mounted on the tractor, and the mechanism may be manually operated or it may be driven from the land wheels, or by an auxiliary engine or by the tractor p.t.o. On most sprayers, the spray is carried in a tank of about 100 gallons capacity from which it is pumped to the nozzles fixed to pendants attached to a horizontal bar across the rear of the machine. On each pendant some of the nozzles face upwards and some downwards to ensure that both surfaces of the foliage are adequately covered by the spray. On one make of sprayer compressed air is supplied to the tank carrying the spray fluid which is thereby forced out of the nozzles. The quantity of spray applied depends on the stage of growth of the crop and may vary from 80 to 100 gallons an acre. A large quantity of water is required, and it is with the object of reducing the time spent in carting water and also of enabling spraying to be done in those areas where there is a shortage of water during the summer months that "low-volume" machines have been developed. These use only a small quantity of water and as little as ten gallons per acre may be all that is necessary. A tractor-mounted British-made atomiser has a high-pressure fan operated by the tractor p.t.o. The air blast is taken to nozzles which also carry small jets connected to the containers with the spray fluid. The spray fluid is under relatively slight pressure and it is the air blast rushing past the jets that causes the fluid to be finely atomised. Some "high-volume" sprayers can be converted for "low-volume" spraying by adjusting the working pressure and fitting special jets. Similar jets are also used on tractor-mounted "low-volume" sprayers which are driven through the p.t.o. The rate of application per acre by "low-volume" machines is so low and is so easily affected by tractor speed that all tractors used for spraying should have accurate speedometers.

Powder dusters are usually employed where large acreages have to be dealt with or where water shortage prevents the use of sprayers. Compared with spraying, dusting can be done more quickly and cheaply, but it is not so effective. Most dusting machines consist of a small hopper from which an agitator causes the dust to fall through an adjustable feed-gate into a fan. The fan, driven by the tractor p.t.o., by a small auxiliary engine or from the land wheels, blows the dust through a number of fish-tails which travel down between the rows of potatoes. Eleven- and thirteen-row power-operated machines enable large acreages to be covered quickly. A recently-introduced duster relies on the exhaust gases of the tractor to carry and distribute the powder.

HARVESTING.—The horse-drawn potato plough probably does less damage to the crop than any other mechanical lifting device, but its prongs do not effect a complete separation of potatoes from soil with the result that the " harrowings " may be considerable. Nevertheless, the plough is used for lifting early potatoes first because of its gentle action and, secondly, because it is not so liable to blockages by shaws as other lifters. The performance of the plough improves when it is mounted on a tractor toolbar because of the increased speed of the tractor compared with the horse. When lifting " earlies," a common arrangement is to have a lifting plough on one end of the toolbar and a harrow leaf on the other, so that as one row is being lifted the last but one row to be lifted is harrowed. Alternatively, for main crops, two lifting ploughs are mounted on the toolbar so that alternate rows are lifted, and the ground is gone over a second time to lift the remaining rows.

The spinner is the commonest potato-lifter in use at the present time. A large share passing below the potatoes loosens the drill so that when the spinner moves the soil sideways the potatoes are left exposed. The tines of the spinner may revolve about a horizontal axis, in which case they are either directly attached to the revolving shaft, or they are mounted in such a way that they are always in a vertical position. Tines with this feathered action do less damage to the tubers than the rigid tines. The spinner may consist of a ring mounted on a vertical shaft and carrying a series of vertical tines. As the spinner revolves, the tines stir the drill and move it sideways where a subsidiary spider spinner assists in the separation of the haulm weeds and soil from the potatoes. Most spinners are driven through gearing from the land wheels, but a few are now being made with power shafts for coupling to the tractor p.t.o. The power-driven spinners may be trailed machines or they may be mounted on the tractor and raised and lowered into work on the power lift. Some of the larger machines are equipped with a self-lift similar to that found on tractor ploughs.

The elevator digger consists of a flat broad share for lifting the drill on to a rod-link elevator or web, which as it passes backwards and upwards is agitated by eccentric sprockets and effects a separation of potatoes from the rest of the drill. The rear part of the web slopes downwards and delivers the potatoes into a narrow band on the ground. Nowadays the web is nearly always driven from the tractor p.t.o. The share is set so that it passes just below the lowest potatoes in the drill and the amount of agitation given to the web is adjusted so that it is sufficient to give a clean sample of potatoes. Excessive agitation bruises the potatoes and results in rapid deterioration of those parts that are expensive to replace, namely the web and its supporting cones and rollers. In wet and sticky conditions the web may be run in two parts, a long front section and a shorter rear section. The slight drop from the front to the rear sections assists in cleaning the potatoes. Some diggers are fitted with a gear box which enables the speed of the web to be varied to suit the soil conditions. The elevator digger does its most satisfactory work on the lighter soils where, if properly set, it leaves the potatoes more exposed and more conveniently placed for gathering, does less damage to the potatoes and leaves fewer " harrowings " than either the plough or the spinner. On heavy land or under wet conditions so much soil may pass over with the potatoes that the digger has to be discarded in favour of the plough or spinner. American experience with elevator diggers suggests that gathering is easier, and therefore quicker, behind a two-row elevator digger than behind a single row, because with the produce of two field rows put into a single narrow band on the ground the picker gathers twice as much at each " stooping " as when gathering from a single row. Only a few two-row diggers are in use in this country, but an effect similar to that of a two-row digger can be obtained with a single-row machine if special large deflectors are used behind the elevator. A French digger has an adjustable cross conveyor behind the main elevator which enables the produce of three field rows to be placed in narrow bands close together so that they can be gathered as a single row.

The high rate of wear and tear on the web and rollers, with the consequent heavy maintenance charges, has led to the development of two other types of lifter which have an effect similar to the elevator digger but are not subject to rapid deterioration. One type has a revolving drum as the cleaning mechanism and the other has a system of reciprocating grids. Both of these are recent developments and are not yet in common use, but, provided they do not damage the tubers, it is probable that they may become attractive alternatives to the elevator web.

Complete potato harvesters are still being developed, and although those already on the market work reasonably well under favourable conditions, they are seriously affected by adverse weather and soil conditions and cannot therefore be relied upon to harvest the potato crop irrespective of the conditions. A complete harvester has a difficult task to perform: it has to lift the crop, free it from about 400 tons of soil, stones, haulm and weeds for every acre lifted, and put the potatoes undamaged into bags or vehicles. Most complete harvesters are built around the elevator potato digger and therefore have all the defects usually associated with this type of digger: blockage and spillage at the share; rapid wear of web and rollers, especially in sandy soil; and damage to the potatoes when agitation is excessive. The digger lifts the whole of the drill, including the haulm and weeds. The potatoes, clods, stones, haulm and weeds pass from the elevator on to a haulm-removing web, similar in construction to the main web except that the links are wide apart to allow potatoes and material of similar size to fall through on to another conveyor, and which drops the haulm and large weeds on to the ground at the rear of the machine. Clods and stones, small weeds and short pieces of haulm are removed by hand from the delivery conveyor of the harvester. If the soil is wet and very cloddy or stony it may be impossible to remove all the foreign matter from the delivery conveyor. Other types of cleaning mechanism which do not have the same disadvantages as the elevator web are incorporated in some harvesters. One make of harvester has a large saucer-shaped grid which is tilted and revolves with the lowest part of the edge behind a long, flat, lifting share. The potatoes roll over the grid as they are elevated, and the soil falls through. This mechanism is satisfactory on light sandy soils at a forward speed of not more than about 1¼ m.p.h. provided all haulm and weeds have been removed beforehand. On another make of harvester a power-driven spinner throws the drill on to a web similar in construction to a haulm removing web. Soil, stones and potatoes fall through the web into a bucket conveyor which elevates them on to an agitated chute leading to a vehicle. Loose, friable soil falls through the bucket conveyor and the agitated chute deals with clods. A recently developed harvester utilises two rotary elevators, one behind the other, to take the drill from the share on to a picking platform. Each elevator consists of a centre plate to the edge of which are attached a number of articulated tines. As the plate revolves loose soil falls through the tines and the potatoes and remaining rubbish are elevated on to the picking platform. Most harvesters are trailed machines, but one incorporating a rotary drum cleaner is built around the tractor. The cleaning problem on harvesters can be alleviated by reducing the amount of soil lifted. Potatoes are concentrated within a strip extending to 9 in. on each side of the original seed and it is therefore unnecessary to lift the whole of the drill to secure the potatoes. The lower edges of the drill are best left on the ground because they hold the soil that has been compressed by the harvesting outfit and by the tractor wheels during the inter-row cultivations and do not contain potatoes. Discs in front of the conventional flat share of the elevator digger can be set to pare away this soil, or a scoop-type of share which takes the centre of the drill only, can be fitted. Haulm frequently causes blockages in harvesters. Two corrugated disc coulters fitted in front of the share cut through the haulm and reduce the amount that passes to the digger. A special haulm-remover, consisting of a power-driven knife-bladed rotor, removes most of the haulm, leaving only the base of the shoots to pass into the harvester. A haulm-puller is being developed, so that even with early potatoes the shaws can be completely removed. The work of all harvesters in main crops or where the haulm has been burnt down can be simplified by using a horse rake to collect most of the dead haulm.

SORTERS.—Potatoes for sale have to be graded according to size usually into three grades—chats, seed and ware. The grading is done by passing the potatoes over square-mesh riddles of two different sizes. The potatoes falling through the smaller mesh are chats; those falling through the larger mesh but remaining on the smaller mesh are seed; and those remaining on the large mesh are ware. The simplest sorter consisting of two hand-shaken sieves is only suitable for dealing with small quantities of potatoes. For larger quantities, hand-operated or engine-driven machines are used. These have either reciprocating flat or rotating cylindrical riddles. The flat riddles are arranged above one another. The ware passes over the top riddle on to a conveyor where blighted or damaged potatoes can be removed before the sound potatoes are put into bags. The seed is taken off the second riddle while the chats fall through and are collected from a small chute at the base of the machine. Machines used for grading potatoes grown for seed, *i.e.* where there is a high proportion of seed-size tubers, are usually arranged so that the seed also travels along the delivery conveyor, which is then divided longitudinally into two sections, one for ware and one for seed. This arrangement allows defective seed potatoes to be removed by hand. The wall of the cylindrical sorter is made of square-mesh riddles, the smaller mesh being near the feeding end. As the potatoes pass through the cylinder the chats and seed fall through the appropriate riddles and pass down chutes into receptacles, and the ware falls out at the lower end of the cylinder on to a delivery conveyor. Some American sorters work on a principle quite different from that employed on British machines. The actual grading portion consists of several diabola-shaped rubber sections mounted on a shaft. Two or more of these shafts placed side by side form a series of holes the size of which varies with the distance between the shafts. The diabola-shaped sections are of two sizes, one for removing chats and one for removing seed. All rollers rotate in the same direction so that the potatoes move up a slight incline as they pass from the chats rollers to the seed rollers. Chats and seed fall through on to their respective flat rubber conveyors which project from the side of the machine, and the ware passes over the end of the grading portion on to another flat rubber conveyor. The seed and ware delivery conveyors are of sufficient length to permit hand sorting. The extensive use of rubber in this machine probably results in less damage to the potatoes than occurs with wire mesh riddles in reciprocating and rotary sorters.

CHAPTER XII

SURPLUS POTATOES ON THE FARM

NORMALLY there is a proportion of small, damaged and diseased tubers that are used each season either on the farm for feeding to stock or sold for the same purpose, there being generally a steady market for such tubers in many districts. Periodically, however, the yield of the potato crop is such that much more is produced than can be consumed. When this happens, growers often reduce their acreage the following year, so that less seed is set aside for planting, and this adds to the surplus. The problem, therefore, is, " What is to be done with this surplus ? "

The increased supply causes the price to fall to such a low level that the surplus potatoes become a more economic food for stock than the usual feeding stuffs; hence more and more ware tubers are withdrawn from the market to replace these cattle feeding stuffs. If this tendency continues, however, there comes a point when no more potatoes can be consumed as stock food before they deteriorate in storage, a process which rapidly sets in after sprouting begins in spring. Before we can profitably discuss ways and means of preserving the potatoes until such time as they can be fed to stock, however, we must have some knowledge of the composition of the tubers.

COMPOSITION OF POTATOES.—As with other crops, there is a considerable variation in the amount of dry matter in different samples of potatoes, the average figure being about 25 per cent. The factors that influence the percentage of dry matter are: (1) the variety, (2) season, (3) soil, (4) manuring and (5) cultivation, *e.g.* time of planting and lifting. The dry matter is highest in dry seasons and soils, and when a well-balanced complete manure (without too much nitrogen) is applied ; it is high also when planting is done comparatively early and the crop is fully matured when lifted.

Among varieties, " earlies " have usually rather less dry matter than the late, maturing kinds, although there are variations within each group as will be seen from the results given below of trials carried out recently when all varieties were planted at the same time, grown under similar conditions and lifted when fully matured. In these trials early varieties such as Doon Early and Ninetyfold had only from 17 to 18 per cent., whereas Epicure and Arran Pilot had 20 per cent., and Duke of York and Sharpe's Express reached 23 and 24 per cent. dry matter respectively. Among second early varieties tested, Ally gave the least dry matter with 20 per cent. ; British Queen, Alness and Arran Comrade were equal with 22 per cent. ; while the rather later Great Scot had 24 per cent. of dry matter. Of the maincrops, King Edward and Majestic gave 22 per cent., Arran Chief and Gladstone 24 per cent. ; Redskin, Arran Consul and Doon Star were equal with only 21 per cent. dry matter ; while Dunbar Standard and Kerr's Pink had 25 per cent. and Golden Wonder 28 per cent.

Starch is by far the chief constituent of the dry matter of potatoes being present to the extent of from 80 to 85 per cent., average figures for the small amounts of other substances in the fresh potato being as follows :—

Protein	1·5 to 2·5 per cent.
Fat	0·1 ,, 0·2 ,,
Fibre	0·6 ,, 0·9 ,,
Ash	0·8 ,, 1·0 ,,

The ash of potatoes is low in lime and phosphates but there is a fair amount of potash, so that unless the other foods used are rich in these constituents it would be well to include a small quantity of " minerals " in the ration for young growing animals.

Potatoes are therefore comparable in composition to such carbohydrate feeding stuffs as barley meal and maize. It may be taken generally that one part of these foods is equivalent to about three and a half to four and a half parts of potatoes. As, however, potatoes are bulky, more work (and consequently more expense) is entailed in preparing them, so that from the financial point of view the value of potatoes would average about one-fifth that of barley meal or maize ; if they are obtainable, therefore, at less than one-fifth the price of these two foodstuffs they are cheap feeding.

USE OF POTATOES AS STOCK FOOD.—Feeding potatoes are usually given to pigs and are often known as " pigs' potatoes," " broke " or " chats " ; it is only when they are plentiful that they are given to other kinds of stock. Potatoes are highly digestible and may be successfully fed raw to cattle or sheep, but are better steamed for pigs. In any case care must be taken that the tubers are clean, for if much soil adheres to them they may induce digestive troubles. It should also be remembered that when fed raw there is a danger of hungry animals choking, especially with medium-sized tubers ; it is therefore advisable to slice the tubers before mixing them with other foods. Mixing with other foods serves another purpose in reducing the laxative effect of potatoes, and for the same reason potatoes should be fed at first only in small amounts which may be increased gradually until the maximum is reached.

When there is a proportion of diseased tubers to be fed it is much safer to boil or steam them beforehand. This avoids the return of the disease to the land in the manure and, incidentally, facilitates the mixing with other foods. Very often, especially near the end of the season, many of the tubers have developed sprouts and these contain a small amount of a poisonous alkaloid called solanin. This substance is greatly increased in tissues exposed to light, so that green sprouts should be removed and " greened " tubers should not be used at all as stock food.

Cooking of Potatoes for Stock.—Provision is made on many farms for the cooking of potatoes for stock-feeding, whilst the " pig's-pot " or " hen's-pot " for boiling potatoes and miscellaneous foodstuffs is an institution on most small farms. Numerous experiments at different American Stations have shown that cooked potatoes are superior to raw potatoes when fed to pigs. Similar results have been obtained in Northern Ireland and at Reading. After being washed, potatoes may be cooked either by boiling in an ordinary copper or by steaming, the latter method being the more economical and convenient for use on a large scale. Steam is best obtained from an approved type of upright boiler, which is usually powerful enough to supply steam for several steamers, each capable of holding up to 10 cwt. of potatoes. A suitable type of force pump must be fitted so that the water supply can be maintained in the boiler without reducing the steam pressure as, if the latter has to be reduced to permit of the addition of water, it is necessary to let the fire down, a procedure which entails much delay. It should also be possible to tip the potatoes, when cooked, from the steamers into convenient receptacles so constructed that the contents can be easily removed.

When filled and the lid securely fastened, the steamer is turned upside down and steam admitted. The cooking lasts from twenty to forty minutes, depending upon the size of the steamer, and, as a certain amount of liquid escapes during the process of steaming, drainage must be provided. The cost of steaming potatoes in this way is from about 12s. to 20s. per ton. Cooked potatoes decay if kept too long, hence it is not advisable to prepare large quantities at any one time. A supply sufficient for two days will generally be found to be most convenient and economical.

Use of Potatoes for Feeding

Both experiment and experience have shown that young pigs require a rich protein diet, so that only a small amount of potatoes, about 4 lb. per day, should be used along with such protein foods as fish meal, soya meal, ground-nut cake and cotton-seed meal. As the animals grow older, up to 6, 8 or 10 lb. of potatoes should be included and the protein reduced. In the case of fattening cattle weighing about 9 cwt., 40 lb. of cut tubers per day may be given along with other suitable foods, a small quantity being given at the start. If given to dairy cows the potatoes should be fed after milking to ensure that the milk is not badly flavoured. Potatoes are not often fed to sheep but they can be successfully used as food for this class of stock; 2 to 3 lb. per day for the younger animals and up to 4 or 5 lb. for fattening sheep can be given without harmful effects. Potatoes are frequently given to poultry, in which case the tubers are usually fed in the cooked state and mixed with other foods. For laying hens about 25 per cent. of the ration may be given in the form of potatoes, while for fattening purposes even more may be used with success.

Potato Silage.—Most surplus potatoes are available when dressing is in full swing during fresh weather in the winter and early spring months; during late spring and summer there is a lean time before the arrival of the new crop.

It is well, therefore, during the time of plenty to provide for the period of scarcity. When the surplus is sufficiently large, provision may be made to ensile or dry the potatoes. They can be ensiled either alone or mixed with grass or any other suitable green material that may be available, different types of silos being used for these purposes.

TANK SILO.—This type is very common on the Continent and may be made either of cement or brick lined with cement. The tanks may be of different shapes, some being long and narrow and others rectangular or square; they should not, however, be more than 3 or 4 ft. deep or there will be difficulty in removing the silage.

The method of filling depends upon the shape of the tank. The long narrow tanks have partitions fixed at intervals so that each section may be filled separately and independently. After the potatoes are washed and steamed, they should be put into the tank as hot as possible and well packed, tightly, so as to exclude air. If there is not sufficient material to fill the tank at one operation, the short type should be filled in layers. After a layer is put in, the potatoes should be covered with empty sacks to exclude air until the next filling. When the potatoes are about 3 or 4 in. from the top of the tank they should be covered with a layer of straw and several inches of soil and, finally, boards or corrugated iron sheets should be placed over the tank to act as a roof to exclude rain.

PIT SILO.—This type can be used either for the mixed silage or for potatoes alone. A level position should be selected for such a silo and it should be situated conveniently both to the steamer and to the piggery when potatoes are ensiled alone. Where there is danger of water collecting at the bottom, drainage should be provided. The usual depth of a pit for potatoes alone is 2½ to 3 ft. and the sides should slope slightly inwards. The width at the top should be about 6 or 7 ft. The length will depend on the amount of material to be ensiled, about one yard being allowed for every 20 to 24 cwt. of tubers. In order to keep the product clean, the sides and bottom should be lined with straw.

As in the case of the tank, the potatoes should be put into the pit as hot as possible and well packed. After the pit is full the material should be ridged up like a potato pit or clamp, beginning at the ground-level, and then covered with straw in order to keep out earth. The straw should be spread lengthways from top to bottom so that a thatch is formed which will help to exclude rain. Finally, a layer of 10 or 12 in. of soil should be placed on the straw.

Potatoes alone, ensiled in tanks or pits, will keep in good condition for at least two years. Although there is little or no loss of liquid from the silage, there is some loss of weight, the cause of which is not known. Such silage may be fed to pigs in the same way as ordinary cooked potatoes. There is some difference of opinion as to comparative values, but practical experience indicates that 2 to 2½ lb. of the silage are equal to 4 lb. of freshly cooked potatoes.

When sound and clean, raw potatoes may be similarly ensiled, but they must first be sliced. Two days before the filling begins, a quantity of maize meal should be saturated with water and allowed to become sour; the mixture, however, should not be sloppy. The maize stimulates the necessary fermentation by inoculating the potatoes with lactic acid bacteria. The sour maize meal should be mixed with the sliced potatoes as they are placed in the pit, the proportions being 1 cwt. of the meal to 1 ton of sliced tubers. The pit is completed with straw and soil in the manner described for ordinary pit silage. A very considerable shrinkage takes place during the fermentation process; hence, in comparison with steamed silage, less raw ensiled potatoes are required to replace a given quantity of meal. This type of silage is suitable for pigs and cattle.

MIXED SILAGE.—The mixed potato and grass silage may be made either in a clamp or on the level. A clamp is similar to a pit, being usually made 2 ft. or so under the level of the ground; but the ends may be open, and it is better made on a slight slope thus providing for drainage and facilitating removal of the silage material.

Mixed silage is largely used in Holland, where it originated, and it is suitable only for fattening cattle and cows. Its preparation requires a supply of young grass and clover, of which, however, there is little to be had when most of the potatoes are available. It would be well, therefore, to prepare beforehand by sowing a mixture of grass and clover seeds with a large proportion of Italian ryegrass, and to give the field a good dressing of a nitrogenous manure as early in the season as possible; by doing so, grass would be available several weeks earlier. For later use it would be better to have another mixture without much Italian ryegrass, but with perennial ryegrass instead, so that there would be a chance of getting a larger proportion of red clover and so enable a silage to be made with a higher protein content. If the potatoes have to be stored until the grass is ready for use, it is likely that desprouting will have to be carried out before the tubers are put into the silo.

About 2 tons of green material are necessary for each ton of potatoes. The site for the silo should be sufficiently wide to enable carts or a tractor to be taken over the heap. A layer of about a foot of green material should first be spread evenly, and on this is a layer of potatoes, also evenly distributed. This is again followed by a layer of grass and so on in alternate layers, the last being grass, until sufficient height has been obtained, usually about 3 ft. above the level ground. A layer of grass fully a foot wide should be built along the sides and should extend about a yard beyond each end. Consolidation is secured by running a cart or tractor, preferably with caterpillar tracts, over the heap continuously from the outset. The ends should be squared up by cutting the material and throwing it on the top of the silo.

On the day after the filling is completed a layer of from 10 to 12 in. of earth should be placed on the top and a similar amount at the sides and ends. If the work is properly done, very little wastage will occur. The temperature of the silo will rise considerably, sufficient partially to cook the tubers. Silage made in this way will keep for at least two years, the potatoes remaining quite sound. Cattle and milch cows consume it readily but the grass makes it unsuitable for pigs.

DRIED POTATOES.—Before the war there was a surplus of potatoes and several factories were erected throughout the chief potato-growing districts for the purpose of drying them. In addition at several sugar-beet factories after the normal operations were finished, potatoes were dried. It may be supposed that if there is a large surplus again some of it may be dried for stock food.

Dried potatoes make a very good mixture with other foods and, being easily digested, agree with all classes of animals.

It may be taken that 100 lb. dried potatoes are equivalent to about 350 to 400 lb. of raw potatoes. Dried potatoes should be soaked in water before feeding, or in milk if the latter is plentiful; skimmed milk in particular, which can often be obtained cheaply, is very suitable. When it is intended to feed the dried potatoes to pigs it is as well to boil the milk before adding it to the tubers. Factory-dried potatoes may thus form a useful addition to the diet of stock and have an advantage over the previously described forms of storing surplus potatoes, in that all that is required to ensure long keeping is that they should be stored in a dry, well-ventilated place.

CHAPTER XIII

THE COOKING QUALITY OF POTATOES

THE main food constituent of the potato is starch which represents from 12 to 18 per cent. of the total weight. Other food constituents include proteins, vitamins and minerals. The proteins, although not present in any high degree, are very valuable from the point of view of nutrition; the potato has a relatively high content of vitamin C and its minerals have considerable dietetic value. These qualities, together with the highly digestible nature of cooked potatoes, make the potato a valuable food.

Before the war we consumed more than 8½ oz. of potatoes per head per day. In other countries the consumption was much higher: in Belgium the average was about 19 oz., in France and Germany about 17 oz., and in certain States the figure was as high as 26 oz. The consumption of potatoes has risen very considerably since 1939 and, as cooking quality has an important bearing on consumption, a brief examination of some of the factors involved and results obtained from experimental work will not be out of place. No attempt, however, will be made to follow in detail chemical processes or to review the results of investigations which as yet are incomplete.

COOKING QUALITY

The meaning of the expression "cooking quality" must be clearly understood. There is, unfortunately, no standard objective method of judging the character, hence much of what is written on the subject is confusing owing to the idiosyncracies of taste in writers. Tastes vary in different countries: in some, yellow-fleshed, non-mealy potatoes are preferred, while in others exactly the opposite qualities are normally demanded. In this country, opinions vary as between individuals and also as to the purpose for which the potatoes are required. Thus, new potatoes and mature potatoes are judged by different standards. The criterion of quality for chipping differs from that for boiling or steaming. There are, nevertheless, certain characteristics which most consumers in this country prefer, and this is reflected in the higher price paid for ware of certain varieties and from certain soils.

For boiling or steaming, a potato should be mealy, retaining its shape when handled, but easily crushed into a dry, crumbly mash ; it should not break down on cooking and a glutinous, waxy texture is a serious fault ; it should be uniform in colour —white to pale yellow being preferred—and without darker patches ; the flavour should be definite, not stale or earthy, and the taste not insipid. Chips should have sufficient potato flavour to retain their taste in combination with the oil but should not taste earthy ; in consistency, they should break cleanly, be mealy and not waxy ; they should retain their firmness for at least thirty minutes after cooking ; in colour, they should be golden brown without patchiness. Potatoes which have low dry-matter contents may lose 45 per cent. and more of their weight when chipped. This allows for the fat absorbed and represents the difference in weight between the raw chips put into the chipper and the cooked chips taken out. Such potatoes are wasteful of fat which is absorbed in greater degree as the amount of expelled water increases. In general, the qualities required in baked and roasted potatoes are similar to those in potatoes which boil well. For crisping, yellow-fleshed tubers which do not colour unevenly are in demand. Apparently only the best-boiling potatoes produce the best potato mashed powder. Hirst and Adam [1] stress the importance of firm texture and absence of cracking and breakdown in potatoes used for canning.

It is clear from the above that quality is a composite character which can be discussed only in relation to the purpose for which the potatoes are required. The main components, however, are mealiness, consistency (*i.e.* the retention of shape combined with ease of mashing), colour and flavour. Because potatoes are usually eaten with more strongly-flavoured foods, flavour, except it be an unpleasant one, may be the least important of these characters.

MEALINESS AND CONSISTENCY.—These two characters are interrelated. Mealiness depends ultimately on the ease with which the cells of the potato separate from one another on cooking so that they become piled up in a loose flour, with air between them, instead of remaining in a solid mass with water in the small intercellular spaces. There is no definite evidence as to how the cells become piled up in a loose flour, further investigation being necessary here, but the character does not appear in potatoes which have low starch contents, *e.g.* immature potatoes. Mealiness and high starch content are associated in American literature with high specific gravity, an association which appears to hold also in this country. Disruption of potatoes in cooking is partly explained by the turgidity of the tissues: the more turged they are, the more easily do they fracture and permit the ready penetration of the boiling water.

COLOUR.—The two main discolorations which appear in cooked potatoes are:—

(*a*) The browning of chipped, fried and crisped potatoes brought about by the caramelisation of sugars, and

(*b*) The blackening or greying of raw tubers, and blackening or greying of cooked potatoes.

Varieties differ in the amount of sugar they contain but the principal cause of high sugar contents is chilling. Where the chilling has not been too severe, storage in warm conditions for some time generally enables the potatoes to become normal again, *e.g.* ten to twenty days at 27° C.

By far the most important type of discoloration is blackening or greying.

When a raw potato is cut and exposed to the air for some time, the cut surface gradually reddens and ultimately turns grey. The chemical changes are complex and are brought by the enzymatic oxidation of tyrosine and O-dihydric phenols into a black compound, melanin. The condition of "bruise," or blackening of potato tissues, appears to have been described first by Horne [2] who found the phenomenon fairly frequently in the late storage season. Dutch workers, [3, 4, 5] investigating the condition described as blueing associated this with the bruising, more particularly of potash-deficient tubers which had lost turgidity. McIntosh [6] and Scott [7] found that blackening of tubers could be obtained by bruising not long after harvest. Mulder [8] states that two factors are responsible for the extreme tendency of potassium-deficient tubers to blacken, viz. the high content of free tyrosine and the liability of cells to sustain injury. Boyd [9] has shown that tubers must be in a relatively flaccid condition before blackening can become serious. He demonstrates also that susceptibility is greatest at the heel end and least at the rose end, and describes factors which render tubers more susceptible to the effects of bruising. Extremes of temperature may cause blackening of tuber tissue, *e.g.* chilling, while an excessively high temperature combined with lack of aeration may produce the condition known as Blackheart.

All the above-mentioned discoloration found in the uncooked potato is attributable to the formation of melanin and is important because it does not disappear with cooking.

The blackening of undiscoloured potatoes after cooking and exposure to air—often referred to as stem-end blackening as it is most frequently found in that region—is not due to melanin. The pigment appearing in cooked potatoes has been found to behave differently from melanin[10, 11]. Blackening after cooking is now attibuted by many authorites [8, 11, 12, 13] to the oxidation of ferrous into ferric compounds. Juul [13] states that the discolouring compound contains iron and O-diphenol. Wager [14] concludes that stem-end blackening is caused by a single pigment whose colour is reversibly affected by *p*H and that variation in the degree of blackening between different stocks is due to the appearance of different amounts of this pigment. In American literature, the appearance of blackening and high *p*H value are often associated. Wager,[15] however, is of opinion that the effect of a high average *p*H serves only to intensify the blackening and that no evidence suggests that the *p*H of the tubers influences the amount of the stem-end blackening pigment. Juul [13] supports Wager's statement about the intensifying effect on the discoloration produced by high *p*H values and draws attention to the fact that the latter are highest at the stem ends. Both he and Mulder [8] agree that discoloration increases with the N/K ratios of fertilisers.

Tinkler [16] and Wheeler [17] have described chemical methods for pre-determining the disposition of tubers to blacken on cooking. Although such tests are interesting, the most reliable test available is cooking itself.

FLAVOUR.—Nothing is known definitely of the causes of flavour in cooked potatoes. Little investigation has been made on this subject. Burton [18] suggests that the strength of the potato flavour may be related to the content of oil. Rathsack [19] has concluded that it depends upon the content of mineral salts and upon the ratio between the contents of potassium and nitrogen. There is, however, one definite aspect of flavour: the burned taste which occurs sometimes in chipped, fried and crisped potatoes is due to the presence of sugars, hence the sugar content in potatoes to be used for these purposes is important.

Factors Influencing Cooking Quality

The Cooking Process.—Cooking may diminish or enhance quality: very rapid boiling, for instance, promotes disintegration. As soon as potatoes are cooked anything which facilitates drying increases mealiness, hence the advantages of careful draining and partial removal of the cover of the cooking utensil to enable steam to escape. The losses of foodstuffs sustained in cooking depend on the methods adopted: unpeeled lose less than peeled potatoes; steaming causes less loss than boiling; and baking and frying cause smaller losses than boiling or steaming. After boiling, the water content of the tubers is slightly higher and the starch, nitrogen, sugar, mineral and vitamin C contents are lower than before cooking. Cooking in salted water seems to conserve more vitamin C than cooking in unsalted water. According to American authorities [20] the addition of calcium salts to the cooking water prevents the disintegration of tubers showing this tendency. Hirst and Adam [1] report that soaking potatoes in a 2·6 per cent. solution of hydrated calcium chloride greatly improved the texture of canning potatoes from certain soils. At Long Ashton [21] it has been found that the colour of potatoes which blacken when boiled in the usual way can be improved by the addition of one tablespoonful of vinegar to each quart of the cooking water and the blackening can be almost completely controlled if, in addition to the vinegar, ½ gm. sodium meta-bisulphite (1 Campden fruit-preserving tablet) is added. There is, however, some loss of flavour and flouriness when this treatment is used.

Variety.—Of the factors determining cooking quality, the variety is in many respects the most important. Some authorities rank site (districts and general soil characters) as being more important than variety. It is probable, however, that data on this point may be influenced by the varieties used for test as, with indifferent quality varieties, the environment effects are more pronounced than with good quality ones. All the major components of quality—mealiness, consistency, colour and flavour—are affected by variety. Sugar content and tendency to blacken are also varietal characters. The requirements for boiling and chipping are not precisely the same, hence some varieties are good boilers and only fair chippers and *vice versa*. For boiling, some varieties, *e.g.* Golden Wonder, are excellent; others, *e.g.* Arran Chief, Kerr's Pink and Dunbar Standard are very good; others, *e.g.* Arran Banner and Great Scot are not so good; and others again vary, for example Gladstone is good at the beginning of the season but may fall off in quality about New Year. The quality of certain other sorts, *e.g.* Ally and King George, can be characterised as poor. No variety, however, is constant in composition and quality. These characters vary with the environment but where a number of varieties are grown in one place and on the same soil, the order of quality is generally fairly constant. The most desirable of the good quality varieties are those least affected by environment and thus most consistent in their characters. It is possible, for instance, in two seasons and with one variety, *e.g.* King George, to have both the good and the poor quality, and, in the same two seasons, to have consistently very good quality in other varieties, *e.g.* Golden Wonder.

CLIMATE.—This is a very important factor. In some northern countries quality is reputed to be poor, probably owing to the short growing season and the immaturity of the tubers when lifted. In hot climates, quality is also stated to be poor and it is possible that the length of day may have an effect. Variations in sunshine, rainfall and temperature during the growing season undoubtedly affect cooking quality but it is difficult, if not impossible, to separate these always from the remainder of the environment, *i.e.* the soil.

In dry years and districts the quality of potatoes in this country is usually good and in wet seasons it is generally inferior. It is noteworthy that in Great Britain the best quality potatoes are stated to come from the eastern and dry districts, *e.g.* Dunbar, Lincolnshire and the Humber area of Yorkshire and not from the west coast or the wet districts. The distribution of the rainfall during the growing season is doubtless important: wetness in the early period does not seem to have the same detrimental effect as wetness nearer maturity, the explanation probably being that environment exercises its greatest effect on tubers when they are swelling. Wager [15] found that the average dry-matter content of a variety varied from season to season, but it always bore an approximately constant relationship to the average value of other varieties. Wet seasons, however, led to potatoes with low dry matter. Wet seasons favour Blight and so may affect quality adversely through the destruction of the haulms before tubers are mature. Immature tubers have never the same high quality as mature tubers. Nash and Smith [22] have dealt with the question of sunshine. They shaded certain plots periodically to reduce the light intensity to that of a very cloudy day. In general, the shading was found to decrease specific gravity, dry weight and mealiness, while in plots to which nitrogen had been added the incidence of blackening was increased. In warm summers, quality is generally good, but such summers are usually also dry. Evidence given by Smith, Nash and Dittman [23] shows that the average air temperature for the three weeks preceding the lifting of the tubers, or the death of the tops, controls the development of stem-end blackening in the tubers, and the authors claim that this is an overriding factor. In their experiments, little or no blackening developed when the average air temperature was between 70° and 80° F.; when between 60° and 70° F., there was a medium development and, when between 50° and 60° F., there was much blackening. Wager,[24] in dealing with this matter suggests that under English conditions, temperature is not the controlling factor in the development of tubers with a liability to blacken. It may, however, either increase or accelerate the production of precursors of the stem-end blackening pigment given the presence of certain other unknown factors. Juul,[13] working in Denmark, found that blackening after cooking was inhibited by early lifting or destruction of the foliage. The dominant factor in blackening appears to vary seasonally, the incidence over the whole country being in some years negligible and in other years severe.

Early frosts which kill the foliage prematurely have the same effect on quality as Blight, producing immature tubers.

So far as climate can be judged as a whole, the best quality potatoes in Britain are produced in years when the rainfall during the latter part of the growing season is small and there is plenty of sunshine and warmth.

SOIL.—Findlay [25] has reported on the quality of potatoes grown on sand, clay and peaty soil transported to Craibstone to make up plots alongside each other. He found that sandy soils gave better quality than clay or peat. In a wet season, the quality was worse in the clay soil potatoes than in those grown in peat. Loams were not investigated. Certain authorities [26] state that the influence of soil on potato quality lies mainly in its effect on consistency and that flavour is apparently unaffected. These writers state that Dunbar red soil gave better consistency in boiled potatoes than medium heavy silt, oolitic limestone, sandy loam and black fen, the last two producing the worst quality. However, as the soils on which the potatoes were grown were situated widely apart, the climate might influence results, hence the differences may not have been conditioned by the soil alone. Crowther [27] reports that the Woburn light soils invariably give better quality than Rothamsted soils. Elsewhere [1, 28, 29] similar results have been recorded.

In reporting an investigation to determine the quality of potatoes in relation to soil and season, Wager [15] stated that the average content of dry matter of potatoes depends on the soil on which they were grown, fen and blackland giving potatoes with low dry matter, followed by skirt, silt and warp, then loam and medium loam, then clay, and the highest dry matter occurring in stocks grown on sands, gravels or light loams. He concluded, tentatively, that the factor responsible for the variation in content of dry matter in potatoes is the available water content of the soils. Wager [15] has also reported that the average amount of blackening in samples from different soil types differ significantly and that samples from fen, blackland, sand, gravel, limestone and chalk blackened more than those from skirt, silt, warp, clay and boulder clay. He also found evidence of an effect of soil type on the amount of yellow pigment in tubers and concluded provisionally that potatoes from clay and red soils were yellower than those from other soils.

General observations indicate that, as with climate, varieties vary in their response to any soil type.

The question as to how soils influence quality is a very complex one, particularly having regard to the interactions of the various components of the total environemnt. However, where there is an early supply of nitrogen, the plant is able to build up much carbohydrate, but, if the soil supplies much nitrogen late in the growth, a potato rich in nitrogen is obtained. In open soils, the oxidation of organic matter proceeds so rapidly that much is available in the early stage but with little to follow later. This, presumably, gives a potato relatively rich in carbohydrate because the maturation process of the plant is not postponed by continued uptake of more and more nitrogen which makes for vegetative growth. Rich peat soils and newly ploughed leys often give poor quality, a fact which may be associated with high nitrogen and low potash. The effect of soil acidity on quality has not been studied. Wager,[15] however, concludes that the *p*H of the expressed sap of tubers is independent of the type of soil on which the potatoes are grown.

MANURES AND FERTILISERS.—Work at Long Ashton[30, 31, 32] has suggested that the quality of potatoes is largely determined by factors other than manures. The application of the latter produced only a limited improvement where the quality was initially poor, but on better " sites " the application of manures may be helpful in decreasing blackening. On poor " sites " (the term " site " includes district and general soil characters), fertilisers have little effect on quality, but on better " sites " the effects are of greater magnitude. On the latter, potash, applied mainly as muriate, has improved both colour and texture, whilst phosphate has increased mealiness. The effects of nitrogen on blackening have been inconsistent, and when nitrogenous fertilisers have been used at both excessive and inadequate levels, the tubers have been close-textured and lacked mealiness. Within the limits set by the " site " the correction of deficiencies gave some improvement in general quality. Dung decreased blackening on potash-deficient soils but also tended there to give excessive mealiness, resulting in broken tubers on boiling.

It appears from all the work done on this subject that the balance of fertilisers used is of great importance. Excessive nitrogenous manuring, particularly when potash is short, is detrimental to quality. Mulder[8] and Juul[13] have recently emphasised the significance of potassium-deficiency and high

N/K ratios in relation to blackening. The various types of fertilisers have different effects: sulphate of potash is the best of the potassic manures while chloride-containing salts, such as muriate or potash salts, are not so good for quality; of the nitrogenous fertilisers, sulphate of ammonia seems to be the least detrimental to quality. Superphosphate [27] is reported as reducing the nitrogen content of the dry tubers in years in which it greatly increases the yield and the omission of phosphates from the manuring has on occasion adversely influenced quality.

Little is known about the effects of the minor elements on cooking quality.

OTHER FACTORS.—Mature tubers are generally of better quality than immature ones. Complete maturity of the crop in late districts is more likely to be obtained if the seed be sprouted and planted early. By such cultural methods, quality can be improved in these districts. The effects of Blight have already been noted; spraying, by controlling the disease, tends to improve quality. There is some evidence pointing to inferior quality in tubers affected with severe virus diseases; as against this, however, such tubers have usually a higher vitamin C content than healthy tubers.

Storage is another factor. Chilling leads to an over-production of sugars, the evil effects of which have already been discussed. Very little investigation has been made into the effect of storage on cooking quality. According to some American workers [23] the amount of stem-end blackening is reduced by exposing tubers to high temperatures, *e.g.* 100° F. for 3 to 4 days. Wager [24] reports that the amount of stem-end blackening increases during storage at +8° C. and that certain samples of potatoes develop much stem-end blackening pigment if stored at low temperature immediately after lifting. Tubers inclined to disrupt on cooking have been found in America to lose this undesirable characteristic after storage for some time in fairly warm conditions when the turgidity of the tissues lessens. The quality of sprouted potatoes is generally inferior if sprouting has been considerable. Anything that can be done to depress sprouting or to organise the quick consumption of rapid-sprouting varieties would help to improve quality in general. Sprout depressants should be useful here.

Tuber shape has an indirect effect on quality: where the eyes are deep and coarse, more of the most floury parts are lost in peeling than occurs in shallow-eyed potatoes. In Kerr's Pink, for instance, the loss on peeling approximates 25 per cent. whereas in King Edward it may be as low as 10 per cent.

General

From the above, the reader will appreciate how complex and uncertain is the question of cooking quality. Much investigation still requires to be carried out and, having regard to the interaction of so many factors, it will doubtless be a long time before clarity on many points is reached. However, breeders can do much to help. It is interesting to note that in the Potato Registration Scheme of the Department of Agriculture for Scotland which both English and Scottish raisers may now enter their new varieties for testing, experts are called in to adjudicate on quality. More could be done also by the industry. Frequently, retailers do not know the names of the varieties they sell and, until they and the public are quality-conscious, the advances will be slower than they need be.

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CHAPTER XIV

SEED POTATOES

SEED potatoes are those planted to produce the new crop and, essentially, they differ in no way from the other tubers of the stock from which they are selected. Commercially, they are drawn from the intermediate-sized tubers, the usual grading including only such tubers as pass through a 2¼-in. and over a 1¼-in. meshed riddle.

This dressing, however, is not altogether ideal as there is too great a difference between the largest and the smallest tubers. It would be much better if there were at least two sizes, say, 1¼ to 1¾ in. and 1¾ to 2¼ in. The small size would suit those who grow ware in England while the larger size would be more suitable for those who grow for seed. This was seen very markedly in many trials carried out at Craibstone where these sizes were compared with the standard seed size. For example, in one trial the variety used was Di Vernon and all the tubers were planted at 12 in. apart in the drills. The ordinary (1¼ dressing to 2¼ in.) produced 2 tons 12 cwt. ware, 9 tons 9 cwt. seed and 39 cwt. chats. The small size (1¼ to 1¾ in.), 3 tons 11 cwt. ware, 8 tons 1 cwt. seed and 27 cwt. chats while the large size (1¾ to 2¼ in.) 2 tons 12 cwt. ware, 11 tons 6 cwt. seed and 37 cwt. chats. With both the large and small sizes not only were the crops more uniform than that produced by the standard seed size, but the small size produced a greater weight of ware (over 2¼ in.) while the large size produced much more seed (1¼ to 2¼ in.).

No aspect of potato growing is more important than the selection of the best possible seed, for the yields obtainable from different stocks of the same variety, under identical conditions, depend more on the quality of the seed planted than on any other single factor. The essentials of a good stock of seed potatoes are :—

(1) *It must be true to Type.*—This involves two different forms of impurities : (a) *Variety.*—The presence of tubers of another variety will give rise to a mixed crop. This may, or

may not, affect the total yield, but will probably cause great irregularity in " stand " and in the time required for maturation. The quality of the ware from such a mixed crop is certain to be affected since different varieties cook differently. Further, the possibility of tubers of a wart-susceptible variety being mixed with a seed stock of an immune variety would be a serious matter to a grower on land contaminated with this disease. The importance, therefore, of ensuring that the seed contains no impurities of this type is obvious. (b) *Abnormalities.*—The crop from which the seed is obtained should not contain abnormal plants which would undoubtedly reappear in the new crop. There are several kinds of abnormal plants, the most common being bolters, wildings and other undesirable variations, these being discussed in Chapter VI. An appreciable number of such plants will certainly affect the yield and will produce an iregularly maturing crop of very unequal vigour.

(2) *It should be carefully graded.*—The standards of size in tubers sold as seed are laid down by regulations and may not be deviated from. The general methods of dressing potatoes have already been considered, but, if possible, even greater care is necessary when dressing for seed than for ware; on this very largely depends the appearance and acceptability of seed consignments. Risk of injury to tubers may be reduced by the use of specially blunted graips for lifting them from the heap or pit on to the riddles. Care should be taken, however, not to use the graips after they are worn, otherwise even more damage may be done by stabbing. Rubber-covered riddles are very useful also, particularly for tender-skinned varieties. All damaged, diseased and misshaped tubers must be removed, and the size kept as uniform as possible; a really good sample of seed will not contain large tubers even though they pass through the regulation riddle.

(3) *It should consist of Tubers as free as possible from Diseases.*—Tuber-borne diseases of the potato are fully discussed in later chapters. Complete freedom from these diseases is not to be expected, but much more can be done than is apparently realised to improve samples of seed tubers in this respect. Some diseases, such as Blight, Powdery or Superficial Scabs, Skin Spot and Dry-rot, etc., are visible on the surface of

the tuber, and the purchaser may refuse to accept delivery of an obviously infected consignment. Other diseases, such as Spraing or Blackleg, may be detected only when the apparently

TABLE XI

Certificate.	1. Standard of Purity.		2. Leaf Roll, Severe Mosaic and Wildings.		3. Mild Mosaic.		4. Blackleg.	
	Per cent.	Rogues per Acre.	Per cent.	Plants per Acre.	Per cent.	Plants per Acre.	Per cent.	Plants per Acre.
A (Scot.) / A (Scot.) N I.	99·5	90 to 120	0·5	90 to 120	2	360 to 480	10	1800 to 2400
H (Scot.) / H (Scot.) N.I.	99·5	90 to 120	2·0	360 to 480	...	...	10	1800 to 2400
Grade B Report	97	540 to 720	2·0	360 to 480	...	...	10	1800 to 2400
S.S. (Scot.) / S.S. (Scot.) N.I.	Including 1, 5 and 6							
1st Inspection	99·9	18 to 24	...	4	0·25	45 to 60	5	900 to 1200
2nd Inspection	99·95	9 to 12	...	4	0·25	45 to 60	5	900 to 1200

	5. Undesirable Variations.		6. Bolters.		7. Semi-bolters.		8. Plants taken out before Inspection.	
	Per cent.	Plants per Acre.	Per cent.	Plants Per Acre.	Per cent.	Plants per Acre.	Per cent.	Per Acre.
A (Scot.) / A (Scot.) N.I.	1	180 to 240	1	180 to 240	...	...	5	900 to 1200
H (Scot.) / H (Scot.) N.I.	5	900 to 1200	5	900 to 1200	...	...	...	...
Grade B Report	5	900 to 1200	5	900 to 1200	...	...	...	...
S.S. (Scot.) / S.S. (Scot.) N.I. / 1st Inspection	Included in 1				2	360 to 480	1	180 to 240
2nd Inspection	...	...	...	...	0·1	18 to 24	...	...

healthy tuber is cut and so may be overlooked both by the grower and his customer. But the most pernicious of the tuber-borne diseases are those due to viruses which produce no visible effects, external or internal, on the tuber, so that the degree of infection of the seed sample only becomes known from the appearance of the resulting crop. Even with these diseases, however, the purchaser is not at the mercy of the seed producer, for the latter is legally bound to supply the buyer with the certificate grade of the consignment, which will indicate the incidence of virus diseases at the time of inspection in the crop from which the seed was obtained. The purchaser is therefore advised to make himself familiar with the precise nature of the information to be gleaned from these certificates ; he should assume that a failure to supply a certificate implies either that the mother-crop was not inspected officially or, if so, that it was adversely reported upon or grown in a district where diseases spread rapidly. The purchase of seed from such a district should be avoided.

CERTIFICATION SCHEMES IN THE UNITED KINGDOM.—Each constituent country has its own Inspection and Certification Scheme, the object being to encourage the growers to produce high-grade seed, true-to-type and as free as possible from virus diseases, and also, by publishing annually a "Register of Certified Crops" to help buyers to select the best obtainable stocks.

SCOTLAND

Table XI shows the essential features of the different classes of certificates issued in Scotland. Similar certificates are issued in England and Ireland. The standards are subject to variation from time to time and growers in their own interests should familiarise themselves with the details.

The number of plants per acre varies from about 18,000 to 24,000 depending on the width of the drill and the distance apart at which the setts are planted. The figures in Table XI give growers some idea of the maximum number of unwanted plants allowed per acre. Of course it is unlikely that all these will be found in one crop.

Crops are considered as unsuitable for seed when

1. the standard of purity is less than 97 per cent., or when (*a*) the crop contains more than 5 per cent. undesirable variations, or (*b*) 5 per cent. bolters, or (*c*) 2 per cent. Leaf Roll, Severe Mosaic and Wildings, or (*d*) 10 per cent. Blackleg.
2. an examination of the roots shows that they are not free from visible infestation of potato root Eelworm.

All certified potatoes sold for seed must be delivered in sound condition and fit for planting. It is an offence under the Sale of Diseased Plants Order to sell or offer for sale for planting any potatoes which are visibly rendered unfit by reason of their being affected by any insect or pest. Inspectors of the Department check the condition of seed going to England from docks, railway sidings and farms, and all seed exported abroad is examined.

All sales of seed potatoes come under the Seeds Act, 1920, and the seller must always give the following particulars in writing :—

1. Name and address of the seller.
2. A statement as to their class, viz. :—
   Certified (Scotch) or Uncertified (Scotch).
3. A statement of the reference letters and number of the relative certificate.
4. A statement of the variety, size and dressing.

There are a few additional conditions in the case of Stock Seed and the chief of these are :—

It will be a condition of Stock Seed Certification in Scotland that the potatoes are grown on land which has been soil sampled and found to be free from infestation by Potato Root Eelworm.

The stocks planted must have been derived from Stock Seed, virus-tested seed or a stock approved by the Department of Agriculture for Scotland.

A crop will not be regarded as suitable for a Stock Seed Certificate unless it is at least 20 yards from the nearest potato crop not obtaining Certificate Standard because of Leaf Roll, Mosaic or Potato Root Eelworm.

All seed sold under a S.S. certificate must be put in new bags and submitted for inspection and sealing by the Department before the potatoes are moved from the farm.

In addition to the ordinary inspection scheme the Department has now a scheme for the certification of virus-tested stocks. In this scheme rigorous conditions are laid down concerning the testing of plants for virus. The raisers' stocks are kept under close observation until they are large enough to be presented for inspection. Only stocks reaching ¼ acre may be presented for inspection and certified crops are awarded a certificate bearing the designation "Virus-tested stocks" which are lettered V.T. (Scot.) or V.T. (Scot.) N.I. for immune and non-immune varieties respectively.

In the next two years certified crops from such seed shall be starred in the "Register of Potato Crops Certified" to denote that they have been once or twice grown from seed derived from virus-tested stocks.

All certificates issued in England and Northern Ireland are in close agreement with the standards adopted in Scotland, the certificates being indicated by the initial letters of each country, thus :—

ENGLAND, WALES AND ISLE OF MAN

S.S. (E) and S.S. (W); A (E), A (W) and A (I.O.M.); H (E), H (W) and H (I.O.M.) for immune varieties.

S.S. (E) N.I. and S.S. (W) N.I.; A (E) N.I., A (W) N.I. and A (I.O.M.) N.I.; H (E) N.I., H (W) N.I. and H (I.O.M.) N.I. for non-immune varieties.

NORTHERN IRELAND

S.S. (Nor. Ir.); A (Nor. Ir.); H (Nor. Ir.) for immune varieties.

S.S. (Nor. Ir.); A (Nor. Ir.) N.I.; H (Nor. Ir.) N.I. for non-immune varieties.

For "H" certificate the crop must not contain more than 0·5 per cent. severe Mosaic or Leaf Roll, or more than 3 per cent. Mild Mosaic. For "S.S." the plants must be killed by having the tops burned off before a specified date.

All seed for export is inspected at the port before it leaves Northern Ireland.

CERTIFICATION SCHEMES IN RELATION TO CHANGE OF SEED.—The scientific principles underlying the need for most growers to change their seed at frequent intervals are fully discussed in Chapters XXVI and XXVII; we are here concerned only with the way in which Certification Schemes can best be used by growers requiring such a change of seed.

The existing Certification Schemes are playing an increasingly important rôle in the improvement of potato stocks in the British Isles, but too much must not be expected of them. It should clearly be understood, for instance, that the health standards adopted in the Schemes refer only to the state of health of the "mother-crop" at the time of inspection; they do not guarantee the state of health of the crop grown from the seed so certified. Indeed, the amount of virus diseases may differ very considerably in crops grown from seed holding the same class of certificate.

The reason for this lies in the fact that virus diseases are spread from diseased to healthy plants mainly by means of "greenfly," most of these newly-infected plants showing no signs of disease, although infected tubers borne on such plants will give rise to obviously diseased plants in the following year. Hence, the state of health of a crop depends not only upon the number of diseased plants in the mother-crop, but also upon the extent to which the mother-crop was infested with vectors, as the insect transmitters of viruses are called. No practicable Certification Scheme has yet been devised which will take into account the relative abundance of insect vectors in different crops. Here, however, the accumulated experience of the past takes a hand, for the old-established precept to "go north for seed potatoes" was unknowingly based on the fact that the exposed areas of the north, or uplands, of Scotland are unsuitable for these insect vectors and, consequently, in such areas there is relatively little annual increase in virus diseases.

Recent work has shown that, in addition to these areas of Scotland, there are districts in Northern Ireland and Eire in which seed of S.S. or (A) standard can be maintained for a number of years without deteriorating from virus diseases. But the quantity of this superior seed is insufficient to plant more than a very small fraction of the total potato acreage of the country. It should be regarded as foundation stock and used only to renovate the stocks in districts which, although somewhat more favourable for the spread of disease, are yet excellent areas in which to produce a good commercially healthy stock of seed potatoes.

These latter areas, situated mainly in central and southern Scotland, provide the vast bulk of commercial seed for the great ware-growing areas of England. By replacing infected stocks with S.S. or (A) seed from the north, or from the uplands, in their own districts, they should have little difficulty in producing seed of (H) standard, whilst most should achieve the high standard required for an (A) certificate. Nevertheless the number of seed stocks receiving only Grade B or "No Grade" reports is evidence that many growers in potentially good seed-growing areas have not grasped the need for planting good certified stocks. Such growers not only fail to take full advantage of their relatively favourable conditions but their stocks serve as sources of virus infection for neighbouring seed crops.

One of the regulations of the recently-formed Seed Potato Growers' Associations in Ross-shire and Aberdeenshire is that only S.S. or "A" seed must be planted. It would be well if there were similar regulations in other districts.

During the last fifteen years or so, research and surveys in England and Wales have disclosed the existence of areas capable of producing high-grade seed (Whitehead, 1943),[1] (Staniland, 1943)[2]; but it is too early as yet to say which, if any, of these areas will rank with the best seed-growing districts of Scotland and Ireland. In any case, their present contribution to the seed market is extremely small and, for as long as can be foreseen, the ware-growing districts of England will continue to rely mainly upon Scotland and Northern Ireland for the supply of commercially healthy seed.

Let us therefore consider this commercial seed from the standpoint of the English ware grower. According to an estimate made by Scott (1941),[3] Leaf Roll will increase fourfold on the average, and severe Mosaic two to threefold year by year in some districts of Scotland. Hence it may be expected that a crop grown from seed which barely reached the 2 per cent. standard required for an (H) certificate will have about 6 per cent. of the crop affected with severe Mosaic and/or Leaf Roll. This amount of disease, large as it may seem, has been shown by Whitehead (1930)[4] to be insufficient to produce any measurable loss in yield. Actually this figure of 6 per cent. is seldom reached, and 5 per cent. is much nearer to the average amount of severe virus diseases found in (H) stocks when

[1] T. Whitehead, "Some Factors influencing the Health of Seed-Potato Stocks in North Wales," *Ann. App. Biol.*, vol. xxx, 1943.

[2] L. N. Staniland, "A Survey of Potato Aphides in the South-Western Agricultural Advisory Province," *Ann. App. Biol.*, vol. xxx, 1943.

[3] R. J. Scott, "The Effects of Mosaic Diseases on Potatoes," *The Scottish Journ. Agric.*, vol. xxiii, July 1941.

[4] T. Whitehead, "A Study of the Degeneration of Certain Potato Stocks," *Ann. App. Biol.*, vol. xvii, 1930.

planted in England. This smaller disease incidence can probably be ascribed to the efforts made in Scotland to attain the (A) standard of health which, by reducing the number of diseased plants in the crop, proportionately reduces the spread of viruses by the insect vectors present. Unless, therefore, the loss in yield due to viruses is accentuated by bad cultivation (Whitehead, 1924 [1]), the ware grower can normally expect a full and vigorous crop by planting seed holding an (H) certificate.

The further history of the crop will depend upon the conditions under which it is grown. If, for instance, it is not grown in close proximity to a heavily diseased crop there may be no more than a three to fourfold increase in infection, and seed saved for replanting may be expected to contain from 15 to 20 per cent. of diseased tubers—a percentage, nevertheless, which will certainly affect the yield in the once-grown crop. This loss, due to increased virus infection, however, may be minimised and often more than counterbalanced by an increase in yield due to sprouting the home-saved setts. On the other hand, new Scotch seed may become so heavily infected when planted alongside once- or twice-grown seed, particularly if the crops show a high infestation with greenfly, that a very substantial loss in yield will occur when the seed is used for replanting, no matter what care is taken in sprouting the setts. Thus, the answer to the question as to whether seed from a commercially healthy crop can profitably be saved for replanting will depend on (*a*) the degree of infestation with greenfly (a factor which is outside the control of the grower) and (*b*) the degree of isolation from a heavily infected crop (which lies very largely within the power of the grower to control).

The farm practice in different parts of Great Britain does, in fact, confirm these scientific conclusions. In the best seed areas of Scotland the same stock of potatoes can be grown continuously for many years without deterioration ; at Craibstone in Aberdeenshire, for instance, drills of Kerr's Pink with Leaf Roll have been grown alongside drills planted with healthy seed, and tubers with and without Leaf Roll have been planted alternately in the drill for twenty-eight years, and in no season has any infection of the healthy plants occurred.

[1] T. Whitehead, "Potato Leaf Roll and Degeneration in Yield," *Ann. App. Biol.*, vol. xi. 1924.

In the main seed-growing areas of central and southern Scotland, on the other hand, it is a common practice for growers to replace their stocks, at intervals of a few years, with seed from the north or the higher-lying land in their own district. Some purchase a proportion only of their seed requirement and keep the whole produce for planting the following year. When care is taken to plant the new seed in a field by itself so as to reduce the risk of mixing or infection, and roguing is efficiently done, the health of the stock can be maintained for several years unless an abnormally high insect infestation occurs in the interval.

As regards England and Wales, it was recently shown by Samuel (1943) [1] that more than 60 per cent. of the potato acreage in Kent, Surrey, Essex, Cambridge and Huntingdon was planted in 1942 with new Scotch seed ; a large number of farmers, therefore, in the warm, dry, south-eastern parts of England find it worth while to buy new seed from Scotland and Ireland every year. About one-half of the rest of England, including the "home counties," the Midlands, Lancashire and Cheshire, Lincolnshire and East Anglia, appear to change their seed every two years. Twenty-five to 40 per cent. of the crop in Durham, Yorkshire, Dorset and the South Midlands was planted with new seed in 1942 ; hence the seed may be said to remain a profitable crop for about three years. Finally, Cumberland and Westmorland, Devon and Cornwall planted only from 10 to 25 per cent. of the crop with new seed, whilst less than 10 per cent. of the seed was changed in most counties of Wales. Apparently, therefore, these areas can maintain the health of potato stocks for from five to more than ten years without serious deterioration, these including just those areas in which seed potato growing is being encouraged.

IMPROVEMENT OF EXISTING SEED STOCKS.[2]—Virus diseases have not been entirely eliminated from even the best of our seed-growing districts. Indeed, possibly because of an occasional high insect count in an area (or for other reasons not fully understood), some crops may show distinct signs of deterioration, particularly with "Mosaic," in what is normally an excellent district for seed production. One effect of the

[1] G. Samuel, "Potato Virus Diseases : Introduction to a Symposium," *Ann. App. Biol.*, vol xxx, 1943.

[2] See article by T. P. McIntosh in the *Scottish Journal of Agriculture*, vol. xxvii, no. 1.

Certification Schemes has been to stimulate many growers, in the best seed areas, to counteract this lapse from perfect health by trying out one of two commercial methods of renovating their stocks.

The first and easier method is to purchase Stock Seed and endeavour to maintain its health by persistent roguing out of every unhealthy-looking plant and variant throughout the growing season. It thus differs from an ordinary " change of seed " only in the care taken to eliminate disease. The second method is to begin with single plants. The crop is searched with meticulous care at the peak of the growing season and a selection made of plants which are vigorous and free from Leaf Roll and, what is a much more difficult matter to determine, showing no sign of mottling (*i.e.* " Mosaic ") when a leaf is examined against a background of white paper. Such plants may be regarded, in a commercial sense, as virus-free and may be staked for later lifting or, better still, dug up at once. The produce of each selected plant is known as a " family," the families being stored separately in boxes and planted apart in the following year. Every plant is then carefully examined several times during growth, the occurrence of even a trace of virus disease in a plant being sufficient to render the remainder of the " family " suspect, and all are removed. The " families " which successfully pass the test again have their produce stored and replanted separately in readiness for an equally stringent examination in the following season. Occasionally the process may again be repeated before the produce is bulked.

The following example with Golden Wonder, which is one of the most difficult varieties with which to deal, will serve as an illustration of the second method. A few healthy-looking plants were selected at Craibstone in the autumn of 1918 and the produce grown on for two or three years, during which time all except one family showed Mosaic. Several selections were made from this family in 1923 and, during the next two years, the crops from each selection were weighed and the heaviest yielding families were kept; in the third year only the best cropping family was reserved for multiplication. Similar selections were repeated in 1928, 1933, 1938 and 1943, so that the present stock has been grown from the healthiest and best cropping single plants on six successive occasions, at least twenty or thirty being selected each time, while in 1928 the number was as much as eighty.

Unfortunately, it is beyond the power of the grower to do more than eradicate plants visibly infected with a virus, yet many varieties (*e.g.* Golden Wonder) may " carry " one or other of the viruses without showing any visible signs of disease. By means of the technique described in Chapter XXVIII, however, the specialist can detect the presence of these hidden virus infections and, by repeated search, is gradually building up small nuclear stocks of completely virus-free plants of a number of varieties. A refinement of the commercial methods described above has already begun with stocks, in which the original selections were tested, virus-free tubers, the produce of which are repeatedly subjected to tests to ensure the continued absence of disease. Virus-tested certificates are issued in respect of such stocks. It is not, however, known yet how long these will remain free from virus. They will have to take the same chances as other stocks with regard to aphid-borne viruses. Theoretically they should maintain their freedom from virus " X " for some years at least. It is essential, even in commercial selections, to isolate the various " families " sufficiently to prevent any possible foliage contact, for in this way the produce of completely virus-free plants can be maintained without contracting virus " X " from a neighbouring family. The isolation should be continued each year until the stock is sold.

It is interesting that in the main seed-growing districts of Canada and America a method called " tuber indexing " is in operation. In these districts the climate is generally no better than that of Lincolnshire. For example, the method at one centre is for the growers to send in about 300 large tubers in the winter months. Each tuber is numbered and one eye is taken out with a sharp-edged teaspoon and planted in a small pot. In about six weeks the plants are examined. The tubers from those with Leaf Roll or Mosaic are destroyed while those from the healthy plants are cut into as many parts as possible and planted,[1] the precaution being taken to plant those from each tuber in families so that if one or more is unhealthy all can be destroyed. The healthy ones are usually able to produce sufficient seed to plant about an acre the following year.

[1] G. Samuel, *Agriculture*, September 1947.

Whatever means may have been adopted to improve the seed stocks, they may be vitiated by failing to take certain precautions when two or more varieties are grown in the same field. These precautions are indeed just as applicable to ordinary commercial fields in which different varieties are being grown for seed. In the first place, the danger of mixing varieties must be avoided by separating them with at least two drills of some other crop such as swedes, this degree of isolation being in fact compulsory for a Stock Seed Certificate in Scotland. Secondly, it has been found that varieties react differently as regards virus diseases (*cf.* Table XXVIII), the various classes into which varieties may thus be divided being (*a*) those which may suffer severely but which are obtainable in a healthy condition; (*b*) those "carrying" viruses without showing symptoms; (*c*) those "field-immune" from certain viruses; and (*d*) those invariably infected with, and showing definite symptoms of, specific viruses. The effect of this difference in behaviour in varieties is discussed later, but here it may be summarised in the form of the following suitable arrangement in the order of planting,[1] so as to minimise the risk of spreading infection from one variety to an adjacent one:—

(1) "Carriers" of the same virus may be planted together, but not next to varieties which show symptoms when infected with the same virus.

(2) Varieties which are "field-immune" from viruses "A" and "X" may be used as buffer crops to separate varieties which are susceptible to, and suffer from, these viruses. If possible varieties of about the same maturity should be planted in the same field otherwise the greenfly may fly to the later sorts from the earlier ones. If this is not possible the early ones should be burned down early.

(3) Varieties invariably infected with, and which suffer from, specific viruses should not be planted next to healthy stocks of varieties which, when infected, suffer severely from the same virus.

Size and Weight of Seed.—The function of the seed-tuber is to provide food for the growth of the plant up to the

[1] T. P. McIntosh, "Mosaic Diseases of Potatoes: The Systematic Planting to reduce their Spread," *Scottish Farmer*, March 1938.

time the roots become established. A large sett may therefore be expected to start the plant off well and enable it to give the maximum yield. That this is true has been repeatedly shown in trials in various parts of the country. A typical result may be quoted from one of the trials carried out at Craibstone with the variety Arran Banner, in which extreme sizes of setts varying from ¼ oz. to 12 oz. were planted at a uniform spacing of 12 in. in the drill. In this trial the 12-oz. setts gave 18¼ tons of ware and 7½ tons of seed, the 2-oz. setts gave 13 tons of ware and 3 tons 3 cwt. of seed, whilst the ¼-oz. setts yielded only 4¼ tons of ware and 2 tons of seed. These figures, however, do not express the whole result as it affects the grower, for 6 tons of the 12-oz. setts were required to plant an acre, whereas 1 ton was sufficient for the 2-oz. setts and the ¼-oz. setts required a mere 2½ cwt. The cost of planting is therefore far from being a negligible item to set against the value of the ware and seed in the crop. The main purpose for which the crop is being grown must be taken into account in deciding on the most economical size of sett to plant. In the illustration given above, a ware-grower planting 12-oz. setts would require an extra 5 tons of setts in order to obtain an additional 5¼ tons of saleable ware, the extra 4 tons of seed-sized tubers being a less valuable by-product. On the other hand, the saving in setts effected by planting ¼-oz. tubers would normally be poor policy since the yield may be reduced by two-thirds. The result, in fact, confirms many other trials in showing that the most economical sett for the ware-grower is one about the size of a hen's egg and weighing about 2 oz. The grading adopted by the Ministry of Food for tubers saleable as "seed," viz., over 1¼ in. and under 2¼ in., is a reflection of this general agreement.

The position is less clear if the ware-grower also has a ready market for the seed-sized tubers in the crop, for the additional weight of both ware and seed obtained by planting large setts may possibly counterbalance the extra cost of using ware-sized setts. Or a compromise may be effected by re-dressing 1¼ to 2¼ in. seed into two classes of 1¼ to 1⅝ in. and 1⅝ to 2¼ in. grades, the larger setts being used for seed production and the smaller either planted close together for seed or at normal spacing to encourage the production of ware in the crop.

When the main object is to produce the maximum yield of seed-sized tubers, the less valuable ware tubers become a by-product and may economically be used as setts for the following crop. In such cases the large setts should be planted close together in the drill. Thus, in a trial at Craibstone with the variety Golden Wonder, setts graded between 2 and 2¼ in. riddles gave 9 tons 8 cwt. of seed and 3 tons 15 cwt. of ware when planted 9 in. apart in the drill, whereas at 12 in. apart they gave 7 tons 14 cwt. of seed and 4 tons 16 cwt. of ware, and at 18 in. spacing the yield was 6 tons 12 cwt. of seed and 5 tons 13 cwt. of ware.

Before deciding on the size of sett to plant, at least in all except the best seed-growing districts, consideration must be given to the risk of an unconscious selection of virus-infected setts. One effect of these diseases is to reduce the average size of the tubers, so that a partially infected crop will give an abnormally high proportion of small tubers, many of which may be used as seed-setts. Efficient roguing is, of course, the best solution, but the use of large setts will usually provide an additional insurance against the perpetuation of the diseases in the new crop. For this reason in many cases it is inadvisable to plant "chats" or "thirds," *i.e.* 1 to 1¼ in. or 1⅛ to 1⅜ in. tubers. In the best areas, however, there is relatively little risk of such an unconscious selection of diseased setts, and the smallest tubers may safely be used for seed purposes. At Craibstone, for instance, the varieties Abundance, British Queen and Great Scot were grown continuously for twenty years from small seed saved from each preceding crop. The seed at the beginning was from healthy plants. The yields over the period showed that, while the small setts produced a rather smaller crop each year when compared with that from larger setts, there was nothing suggestive of progressive deterioration such as would undoubtedly have occurred had the percentage of virus-infected plants, or of wildings, increased. When produced under similar excellent climatic conditions, therefore, "thirds" form a useful additional source of income to the seed-grower. He may either extend his own acreage by planting the "thirds" closely in the drills or, by selling them at a relatively low price for planting, help to encourage seed-growers, in a somewhat less suitable area, to improve the health of their stocks.

The general conclusions which can be drawn from the foregoing discussion may be summarised as follows :—

1. Large setts usually produce a heavier total crop than do small setts ; it may, however, not always be a sufficiently large increase to offset the extra weight of setts required.
2. Large setts produce both a larger proportion and a larger amount of seed-sized tubers than is the case with smaller setts. For this reason it is usually profitable for seed-producers to plant large setts (2 to 2½ in.), since their market value is much less than that of seed-sized tubers, especially in the case of Stock Seed.
3. When growing for ware, medium-sized setts usually produce the most economic crop ; a relatively small amount of seed is required for planting and the crop contains a high proportion of ware.
4. The highest proportion of ware is produced by the very small setts, but the total yield is below that of seed-sized setts.
5. When healthy and sprouted small setts are planted under good soil conditions, however, the small outlay in setts is far more than counterbalanced by the yield obtained.
6. Small setts sprout late and are slow in maturing. Conversely, if early ripening is sought for, larger setts should be planted.

Finally, it should not be overlooked that whilst seed-tubers are graded according to size, they are sold by weight, and a heavier weight of kidney or oval tubers will pass through a given riddle than is the case with round varieties. Hence the weight of seed required per acre will depend not only upon the size of sett, the width of the drills and the tuber-spacing in the drill, but also on the shape of the tubers. With these reservations in mind it may be accepted that, using tubers of the statutory 1¼ to 2¼ in. grading, from 25 to 36 cwt. per acre are necessary when seed production is the object, while from 18 to 20 cwt. will suffice if the crop is grown mainly for ware. When large tubers (say 2¼ to 2½ in.) are planted for seed production, as much as 3 tons are required for round varieties such as Great Scot or Arran Banner, and up to 3½ tons for longer varieties such as Majestic. From 5 to 10 cwt. are usually sufficient to plant an acre with small setts (" thirds ").

CUTTING OF SEED.—The practice of cutting large tubers into two or more setts is much less common now than was formerly the case, but is still to be seen in certain districts such as South Lancashire. The advantage gained in cutting tubers is obvious in seasons in which there is a scarcity of ordinary seed-sized tubers. Seed-growers, who frequently use large tubers as setts, may also find it necessary to cut the ware of varieties which tend to produce abnormally large tubers, in order to avoid an extravagant waste of tuber-material.

On the other hand, it is possible that some virus diseases of the " Mosaic " type may be spread from diseased to healthy tubers by means of the cutting knife; Spindle-Tuber and Blackleg are undoubtedly transferred in this way. There is no reliable information at present as to the extent of the risk involved in spreading tuber-borne diseases during the process of cutting tubers, but it will certainly be minimised by keeping the knife damp with a disinfectant; whilst the very act of cutting may disclose the presence of Blackleg in a tuber which otherwise would be planted as sound.

The chief objection, however, to the use of cut setts is the tendency of such setts, particularly of some soft-fleshed varieties, such as Majestic and Arran Pilot, to produce " misses " or " blanks " in the crop. These failures are due to premature rotting of setts in the soil before the roots become established. The problem therefore resolves itself into one of providing the tuber with the most suitable conditions for healing the cut surface, and so preventing the entrance of pathogenic or putrefactive organisms. The sequence of events during the healing of the cut surface has been studied by Priestley and Woffenden [1] (1923) and Priestley and Johnston (1925) [2] and their results may be summarised as follows:—

1. The first process in the healing of the tuber is the

[1] J. H. Priestley and L. M. Woffenden, "The Healing of Wounds in Potato Tubers and their Propagation by Cut Setts," *Ann. App. Biol.*, vol. x, 1923.

[2] J. H. Priestley and G. C. Johnston, " The Cutting of Potato Setts," *Journ. Ministry Agric.*, vol. xxxi, 1925.

deposition of a fatty suberin layer in the tissues at the cut surface.

2. If the cut surface is exposed in a moist atmosphere the fatty layer is continuous ; if, on the other hand, the surface is exposed in a dry atmosphere, especially in sunlight, the layer may not be continuous.

3. This layer forms within twelve to forty-eight hours. Later, cork is formed below this suberin deposit as a result of cell division in an actively dividing layer of cells known as the cork phellogen.

4. The activity of the cork phellogen may be estimated roughly by the numbers of layers of cork produced. Comparative data showed that Majestic, King Edward and Bishop are particularly deficient in this important activity connected with the healing of wounds.

The optimum conditions for healing, therefore, require the cutting to be carried out in a moist atmosphere and at a warm enough temperature to allow of normal cell activity, whilst exposure to drying winds, bright sunlight or other drying conditions must be avoided. Under such conditions there is strong evidence that cut setts can be used on a field scale with satisfactory results. Thus, Lombard (1937) [1] and Smith (1940) [2] state that cutting is quite practicable in U.S.A. provided the cut setts are allowed to heal satisfactorily. Good results from the use of freshly cut setts planted immediately are reported from Northern Ireland by Megaw and Bankhead (1938),[3] and in this country by Brandreth and Bryan (1937) [4] and Tinley and Bryant (1939).[5] The most recent work in this country is that of Bell, Gilson and Dillon Weston (1942),[6] in which replicated trials with sprouted cut and uncut ware tubers of Arran Banner, King Edward and Majestic were carried out. The results showed that no material loss of plants due to "misses" was suffered by the use of cut setts,

[1] P. M. Lombard, *Amer. Potato Journ.*, vol. xiv, 1937.

[2] O. Smith, *Amer. Potato Journ.*, vol. xvii, 1940.

[3] W. J. Megaw and J. Bankhead, *Journ. Ministry Agric., Northern Ireland*, vol. vi, 1938.

[4] B Brandreth and H. Bryan, *Journ. Nat. Inst. Agric. Bot.*, vol. vi, 1937.

[5] N. L. Tinley and D. M. Bryant, *Journ. South-East Agric. College, Wye*, vol. xliv, 1939.

[6] G. D. H. Bell, M. R. Gilson, and W. A. R. Dillon Weston, *Journ. Agric. Sci.*, vol. xxxii, 1942.

whether these setts were planted immediately after cutting or were stored under good conditions for periods up to six days.

An important conclusion reached by Bell *et al.* is the high degree of protection afforded against the penetration of putrefactive organisms by the natural healing power of the cells underlying the cut surface of the tuber. Thus, practically no rotting occurred in a large number of tubers of seventeen varieties which were planted immediately after they had been cut and the cut surface painted with a watery infusion of organisms from diseased tubers. The cork layer formed under the cut surface, however, is not as efficient in preventing water loss, and consequent shrinkage, as is the "peel" or skin of the tuber, and an excessive loss of water seriously reduces the resistance of the cut surface to the entrance of rotting organisms. Thus, when tubers were cut, painted with an infusion of tuber-rotting organisms, and then exposed to varying conditions of drying, the following percentages of tubers eventually rotted in the soil: (1) Exposed to strong sunlight, 58·3; (2) exposed in shade out of doors, 20·8; (3) covered out of doors with a dry sack, 12·3; and (4) covered out of doors with a damp sack, 7·0. The duration of exposure out of doors also had a marked effect on the resistance of the inoculated cut surface to infection, for after (1) half an hour's exposure, 5·6 per cent. developed rotting to a greater or less extent; (2) after one hour, 19·5; (3) after two hours, 61·1; and (4) after three hours, 64·7 per cent. eventually rotted.

Any condition, in fact, which impairs the recuperative power of the cell will weaken its resistance to invading organisms. The various means adopted in different localities to protect the newly cut surface of tubers must therefore be examined from this point of view. The treatment usually consists in dusting the cut surface with lime, slag or ashes, in order to "seal" the wound and prevent water loss. Bell *et al.* (1942), however, showed that none of these methods possessed any advantage over the untreated tuber in preventing loss from "misses," whilst Priestley and Woffenden (1923) concluded that lime, in any form, increased the loss of water from the cut surface. Similarly, Bell *et al.* found that cut setts showed increased loss of water, and an increase in rotting, when treated with alum as a drying agent.

From all this evidence it cannot be doubted that, given fairly cool, moist conditions from the time the tubers are cut, and a moist soil in which to plant them, there is little or no risk involved in cutting tubers even of varieties like Majestic. The problem as to whether the cut tubers should be planted immediately, or only after storing for a few days, is answered by the means available for keeping the cut surfaces moist. Therein lies the sole virtue of leaving the tuber almost, but not quite, severed into two halves ; for the unsevered portion acts as a hinge which keeps the two cut surfaces together and reasonably moist until the cork layer is formed. Air is essential to the healing process, so that the cut setts should be stacked in boxes or in a single layer on the floor, in both cases with the cut surface uppermost, for if air is excluded by placing the setts face downwards, some rotting will certainly occur. When cutting is carried out under unsuitable conditions dusting with lime appears to be beneficial. Thus, at Craibstone, dusting the cut surface with lime is useful (1) when cutting is carried out in the sun, as is often done on farms when tubers are taken direct from the pit to the field ; (2) if cut tubers are left for some hours in the drill before being covered ; (3) when cut tubers are spread too thickly on a floor for a few days ; or (4) when kept in bags for even a short period. It may be that in these practical tests some factor is present which is not taken into account in the scientific experiments described above, but it would seem that the best farm policy to pursue is to avoid cutting tubers under unsuitable conditions rather than to use lime as a palliative.

A closely related practice is that, common in some countries, of treating the cut surfaces with one or other fungicide to protect them against infection by disease organisms. On the whole, the practice is not to be commended owing to the direct injury inflicted on the cells by the chemicals, with the result that treated tubers may actually show more rotting than the untreated controls ; in other words, the healthy plant cell is a better protection against disease than is one in which the resistance has been impaired by chemical treatment. Cunningham (1936),[1] for instance, states that whilst treatment in U.S.A. with yellow oxide of mercury at the time of cutting or planting did not prevent normal healing of the wound,

[1] H. S. Cunningham, *Bull. N.Y. State Agric. Exp. Sta.*, No. 668, 1936.

and in one case prevented the decay of the sett in the soil, there was usually a reduction in yield, and treated tubers, whether cut or uncut, showed delayed emergence after planting. Lutman (1937)[1] emphasises the damage which may result from the use of disinfectants such as formaldehyde, which are very soluble in water, as fungicidal treatments of cut tubers. He states that formaldehyde may kill cut tubers by penetrating the newly formed suberised layer and passing via the vascular bundles to the sprouts ; whilst corrosive sublimate can cause much damage by coagulating the proteins of the tuber. Lutman finds, however, that calomel, yellow oxide of mercury and organic mercury compounds can be used successfully on cut tubers if these are allowed a period of at least five days in which to heal before application of the fungicide, and that, under such circumstances, calomel and yellow oxide of mercury can inhibit the action of soil parasites. Bell *et al.* (1942) found that both alum and a proprietary substance, the basis of which was copper sulphate, produced delayed and irregular emergence of plants after cut tubers of Majestic had been treated and then immediately planted. They also report that cut tubers of Sharpe's Express showed a high percentage of rotting after being covered by sacks moistened with either 2½ or 5 per cent. copper sulphate, the effect being as serious as occurred with uncovered tubers stored under conditions unsuitable for wound healing.

It would appear that the total crop obtainable from cut setts varies with the size of the setts in much the same way as in whole tubers. This, however, does not necessarily mean that the crop from a cut sett will equal that from a whole tuber of the same size. Indeed, after several careful field trials Stewart (1922)[2] came to the conclusion that uncut tubers of between 1 and 2 oz. in weight are at least as good as, and probably a little better than, pieces of equal weight cut from large tubers of the same plant. On the other hand, Bell *et al.* (1942) in comparing the yields from halved and whole ware tubers of the varieties Arran Banner, King Edward and Majestic, found the yield from half-tubers to be most usually over 90 per cent., and never less than 79 per cent., of

[1] B. F. Lutman, *Bull. Vermont Agric. Exp. Sta.*, No. 418, 1937.

[2] F. C. Stewart, *Bull. N.Y. State Agric. Exp. Sta., Geneva, N.Y.*, No. 491, 1922.

that of the whole tubers planted under the same conditions, thus implying that an uncut tuber will yield more than a cut tuber of the same size. Hence, a grower who plants an acre with halved ware setts will effect a 50 per cent. saving in the cost of the setts, and may expect to get from 10 to 20 per cent. less total crop than would have been obtained from an acre of whole tubers of similar weight.

Trials were carried out at Craibstone for several years with about 50 varieties when whole seed was compared with cut seed of the same size. Cutting was done several weeks before planting and the tubers were kept in boxes. In every case the cut surfaces healed nicely and there were practically no blanks. When both were equally sprouted the yields were almost the same.

The manner in which the tubers are cut will influence the yield, owing to the greater power for growth possessed by the buds in the " eyes " at the rose end over those at the heel end of the tuber. There is no innate inferiority in the heel end buds but their growth is suppressed by the " apical dominance " of the buds at the rose end, a fact which is common knowledge to anyone familiar with the appearance of sprouting potatoes. By cutting a sprouted tuber crossways (*i.e.* midway between rose and heel ends), it is divided into a rose end half with several strong sprouts and a heel end half with, usually, only rudimentary sprouts. The act of cutting removes the dominance of the rose end, but the " leeway " in growth of the heel end means later emergence of the shoot and a smaller yield than that obtained from the rose end. There are many experimental results to confirm this statement, amongst which are those of Chittenden (1918 and 1919) [1] in this country and Stewart (1933) [2] in U.S.A. For this reason, therefore, sprouted tubers should always be cut lengthways (*i.e.* with the knife passing through both rose and heel ends) in order that each half-tuber planted may have strong sprouts and that the resulting plants may emerge and mature uniformly. If, however, cutting is carried out sufficiently early with unsprouted tubers there appears to be no objection to cutting crossways,

[1] F. J. Chittenden, *Journ. Roy. Hort. Soc.*, vol. xliii, 1918; vol. xliv, 1919.

[2] F. C. Stewart, *Bull. N.Y. State Agric. Exp. Sta. Geneva, N.Y.*, No. 633, 1933.

since the heel halves now have abundant time in which to develop sprouts as sturdy as those from the rose ends (Appleman, 1918).[1] This statement was corroborated by trials at Craibstone. When tubers were cut crossways early and the halves equally sprouted the yields were similar. It must also be remembered that this early cutting entails the maintenance of the tubers in the store, for long periods, under conditions favourable for healing the cut surfaces.

SPROUTING OR CHITTING.—Practical experience in the great majority of cases is in favour of sprouting seed-tubers before planting, and the practice, always common amongst gardeners, is being adopted by an ever-increasing number of farmers.

Sprouts developed under suitable conditions will be short sturdy growths about 1 to 1½ in. in length and with the rudiments of roots already well advanced at the base. Growth begins almost immediately such tubers are planted, even when the soil temperature is rather low, and the shoot soon emerges above ground. With this initial advantage there is also a hastening in the maturation of the crop, an important consideration with early varieties competing for the high prices obtainable in the early summer markets. Late varieties should always be sprouted, particularly in late districts where frost or Blight may cut down the tops before they are fully mature.

A higher yield is almost invariably obtained from sprouted than from unsprouted tubers. Thus, in trials at Craibstone, in which plots of sprouted and unsprouted tubers were planted at fortnightly intervals from the beginning of March to mid-June, the average increase in yield from sprouted setts of Arran Banner was 2 tons 16 cwt. or 13·7 per cent., and in the case of Golden Wonder the increase amounted to 3 tons or 24·9 per cent. Similar trials in another season gave the following increased yields due to the use of sprouted setts: Di Vernon, 1 ton 4 cwt., or 11·2 per cent.; Kerr's Pink, 2 tons 8 cwt., or 20·8 per cent.; and Golden Wonder, 2 tons 10 cwt., or 19·6 per cent. The increased yield is usually most evident in late varieties, especially in late districts. Further, the increase occurs mainly in the weight of ware-sized tubers, there being little difference in the seed, whilst the weight of chats is usually reduced. It is not surprising, however, that

[1] C. Appleman, *Science*, N.S., vol. xlviii, 1918.

adverse weather or soil conditions in spring may sometimes have a more severe effect on the advanced growth from sprouted tubers than on the comparatively retarded plants from unsprouted setts, and in such cases no increased yield is to be expected from the former. Thus early varieties, especially when planted early may be frosted while second early varieties, especially when planted in light soils, often experience a check to growth when a long dry period coincides with the beginning of tuber formation in plants grown from sprouted setts, and this may go far towards eliminating the benefit they had gained from their advanced growth.

There are other advantages, in addition to increased yields, to be obtained from the use of sprouted tubers. Amongst these are: (1) In late seasons planting may be delayed until soil conditions are favourable, without making the crop unduly late; (2) advantage can be taken of the fact that the sprouts of different varieties vary in colour to discard tubers of "rogue" varieties; (3) tubers which show delayed or weak sprouts should be suspected of being infected with some disease and, by removing them, blanks in the field may be avoided; (4) the haulms from sprouted tubers, especially when planted early, are comparatively short, strong and sturdy, whereas those from unsprouted tubers are taller and softer, with the result that they are readily beaten down by heavy rain or high winds; (5) potato haulms, particularly those of late varieties, are frequently destroyed by frost or Blight in early autumn. At this time, however, the crop from sprouted seed may be almost mature and, in consequence, suffers less and gives a much higher yield than the relatively immature crop from unsprouted setts, and (6) the cooking quality also improves with approaching maturation of the tubers. Much of the poor quality potatoes on the market are due to the late planting of unsprouted seed.

SPROUTING OR CHITTING BOXES.—The practice of encouraging sprouting by spreading the tubers in a thin layer on the floor has fallen almost wholly into disuse with the recognition of the convenience with which tubers stored in boxes can be handled. Seed tubers so stored can be kept under observation with ease and moved, as occasion demands, so as to ensure the uniform warmth, light and ventilation without which sprouts will not develop to the best advantage.

Boxes are constructed on a common principle in different areas, but the size preferred varies considerably, as can be seen from the following examples :—

$24 \times 12 \times 3$ in.	to hold about 20 lb.
$28 \times 13\frac{1}{2} \times 3$,,	,, ,, 28 ,,
$36 \times 16 \times 3$,, or $32 \times 18 \times 3$,,	,, ,, 40 ,,

One person can easily handle up to 28 lb. of seed, but for 40 lb. two persons are required for easy and efficient planting. The tray is made of thin pieces of wood of which two or more form the bottom, a space of $\frac{1}{2}$ or $\frac{3}{4}$ in. being left between them to allow of ventilation from underneath. At each corner is an upright 7 in. high, these being joined together across the narrow ends of the tray by a piece of wood 2 in. wide. Except in large boxes a handle is provided by connecting the two end pieces by means of a spar. The thickness of timber used will of course vary with the weight of tubers they have to support. Suitable thicknesses for the sizes of boxes described above would be $\frac{5}{16}$, $\frac{3}{8}$ and $\frac{7}{16}$ in. respectively, with 1, $1\frac{1}{8}$ and $1\frac{1}{4}$ in. for the handles and corner posts. Care should be taken that no more than the weight of tubers given above for each size should be placed in the box, the tubers being stacked (preferably but not necessarily) with the rose ends uppermost. When the filled boxes are built one upon the other there is ample space between them for effective ventilation of the tubers.

Sprouting or Chitting Houses.—It is now well understood that success in sprouting seed tubers depends very largely on securing good conditions of storage. At one time most growers stacked the sprouting boxes in barns, sheds or in byres, either on the rafters or behind the cattle when space was available, and sometimes in empty stalls ; indeed, in some districts this is often still to be seen. Byres, owing to their comparatively high temperature, are usually believed to be very suitable for the slower sprouting varieties, but, apart from other considerations, it is unlikely that sufficient light for proper sprouting can be obtained under these conditions. Even when there is not much light, however, byres are very suitable for starting the sprouts after which the boxes can be removed to an airy shed.

The need for controlled warmth, light and ventilation has led to the use of special "chitting" houses, which, in England, are usually glasshouses which may be used during the summer for tomato growing. They are, however, much higher to the eaves (say, 8 ft.) than is customary for ordinary glasshouses, so that they can accommodate the maximum number of boxes. The structure should rest on brick foundations, but the brick sides should be kept low to allow of ample light reaching the lower boxes.

A convenient width is 20 ft. for a house 40 ft. in length. Such a house will hold about 25 tons of potatoes when the boxes are properly spaced, or about 40 tons if placed close together. The boxes should be stacked lengthways in tiers, from a centre pathway of 3 ft. towards the sides of the house, leaving a space of 18 in. between the tiers. Ventilation should be provided along the top and bottom of the house and all ventilators should open from the outside. This is particularly important for bottom and side ventilation owing to the difficulty of access when the house is full. Double doors are useful to enable carts to be backed into the house for unloading or loading purposes. A hot-water heating system is advantageous, but, in its absence, a few Valor Perfection stoves will be useful during frosty weather. Protection against frost is important, for it has been shown by Wallace (1935) [1] that exposure to only 1·8° F. of frost for a period of forty hours caused a significant reduction in yield from tubers which showed neither external nor internal signs of injury.[2] When subjected to a low temperature for a prolonged period the tubers became soft and rotted. Once sprouting has begun it is essential to give each tuber access to an ample amount of light. When storage conditions prevent this being carried out the sprouts may become blackened and die at the tips, a condition which may be accentuated by injury or bruising (Bates and Dillon Weston, 1936).[3] These writers advise that the position of the boxes should be changed at least once during the sprouting period, those at the ends of the tiers being moved to the centre and those at the top being moved to the floor. The extra labour

[1] E. R. Wallace, *Journ. Ministry Agric.*, vol. xli, 1935.

[2] See also T. P. McIntosh, *Gardeners' Chronicle*, 2nd Sept. 1944.

[3] G. H. Bates and W. A. R. Dillon Weston, *Scientific Hort.*, vol. iv, 1936.

involved will be well repaid by the greater uniformity in sprouting.

When the temperature of storage is too high, and particularly with poor ventilation, the sprouting tubers may become infested with aphides or greenfly in the early spring. This infestation may be a serious source of danger in that virus diseases are very readily spread in this way. Greenfly, however, can be effectively controlled, without damage to the sprouts, by the use of nicotine sulphate. This is applied either as a dust from a hand-dusting machine or as a fumigant, in which latter case it is volatilised by means of a spirit lamp after the store has been made air-tight.

CHAPTER XV

ANIMAL PESTS OF THE POTATO

I. GENERAL AND CLASSIFICATION

Introduction

UNDER natural conditions the multitudinous forms of life, both plant and animal, exist only as a result of constant struggles against each other and their common, and fluctuating, environment. Thus in the course of time a " balance of nature " is arrived at in which each plant and animal finds its proper place or " level," a condition which is to be seen in any untouched hedgerow or waste land in the countryside. If this balance is altered, even temporarily, to the advantage or otherwise of some particular species the reaction will be immediate and profound. Thus any unusual increase in the numbers of a plant will almost certainly result in a rapid increase in the number of the lower forms of animal life, such as insects, which rely on the plant as food. But this, in turn, has the effect of stimulating the breeding of more carnivorous animals which prey on the herbivorous forms. The excessive numbers of the plant are once more reduced to something approaching their original level, as are the herbivorous pests by their predators and parasites until these latter decline in numbers owing to the increasing shortage of their prey—and so, by this rather over-simplified illustration of the factors involved, we again see the restoration of the original " balance of nature."

Nothing is more likely to upset the balance of nature so readily as the cultivation by man of vast quantities of plants grown to produce the maximum amount of food for himself and his stock. The crop plant is " improved " out of all recognition by the plant breeder who, until recently, has striven for " useful " characters at the expense of other qualities which, if developed, might enable the plant to resist pest or fungus disease attack. Susceptibility may indeed increase by the loss of innate powers of resistance, and the effect is intensified by all the cultural operations aimed at producing " lush " growth from the crop. The serious effect of the consequent encouragement of pests is increased by the extraordinary rate at which many of these pests breed, so that the time-lag before the carnivorous species can re-establish the balance may be quite sufficient for the unfortunate grower to lose his crop. Hence the need for continuous research on the conditions favouring the development of specific pests, and on the most effective means of destroying them without awaiting the action of their natural enemies.

The first essential is a thorough study of the life-history and habits of the pest. Many pass through a complicated cycle of development (metamorphosis) or change their feeding habits, and it may happen that they are most easily, and cheaply, killed on some weed plant or at some stage of development when they are harmless to the crop plant we are endeavouring to protect. The methods of control, requiring thorough testing under varied conditions, may be either "*direct*," *i.e.* they may aim at killing the pest by some poison or mechanical means, or "*indirect*" by so altering cultural operations as to favour the plant and, at the same time, check the feeding and breeding of the pest. A third, or "biological control," is sometimes possible by the introduction of some parasite or predator of the pest whereby the numbers of the latter may be reduced until a new "balance of nature" is set up.

Direct methods usually involve the spraying or dusting of chemicals which act either as stomach poisons or as contact poisons, though sometimes the chemical is mixed with an attractive food and either broadcast or deposited in small heaps on the soil to serve as "poison-baits" *e.g.* "meta-fuel." Animals with biting mouthparts, such as beetles or the larvæ (caterpillars) of butterflies and moths, are usually best killed by a stomach poison, the basis of which is frequently some arsenical compound. But stomach poisons are of little or no use against such sucking insects as aphides which bury their stylets deep in the plant tissue; in these cases the best results are obtained by a contact poison (in the form of spray, smoke, dust, or gas) which is able to penetrate through the skin of the pest. Among the most commonly used of contact poisons are nicotine or nicotine sulphate, derris extract and pyrethrum or hellebore powders. One great advantage of some of the new insecticides, *e.g.* D.D.T. is their ability to act both as stomach and contact poisons; thus considerable success appears to have been achieved recently in U.S.A. in the use of D.D.T. against aphides.

Indirect methods of reducing loss due to pests include (*a*) modification of the rotation. Thus it may be lengthened to control potato root eelworm, or a resistant crop may be interpolated to increase the interval between susceptible crops in order to try to reduce the pest population, *e.g.* mustard for wireworm and root eelworm infestation, beans and peas for wireworms. (*b*) Varieties of a normally susceptible crop which may escape severe damage may be planted, *e.g.* early potato varieties on land infested with slugs, root eelworm or wireworm; or which are claimed to show actual resistance to attack, *e.g.* Arran Peak in the case of slugs or Epicure and Doon Star for root eelworm. (*c*) Thorough consolidation of the soil to the full ploughing depth may restrict the movement of subterranean pests and may force wireworms and cutworms to the surface where they are exposed to their natural enemies. (*d*) The planting of well-sprouted seed, and heavy dunging, may encourage root development and so materially reduce the loss due to root eelworm; on the other hand artificial fertilisers act as correctives against slugs and millepedes in soils rich in organic manures. (*e*) Thorough cleaning of the land, including hedgerows and ditches, may be of great importance in destroying cover or alternative food plants for many crop pests. (*f*) Finally, the Government takes a hand in preventing the introduction of pests from abroad by inspection and quarantine regulations. As regards foreign pests of the potato, two are scheduled under the Destructive Insect and Pest Acts (Importation of Plants Orders, 1939-45), *i.e.* the Colorado Beetle (page 266) and the Potato Moth (page 263). The former has several times gained a footing in the country but constant vigilance has prevented it, as yet, from establishing itself. So far, the Potato Moth also has been successfully intercepted but some risk must always be faced from imported continental produce. Biological control by the introduction of an animal or fungus parasite of the crop pest has not been tried against potato pests in this country although many naturally occurring parasites frequently are of great importance. Unless the parasite relies wholly on the pest as its food there are obvious dangers in encouraging the unlimited breeding of a newly introduced insect or other animal. Spraying and the use of some parasite are often mutually exclusive methods, for the spray may destroy more of the parasite than of the pest.

CLASSIFICATION OF POTATO PESTS, AND THEIR RELATION TO OTHER FORMS

The pests of the potato with which we are concerned all belong to the *Invertebrata* division of the animal kingdom, *i.e.* none of them possesses a backbone or internal bony skeleton, but many are protected by an external horny (chitinous) covering or exoskeleton. Among the main groups, or *Phyla*, of the invertebrates we are chiefly interested in (*a*) the *Aschelminthes*, (*b*) the *Mollusca*, and (*c*) the *Arthropoda*; the distinguishing characters of which are given below.

(*a*) *Aschelminthes* comprise many diverse types of minute, usually "worm-like" animals, with a false "body-cavity" in which is contained a relatively straight (*i.e.* not looped) digestive tract. An important Class of this Phylum is the *Nematoda*, to which belong the potato Root Eelworm (page 205) the Stem Eelworm (page 231), and the Tuber-Rot Eelworm (page 236).

(*b*) *Mollusca*, to which belong the mussel, whelk, snail and slug (page 240), are unsegmented invertebrates devoid of legs, with or without a "shell," and typically breathing by means of gills except in the land-forms such as snails and slugs which breathe with the aid of a rudimentary "lung."

(*c*) *Arthropoda* includes all the remainder of the potato pests described in this book; the distinguishing features being the possession of a segmented body covered with a horny (chitinous) exoskeleton, and a number of many jointed legs. To this very large phylum belong the

i. *Crustacea* or crabs and woodlice, with at least five pairs of legs and two pairs of "feelers" or antennæ;
ii. *Arachnida* or spiders, mites and ticks, having no antennæ, four pairs of legs in the adult and a body divided into a front portion or cephalo-thorax and a rear abdomen;
iii. *Myriapoda* or centipedes and millepedes, with one pair of antennæ and a many-segmented "worm-like" body carrying one or two pairs of legs on each segment (page 250);
iv. *Insecta*, an important and extremely large class separated from all others by possessing a body

divided into three parts (head, thorax and abdomen); the thorax consisting of three segments, each of which in the adult carries a pair of legs, and the last two are often provided with wings. The mouth-parts, which are of particular interest to us, are extremely varied but, fundamentally, they consist of (*a*) a *labrum*, forming the roof of the mouth and hinged posteriorly to permit of limited up and down movement, (*b*) a pair of *mandibles* or jaws, hinged to give only a side to side movement. In phytophagous (vegetarian) insects these are bluntly toothed and with a grinding surface, in contrast to the sharply pointed mandibles of the carnivorous forms, (*c*) two pairs of *maxillæ* with appendage-like "palps"; the first pair acting as auxiliary jaws while the second pair are fused into a plate (*labium*), serving as the floor or base of the mouth. In the *Hemiptera* (page 255) the mandibles and maxillæ are modified to form bristle-like stylets which serve as piercing and sucking organs and, when at rest, lie in the grooved labium.

Insects are divided into the *Apterygota* or primitive wingless forms, to which belong the *Collembola* or "springtails" common on potato foliage, (page 253), and the *Pterygota*, *i.e.* those with wings at some stage in their life-history or, as in the case of "fleas" and "lice," believed to have lost their wings in the course of evolution. Finally, the *Pterygota* are sub-divided into

(*a*) the *Exopterygota* with a slight or simple metamorphosis and wings which, arising from the outer tissues of the thorax, are seen as "buds" at an early stage of development of the insect. To this group belong the *Thysanoptera* or "thrips" (page 253) and the *Hemiptera* or plant-bugs (page 255), jassids (page 256), psyllids (page 257) and aphides (page 258).

(*b*) the *Endopterygota* with a complex metamorphosis, wings which arise from internal tissues, and larvæ which are usually highly specialised. This group includes the *Lepidoptera* or butterflies and moths (page 262), the *Coleoptera* or beetles (page 266), and the *Diptera* or two-winged flies (page 278).

The interrelationships between the various pests of the potato are shown graphically in Table XII.

TABLE XII

Scheme of Interrelationship between Various Pests of the Potato

- (A) ASCHELMINTHES (*NEMATODA*). Microscopic, unsegmented, "worm-like" body
  - Cysts on potato roots — Root-Eelworm (p. 205)
  - Cysts absent
    - affecting tubers and aerial organs — Stem-Eelworm (p. 231)
    - affecting tubers only — Tuber-Rot Eelworm (p. 236)
- (B) MOLLUSCA (*GASTEROPODS*). Unsegmented; limbless
  - Prominent shell — Snail (p. 240)
  - Shell rudimentary or absent — Slug (p. 240)
- (C) ARTHROPODA. Segmented body and limbs
  - *Myriapoda*. "worm-like," segmented body; many pairs of legs
    - One pair of limbs per segment — Centipede (p. 250)
    - Two pairs of limbs per segment — Millepede (p. 250)
  - *Insecta*. Body divided into head, thorax and abdomen; three pairs of legs
    - *Apterygota*. Primitive and wingless — *Collembola* or "Springtails" (p. 253)
    - *Exopterygota*. Simple metamorphosis or none; pupal stage absent or incipient
      - *Thysanoptera*. Two pairs of "feathery" wings; asymmetrical mouthparts — Thrips (p. 253)
      - *Hemiptera*. Two pairs of membranous wings
        - *Heteroptera*. Forewings horny at base — Plant (Capsid) Bugs (p. 255)
        - *Homoptera*. Wings wholly membranous — Jassids (Leafhopper) (p. 256); Psyllids (p. 257); Aphides (p. 258)
    - *Endopterygota*. Metamorphosis complex; pupæ
      - *Lepidoptera*. Two pairs of wings; membranous and scaly — Rosy Rustic Moth (p. 262); Potato Tuber Moth (p. 263); "Cutworms" (p. 264)
      - *Coleoptera*. Forewings (elytra) horny — Flea-Beetles (p. 266); Colorado Beetle (p. 266); "Wireworms" (p. 269)
      - *Diptera* (Flies). One pair of wings — Seed-Corn Maggot (p. 278)

CHAPTER XVI

NEMATODA—EELWORMS OR THREADWORMS

NEMATODES or eelworms are extremely simple animals belonging to the Phylum *Aschelminthes*, which includes not only the plant parasites with which we are directly concerned, but also such important parasites as *Ascaris* (the "round-worm") of which different species infest the small intestine of man, horse, ox and other animals. The nematodes are minute, almost microscopic, and "eel-like" animals usually about 1/25th of an inch long. Their almost transparent bodies taper to the ends but are rounded somewhat at the fore-end or "head" where the suctorial mouth is placed. The body-wall consists of longitudinally-arranged elongated muscle cells and is covered by a well-developed cuticle which is shed on "moulting." The alimentary canal is almost straight, *i.e.* without convolutions, and runs almost the whole length of the eelworm, terminating anteriorly in the three-lipped mouth and posteriorly in the anus. Behind the mouth lies the œsophagus or gullet, which in some forms has a muscular swelling in the middle and a glandular dilation or "bulb" near the point of junction with the middle-gut; surrounding the œsophagus is a nerve-ring from which, usually, six nerves pass forward and six pass backwards. There is neither a respiratory nor a vascular (blood) circulatory system and the excretory system consists of two lateral canals opening by a single pore near the œsophagus. The sexes are distinct and there is usually well-marked sexual dimorphism, *i.e.* the one sex differs conspicuously from the other. It will be clear from this description that the only resemblance the eelworm has to the earthworm is its cylindrical shape; nor is there much reason to confuse eelworms with the small (1/3rd inch) white, opaque and segmented Enchytræids or "potworms" which often swarm in rotting potato tubers in company with the scarcely larger larvæ of various flies.

By far the majority of eelworms are saprophytic scavengers of decaying organic matter, some can invade wounded tissues and exist as semi-parasites but are of little economic importance, while others are true parasites able to cause serious loss in otherwise healthy plants. The parasitic forms are readily identified under the microscope by the presence of a pointed spine, the so-called stylet or " buccal spear " buried within the mouth, and believed by many observers to be capable of being protruded as a means of penetrating unwounded tissues, Filipjev and Stekhoven, (1941). Parasitic eelworms usually exhibit marked preferences for particular tissues as a " feeding zone," and it is due to this selective feeding on the part of different eelworm species that they can be grouped, for instance, as " root eelworms " and " stem eelworms." Nematodes do not escape their full share of natural enemies. Filipjev and Stekhoven (1941) give authority for stating that nematodes are consumed by amœbæ, *Hydra*, enchytræid annelids, and even fishes. Bacteria set up a general septicæmia which completely destroys the internal organs of nematodes. Fungal spores are swallowed and, on germinating, destroy the organs and cause death. The " Bunt " fungus of wheat (*Tilletia caries*) is said to kill the wheat " ear-cockle " nematode (*Anguina tritici*). Many fungi (Phycomycetes and Fungi Imperfecti) are known to trap nematodes by means of hyphal loops smeared with a plasmatic gum (Drechsler, 1933-35) while, according to Duddington (1950), the hyphomycete *Dactylella ellipsospora* employs adhesive knobs ; and *Dactylella bembicoides* closes a hyphal loop, into which a nematode has entered, by the swelling of the hyphal cells. In all these cases a fungal infection thread penetrates the nematode and parasitises it.

In this country only one species, *Heterodera rostochiensis* Woll, is known to attack the root system of the potato and, incidentally, also the roots of tomato (Thompson and Johnson, 1936). A second species, *Heterodera marioni* (Cornu) Goodey, well known as the " root-knot " eelworm of tomato, is regarded in some countries, *e.g.* U.S.A. and New Zealand, as a serious pest on potato roots. This fact emphasises the urgent need, already sufficiently obvious from Chitwood's (1949) analysis of the American " root-knot " eelworms, for a re-examination of the identity and host-range of the forms occurring in Britain. Chitwood pointed out that not only is *Heterodera marioni* a conglomerate of species, but that it differs generically from the type *Heterodera* of Schmidt (1881). Thus, among other structural differences, the body-wall of the female never becomes leathery nor forms a cyst as in *Heterodera* nor, in fact, are the eggs retained within the female body. Further, in the type *Heterodera* the host does not usually form galls and the females tend to live superficially on the roots, in both of which respects the "root-knot" forms differ from *Heterodera*. Chitwood has therefore resuscitated the genus *Meloidogyne* Goeldi and, within this genus, has erected a number of species covering the forms now collectively known as "*Heterodera marioni*." Christie's (1949) results have led him to conclude that the difference in resistance shown by various plants to "root-knot" may be due to the varying ability of the larvæ of different species of *Meloidogyne* to penetrate the roots, and to the fact that each species reacts to specific stimulants excreted only by certain plants.

Questions of nomenclature have also arisen recently with regard to the eelworm species parasitic on tubers and/or the aerial parts of the potato, but which do not invade the root system. In some continental countries, notably Holland, the species *Ditylenchus* (*Anguillulina*) *dipsaci* (Kühn) Filipjev, is not only a serious pest of tubers, but at least three biologic races are able to invade the aerial haulm and foliage (Seinhorst, 1949). Another and distinct species, *Ditylenchus destructor* Thorne—first named and described from Idaho, U.S.A., by Thorne in 1945—is parasitic both in America and Holland on the potato tuber alone. In the British Isles, attacks are confined to the tuber and underground parts of the haulm (Goodey, 1951) and the responsible agent was, until recently, regarded as a biologic race of *D. dipsaci*. Further studies, however, have convinced the British workers that here, also, the species involved is *D. destructor*. The nomenclature and distribution of these two forms of potato-tuber eelworm are further discussed on page 231.

THE POTATO ROOT-EELWORM
(*Heterodera rostochiensis* Wollenweber)
as a cause of "Potato-Sickness"

NATURE AND EXTENT OF DAMAGE.—A new attack of "potato-sickness" can be suspected at once by the occurrence of patches in the crop in which the plants are stunted, yellowed, and with weak spindly haulms (*cf.* Fig. 30). The leaves turn brown, wither, and the margins roll inwards; often all the leaflets on one side of the midrib appear "scorched" while those on the other side remain green. As the attack proceeds the lower leaves hang as a withered mass or fall off to give a "palm-tree" effect to the whole plant. It is possible to confuse these foliage symptoms with those characteristic of Leaf Roll (page 437), Leaf-Drop Streak (page 461), Stem Canker (page 295), or Blight (page 334), but any doubt is removed at once when the roots are examined. The root system is sometimes poorly developed and consists of brown, decaying rootlets, from which the outer surface or cortex is readily peeled; but more often there is an abundant production of secondary fibrous roots near the ground level, and always there is the characteristic occurrence of numbers of tiny bladders, about the size of a pin-head ($\frac{1}{50}$ in.) attached to the rootlets and varying according to their degree of maturity from white to dark-brown in colour (*cf.* Figs. 31, 32). These "bladders" are the female eelworms which, attached to the rootlet by their narrow, pointed heads, have bodies swollen with eggs, for which they form a protective case known as a "cyst."

When potatoes are taken too frequently in the rotation the attack may be intensified and the diseased patches join up until the whole crop is affected and the yield may be negligible. Leiper and Triffitt (1934) quote a case in which 7 cwt. of seed planted in Cambridgeshire yielded only 5½ cwt. of crop, and record that, in Yorkshire, land which let at £2 per acre in 1930 failed to let at a rental of 10s. per acre in 1933 after a severe attack by eelworm. Potato Sickness is prevalent throughout the British Isles in gardens and allotments, and is becoming alarmingly serious in some of our best potato-growing areas. Peters (1949) records four major areas of infestation in England: (*a*) Around the Wash in Lincolnshire, Norfolk and the adjacent areas of Cambridgeshire, Huntingdon and the Isle of Ely; (*b*) The lower valley of the Yorkshire Ouse and Trent; (*c*) The coastal plain of Lancashire, and (*d*) The greensand area of Bedfordshire. Bad patches also occur in Durham, Notts, Stafford, Worcester, Cornwall, Devon, Dorset, Isle of Wight and Surrey. The distribution in England has been described in detail in the four northern counties by Cohen (1949); in Yorkshire by Johnson and Thompson (1945), and Thompson (1949*a* and *b*). In Devon and Cornwall, according to a survey made by Staniland (1946), although most of the commercial

FIG. 30.—"Gappiness" due to Potato Root Eelworm (page 205)

FIG. 31.—Immature Cysts of Potato Root, Eelworm on root (magnified).

FIG. 32.—Mature Cysts of Potato Root, Eelworm on root (magnified).

FIG. 33.—Potato Root Eelworm (page 205). Ruptured Cyst enlarged to show eggs and larvæ (magnified).

holdings are free, the position is serious in many of the early-ware growing areas ; out of 86 fields examined only 5 were free from eelworm and, in a second survey, all but 2 in 400 fields were infested. Wood (1946) states that, in 1944 and 1945, 20 per cent. of all the arable land in the county of Holland (Lincs.) was badly infested, 25 per cent. of which failed as a result of the encouragement of eelworm by allowing too short a rest between potato crops. Potato Sickness is widespread in Eire, particularly in the light sandy areas and in cut-away peat-bog land in the midland counties (Carroll and McMahon, 1944) ; it does not yet appear to be very serious in Northern Ireland or in Wales. In Scotland there are areas where the Potato Root Eelworm is assuming considerable importance and severe losses in yield have been recorded, *e.g.* in a survey of S.W. Scotland, Grainger (1949) found 2500 acres of the 3000 under early potatoes in Ayrshire heavily infested with root eelworm ; about 1 per cent. of the crops of late varieties appeared to be infested in Stirling, Perth, Dumfries and Kirkcudbright, with probably a still higher infestation in Lanark. Gemmell (1944) assessed the loss in early potatoes in Ayrshire at 10 to 15 per cent. in wet years and at from 50 to 60 per cent. in dry seasons. In such main crop varieties as Kerr's Pink he reports a loss of 40 per cent. following a moderate attack, and up to 95 per cent. when infestation is severe. According to Grison and Ritter (1948) *Heterodera rostochiensis* is unknown in France, but it is certainly widespread in many continental countries. In U.S.A. it appears to be confined to Long Island, New Jersey, where some 6000 acres are known to be heavily infested (McCubbin, 1948).

LIFE-HISTORY AND BIONOMICS OF THE EELWORM.—The egg-cases or " cysts " formed by the dead bodies of the female eelworms eventually fall off into the soil, where they remain well protected by the hardened cyst-wall throughout the winter. With the coming of suitable temperature and moisture conditions, and under the stimulus provided by excretions from the roots of growing potatoes, or of certain grasses, the larvæ (each about $\frac{1}{60}$ in. long) hatch out from the eggs in large numbers (*cf.* Fig 33). In the absence of this special stimulus from root excretions very few larvæ emerge but they remain alive within the cysts for at least ten years (Triffitt, 1932). Once liberated, the larvæ are more vulnerable but, even so, it has been shown by Franklin (1937) that they can survive during a normal winter and spring for a period of nine months, or for as long as sixteen months under sheltered conditions. However, hatching is at a maximum when potatoes are growing and the larvæ quickly invade the rootlets near the tips, from which point they migrate upwards in the cortical tissue until at length they come to rest where they feed and continue their development. After a period of feeding the male eelworm " moults " and then elongates into a worm-like form which remains coiled within the skin of the second-stage larva until maturity ; this is followed by a second moulting or " ecdysis " and the mature eelworm frees itself from the host tissues and reaches the soil. The female similarly undergoes a first ecdysis and then swells until all but its head protrudes through the root tissues, where it is fertilised by the male eelworm now in the soil. Egg production now goes on rapidly until from 200 to, occasionally, 800 eggs may be formed. The embryo eelworms begin to develop with the death of the mother, whose body becomes the cyst-wall. During the active feeding period of the larvæ within the root tissues, the cortical cells of the potato are stimulated to grow into " giant " cells which actually press apart and disrupt the conducting elements of the root and so prevent movement of water from the roots, or soluble food from the aerial parts to the roots. One effect of this is to stimulate the production of more and more fibrous roots by the plant (the so-called " hunger " roots) which, by their excretions, stimulate yet more larvæ to hatch from soil cysts, and lead to further secondary eelworm invasions. These invasions of the fibrous roots often constitute the main eelworm attack (Miles, 1930).

The rate at which larvæ hatch from the cyst depends upon many factors, among them being soil temperature for, according to O'Brien and Prentice (1930, 1931), hatching reaches a maximum at a soil temperature of about 18° C. (64·4° F.). Perhaps the most important of these factors, however, is the reaction to certain chemical stimuli. Triffitt (1930) and O'Brien and Prentice (1930, 1931) showed that very few cysts liberated their larvæ in water, whereas under the stimulus of excretions from the roots of growing potato plants there was abundant hatching. The latter authors state that, under such stimulation, the rate of hatching increases to a maximum at about the fourth day and then falls off rapidly, to become negligible within twenty-eight days. They believe this decrease is due to the staling effect of the root excretions since newly formed cysts will also fail to hatch in the same liquid, while even the old cysts, remaining unhatched, become stimulated if fresh root excretions are added to the staled liquid. On the other hand Ellenby (1946*b*) postulates the formation, within the larvæ, of an " inhibitory " substance as a result of modification in their metabolism under the influence of the stimulant ; the accumulation of which causes cessation of hatching. He found considerably more hatchings from cysts which had been punctured than from undamaged cysts, and this he supposes is due to the escape of the inhibitory substances. It has been shown by Triffitt (1934) that certain grasses (*i.e.* smooth and rough-stalked meadow grasses and cocksfoot) also stimulate hatching ; to which may be added *Solanum capsicastrum* (winter cherry), *S. nigrum* (black nightshade), *S. dulcamara* (bitter-sweet) and tomato (Franklin, 1940*b*). Even earthworms have an influence on the rate of hatching, and Ellenby has demonstrated that cysts which had been acted upon by the digestive fluids of earthworms (mainly *Allolobophora longa* Ude), and which were recovered from the worm-casts, liberated 34·5 per cent. of their larvæ as compared with 14 per cent. liberated from cysts from the rest of the soil ; boiled trypsin or boiled digestive fluids from earthworms had not the same effect. On the other hand Morgan (1925) accidentally discovered that potatoes grown with mustard carried fewer cysts than normally, and Triffitt (1929, 1930) showed that this was probably due to the inactivation of the potato root excretions by mustard oil ; an observation which has been confirmed and extended by Ellenby (1945*a*). In view of this retardation of hatching by mustard it would be unwise to assume that the rate of hatching under field conditions may not be affected by other plants, immune from eelworm attack, and common in potato fields.

Identity of the Potato Root Eelworm.—Until 1940 the Potato Root Eelworm was identified with the form attacking sugar-beet (*Heterodera schachtii*), and Leiper and Triffitt (1934) expressed the concern felt by many growers as to the possible effect on the potato crop in East Anglia following the increased cultivation of sugar-beet. However, it soon became clear that considerable biological differences existed between the two forms of root eelworm. Thus Triffitt (1930) had already pointed out that the potato form produced only one generation of larvæ each year as compared with several produced by the Sugar-beet Eelworm, and O'Brien and Prentice (1930, 1931) had stated that the time required for penetration, migration to the feeding zone, and subsequent feeding is twenty-five days in the case of the male Potato Root Eelworm, and more than sixty days for the female; the total time taken to complete the life-cycle being therefore from eighty to one hundred days. These authors pointed out that in this respect, as in others, the Potato Root Eelworm differs from the form which attacks sugar-beet; these differences being summarised as follows :—

(*a*) The cysts of the potato form are spherical, whereas they are lemon-shaped in the case of the Beet Eelworm.

(*b*) A whole growing season is required for the completion of the life-cycle (Triffitt, 1930; O'Brien and Prentice, 1930, 1931), as compared with only thirty days for the beet strain (Rensch, 1925).

(*c*) Only immature larvæ are present in the white cysts of the Potato Eelworm, whereas the Beet Eelworm produces white, summer, cysts containing fully mature larvæ (Baunacke, 1922).

(*d*) The larvæ of the potato form will only hatch from the cysts in appreciable numbers when in the presence of root excretions from potato, certain grasses, or certain chemical compounds, and are not affected by the presence of beet. On the other hand, the Beet Eelworm, at suitable temperatures, will hatch out in water, and is not affected by the presence of potato root excretions.

(*e*) The optimum temperature for hatching Potato Eelworm is 18° C. (64·4° F.); and 25° C. (77° F.) in the case of the beet form (Rensch, 1925).

(*f*) The larvæ of the potato form escape mainly through the open neck of the cyst, while in the beet strain they escape through the vulva (external opening of the vagina).

The importance of these biological differences between what were believed to be strains of the same species of Eelworm lay in the fact that they showed the extent to which each strain had become specially adapted to parasitise only one, or at most a few closely related, kinds of plants; and it was hoped that this would prove equally true of the forms occurring on cereals, peas, and clovers. There seemed at any rate little need to fear that the Potato Eelworm would attack beet or *vice versa*, though the possibility could not wholly be ignored. However, the belief that sufficient stability had been reached by the various forms as to make it extremely unlikely for any strain to revert to a more generalised parasitic habit was reinforced by Franklin's (1940*a*) demonstration of important structural differences between the various strains, and there is now general acceptance of her conclusion that these so-called strains are, in fact, distinct species; the form on beet retaining the name *H. schachtii* and the Potato Eelworm being designated *H. rostochiensis* from the German port of Rostock which supplied the material originally described by Wollenweber. Jones (1950) has recently studied the wide differences in host-range of the cyst-forming species of *Heterodera*. Thus he showed that while the beet form, *H. schachtii*, attacks plants in the Polygonaceæ, Chenopodiaceæ, Amarantaceæ, Aizoaceæ, Caryophyllaceæ, Cruciferæ, Onagraceæ and Labiatæ, *H. rostochiensis* is confined to potato, *Solanum dulcamara* L, and tomato. The Potato Root Eelworm did not attack *Solanum nigrum* L, or *S. sarrachoides* Sendt, and there was no evidence that it is capable of attacking weeds in natural orders other than the Solanaceæ.

RESPONSIBILITY OF *H. ROSTOCHIENSIS* FOR "POTATO-SICKNESS."—Many of the facts brought out by research have seemed to suggest that a number of distinct causes contribute to the development of "potato-sickness," so that much doubt has been cast upon the degree of responsibility to be assigned to the eelworm. The established facts which require explanation appear to be :—

(1) There is, in general, no correlation to be found between the number of eelworm cysts in the soil and the severity of the disease (Morgan, 1925, 1926; Morgan and Peters, 1929; Miles and Miles, 1942), although as Smith and Prentice (1929) stated, a definite correlation did exist in the case of newly infected land.

(2) In a partially affected crop there is a similar lack of correlation between the number of cysts on "sick" and on normally vigorous plants; indeed the latter may have the higher number (Miles, 1929; O'Brien and Prentice, 1931).

(3) Potato "sick" land, after a few years' rest from the crop, will make a fair recovery and may yield well although

the roots still give a high count of cysts. Indeed, if the fertility of the land has been improved the new crop of potatoes may show increased infestation with eelworm (Miles *et al.*, 1943).

(4) Buckhurst and Fryer (1931) found that " sick " soil which was partially sterilised by steam and then re-infested with cysts, produced in the first year a healthy crop of potatoes, although there was a greater increase in the cyst content of the soil than in the unsterilised soil carrying typical " sick " plants. With no further treatment, however, the second crop became badly affected. They concluded that some other factor, probably nutritional, was involved as well as the eelworm in producing the condition known as " Potato-Sickness " ; this factor being destroyed by sterilisation and becoming operative only after the first potato crop had been grown. Similar results were obtained by Millard *et al.* (1932). In 1935 Carroll and McMahon confirmed the conclusions of Buckhurst and Fryer, and showed also that pronounced symptoms of " sickness " could be induced by the addition, to the newly sterilised soil, of water washed through unsterilised soil in which potatoes were growing. The same effect was produced by lengthening the interval to six months between sterilisation and re-infestation with cysts.

(5) A further complication noted by most workers was the almost constant association with eelworm, in potato-sick soil, of the fungus *Rhizoctonia* (*Corticium*) *solani* (page 295) and, occasionally, of *Colletotrichum atramentarium* (page 331) ; though in the case of the last-named fungus no evidence has been found to implicate it as a cause of " sickness." As to the former, Morgan (1925) believed that *Rhizoctonia* contributed largely to the failure of the crop, while in Edward's (1929) pot experiments the potatoes succumbed only to a joint attack by eelworm and the fungus. O'Brien and Prentice (1930, 1931), however, were convinced by a careful examination of affected roots that the fungal attack is always subsequent to that of the eelworm. Larvæ could be found in the rootlets within fourteen days after the " sett " was planted, whereas a further fourteen days' growth occurred before the fungus could be isolated and, only then, from roots already largely destroyed by the eelworm. Buckhurst and Fryer (1931) obtained typical " Potato-Sickness " symptoms with the eelworm, whether alone or with the fungus, but the fungus alone had little effect on

the vigour of growth. They conclude therefore that, while the fungus, under suitable conditions, may be an important parasite of the potato, the development of typical " Potato-Sickness " is a distinct malady due to eelworm attack.

Although all recent work has served to confirm the responsibility of *H. rostochiensis* for " Potato-Sickness," the lack of any correlation between the severity of the malady and the number of cysts—whether in the soil or on the plant, is an important fact requiring explanation ; the more so since a count of cysts present in the soil is still regarded as a measure of the degree of infestation. The best approach is probably to remember that the infecting unit is the larva, and not the cyst, and that the number of larvæ per cyst may vary widely. Thus Franklin (1938) found in samples of " sick " soils from Yorkshire, that whereas one-year-old cysts contained an average of 173·9 living larvæ, there were only 25·5 in each five-year-old cyst and 18·8 in six-year-old ones. She points out that in order to obtain the same concentration of infective units (larvæ) per 10 c.c. of soil she therefore required 210 of the six-year-old cysts, 160 of the five-year-old and only 20 one-year-old cysts. Again, Miles *et al.* (1943) found in a soil from Lancashire that the *effective* cyst concentration (*i.e.* those containing viable larvæ) fell, between 1929 and 1935 (six years), from 12·7 per c.c. of soil to 2·7, although the actual number of cysts recovered fell only from 14·6 to 12·4 per c.c. of soil. It is not surprising therefore that no correlation has been traced between cyst counts in the soil and the intensity of plant symptoms. The benefit accruing from giving the land a prolonged rest from potatoes is due, of course, to the gradual liberation of larvæ from cysts, and their limited existence as " free-living " forms. What happens to the, as yet, unhatched cysts during the period in which the land is free from potatoes was shown by Triffitt (1934) to depend partly, at least, upon the cropping, for some further stimulation to hatch was provided by root excretions from certain grasses (smooth and rough-stalked meadow grasses and cocksfoot ; other grasses tested being ineffective). The grasses themselves are immune from attack from the eelworm, so that after eighteen months under a suitable ley the viable cyst content of the soil had been reduced by 48·63 per cent. Fenwick (1950*a*) points out that although the variability in the rate of hatching is well known, *e.g.* that it rises to a maximum and then tails off to nil, there is insufficient knowledge of the form of the hatching curve or of the rate of emergence, to make an accurate study of the effect of different factors on hatching time or, knowing the number of larvæ hatching over a period, to forecast the ultimate total hatch. The effect of a stimulant such as root-diffusate on hatching depends on (*a*) penetration of the diffusate; (*b*) the response of the larva and (*c*) the mechanical difficulties and larval competition in freeing themselves. Of these, (*b*) is likely to be the limiting factor capable of direct measurement, although some (and perhaps large) departures from the norm may be expected from the operation of (*c*). Fenwick showed that the individual response to root-diffusate followed a normal frequency curve, and that therefore the results could be treated according to the "probit" method of analysis (Bliss, 1937). This method resolves the normal curve in a linear manner so that it becomes possible, by expressing susceptibility to stimulation as a function of either concentration or time, to obtain the linear relationship between dosage and response, with obvious advantages in any comparative work. In a second paper (Fenwick, 1950*b*), he states that even in the absence of root-diffusate about 50 per cent. emergence occurred as compared with 84 per cent. in soils treated with diffusate. If this figure of 50 per cent. is regarded as normal, and if only a short "free-living" stage may be assumed, it would take two years to reduce the eelworm population to 25 per cent. of the original level, and this would still be at 3 per cent. after a lapse of five years; a population which, according to Chitwood and Feldmesser (1948), might only permit of one potato crop with any degree of safety. Fenwick also found significant differences in the degree of emergence with diffusates from the roots of different potato varieties—that from Ulster Chieftain having the greatest effect. Similarly significant differences were observed with three different soils (a stiff heavy loam; a blackland peat and a light greensand); larval emergence being lowest in the greensand. Yet in each soil the same proportion (16 per cent.) remained in the cysts, so that, other things being equal, the rate of fall of infectivity would be fairly constant for all the soils.

The explanation of the lack of correlation between the intensity of symptoms and the number of cysts on the *plant* is more elusive because of the interaction of other factors, fungoid and nutritional, which may be involved. It is, however, known that the *time* at which infection occurs is important since any delay will enable the plant to produce a root system sufficient to withstand a severe drain upon the food supply; indeed it has been shown that an established plant exhibits great tolerance to a relatively high eelworm infestation. Thus O'Brien and Prentice (1930, 1931) record 200 cysts on the roots of a plant showing only slight symptoms, and Miles (1930) states that an average of 75 eelworms per in. of primary root may occur without setting up pathological conditions, even though invasion has taken place within a fortnight of planting the tubers.

Apart from a seasonal fluctuation in the rate of hatching, which gives a maximum response to a stimulant in mid-summer, and is at a minimum in mid-winter under uniform conditions of stimulant and temperature (Triffitt, 1930), and for which no explanation can be offered, there is a good deal of evidence of delays in hatching under natural conditions. Temperature may sometimes be the deciding factor, for O'Brien and Prentice (1930, 1931) record that maximum hatchings occur within twelve days at a temperature of 18° C. (64·4° F.) but are only reached after three weeks at 14° C. (57·2° F.); and to this fact they attribute the less severe effect the disease has upon "first early" varieties in Ayrshire where the crop is well advanced before a soil temperature of 19° C. is reached. The same authors state that heavy dressings of organic manure delay infection and suggest that the larvæ may live saprophytically for a time on the manure before attacking the growing plant. They explain the severity of symptoms on groups of plants, in an otherwise slightly attacked crop, as being sometimes due to the occurrence of light, sandy areas, low in organic matter and therefore easily warmed, so that larvæ are liberated early from the cysts and the plants attacked before many roots have formed. Triffitt (1930) demonstrated a marked retardation in hatching when the oxygen supply was reduced, and suggested this as one reason for the greater prevalence of the malady on light soils. Experimentally, she found after uniform infestation of clay and a sandy loam, that the former gave only 15 cysts as opposed to 340 on plants growing in the lighter soil; she estimated that in the heavy soil only 15·2 per cent.

of the available larvæ succeeded in causing infection. Reinmuth (1929) had already had similar results and showed, in addition, that fewer and smaller cysts, with a smaller number of larvæ per cyst, were produced in clay soils as compared with lighter soils.

The unexpected results following partial sterilisation of infested soil and its re-infestation, described under (4) page 212, also become rather more intelligible in the light of present knowledge, though a full explanation is still not possible. Buckhurst and Fryer's (1931) results, as well as those of Carroll and McMahon (1935), could be explained either on the assumption that sterilisation by steam destroyed the potato-root excretion permeating the soil so that the stimulation of cyst-hatching was restricted to those in the immediate neighbourhood of the newly-planted tubers, or to the production in the soil of a chemical having a similar inhibitory effect on potato excretion as that displayed by mustard. Either explanation is consistent with the renewal of a heavy attack after the addition of washings from unsterilised potato soil, and with the severe attack in the second crop of potatoes taken, by which time the hypothetical inhibitors may have been dissipated in the accumulation of potato-root excretion. The increase in the cyst content of the re-infested sterilised soil as compared with the untreated control was presumably due to the reduced competition permitting a higher rate of survival among the larvæ hatching out, while the vigorous plant growth induced in partially sterilised soil enabled the plants to withstand a higher larval infestation. The delay in the hatching of cysts in partially sterilised soil is explained by Johnson and Townsend (1949) as probably due to the accumulation of ammonia, for they found that the addition of ammonium carbonate to potato-root water inhibited cyst-hatching when the concentration of ammonia reached 100 p.p.m. Professor A. R. Todd is quoted as stating that he has identified the " hatching factor " as eclептic acid and that this acid is readily destroyed by alkalies. Chitwood and Feldmesser (1948) have shown that the rate of cyst population increase is greater in less populated soils, *e.g.* there was a 23-fold increase when only 10 cysts were added to sterilised soil and only a 0·5 times increase when 12,000 cysts were added. It is not unusual in the field to find that the first potato crop taken after a rotation is relatively healthy though heavily infested with eelworm cysts, and this may, in part, also be explained by a sluggishness to infect on the part of larvæ liberated from old cysts. Franklin (1938) indeed, has shown that, although the maximum rate of hatching from old cysts—as from newly matured ones—occurred during the second week of exposure to potato-root excretions, the liberated larvæ were slower in invading the growing roots, and fewer succeeded in doing so, than in the case of larvæ from new cysts.

It is clear that root-eelworm is a major problem which, unless it is solved, will have serious effects in the main potato growing areas. In Great Britain, Johnson and Thompson's (1945) estimate that the critical level of cyst population, above which "potato sickness" may be expected, is 0·5 viable cysts/gram of air-dried soil, is generally accepted as a useful, if arbitrary, standard for advisory purposes. The technique adopted is based on suggestions by Anscombe (1950) and involves the counting of cysts in a sample of 50 grams of air-dried soil. To obtain this sample, 25 auger-borings per 10 acres are taken at random and, after precautions to reduce the sampling error, 1000 grams are withdrawn and air-dried. From this, 50 grams are floated on water and decanted twice, through graded sieves, on to filter paper, bolting silk or a "Fenwick's tray." The cysts so exposed are collected on a glass slide and counts are made of (1) number of spherical cysts (assumed to be *H. rostochiensis*—the inclusion of *H. punctata* would not involve an error of more than 2 per cent.) and (2) number of viable cysts, grouped into those containing few (1-20) eggs and those with many. A count of 50 or more cysts from the sample of 50 grams of soil will, of course, leave no doubt as to the risk involved in planting the field with potatoes, but a count falling well below 50 should be checked on another sample. If the square roots of the two counts do not differ by more than 1·5 it may be assumed that no important error in technique has been made and the mean count can be accepted for advisory purposes. The problem is rather different when an area is surveyed for its suitability for seed production. In that case it may be assumed that infestation, if present, will be of a relatively low order and caution in interpretation is necessary before complete absence of infestation can be accepted. Thus Anscombe (1950) states that the chance of a zero count is about one in ten in cases where the true cyst population is really 0·01 cysts/gram of soil. This is equivalent to 2·5 cysts/250 grams of soil, or about ten million cysts per acre; this (250 grams) should therefore be the minimum weight of air-dried soil floated. If a considerable proportion of the fields sampled give no cysts in 250 gram-units one can feel fairly sure that most, if not all, of the fields have populations substantially less than 0·01 cysts/gram; but if less than 10 per cent. give no cysts it may well be that all the fields have populations of more than 0·01 cysts/gram and that the zero counts are accidental. In other words, the presence of a potentially serious infestation can be demonstrated, but not its absence.

Control of Potato-Root Eelworm

(1) Initial Infestation and Rate of Spread.—The most frequent means of infesting clean land with eelworm is probably the planting of seed tubers to which soil containing cysts adhere. O'Brien and Prentice (1930, 1931), found in one sample of seed an average of 15 cysts per tuber; this means that an acre would thus receive some 300,000 cysts with a potential one million larvæ. True, this represents only $\frac{1}{320}$ of one cyst in 10 c.c. of soil, which might seem negligible when it is remembered that counts as high as 141 cysts per 10 c.c. of soil have been found and that, according to Miles *et al.* (1943), crops free from any sign of "sickness" can be grown on land with a cyst population exceeding 25 per 10 c.c. of soil, so long as other conditions remain favourable for growth. Much higher tuber-contamination sometimes occur and Robertson (1940) estimated that one ton of seed tubers, sampled from clay soil, carried 28½ million larvæ; from which it is clear that from such sources many very serious attacks on new land must have originated. The rate at which a localised attack may spread can be conjectured by O'Brien and Prentice's (1930, 1931) estimation that soil contamination spreads at the rate of 9 ft. each year on level ground with, of course, an acceleration downwards on land with a gradient. Strachan and Taylor (1929) instance a field in Yorkshire in which a small patch, noted first in 1904, had covered the field by 1917; meanwhile a second field had become infested in 1914 and, by 1923 the third, and only remaining, field of the farm showed several bad patches. On the other hand Thompson *et al.* (1949)

found little or no evidence of any serious dispersal of viable cysts by the extensive floods of 1947 around Selby (Yorkshire Ouse), East Ferry (Trent), Kesteven Fens (Witham) and certain Welland and Nene areas; the cysts found, however, were mainly in the flotsam at flood margins.

Clearly, the first consideration should be the prevention of sale of seed-tubers from land known to be infested. Although the practical difficulties in enforcing such a prohibition are great, steps to overcome them are being made. Thus, both in Great Britain and Northern Ireland, all land on which it is proposed to grow seed for S.S. certification must previously have been inspected by Entomologists and found to be apparently free from eelworm. In Northern Ireland the Potato-Root Eelworm Order makes the eelworm a notifiable pest and on such land potatoes may not be planted or, if growing, may not be moved to another part of the same farm or elsewhere except under licence; nor may affected soil be moved from one part of the farm to another and affected "tomato" soil must be steam-sterilised (Patterson, 1948). The same technique as described above (page 217) is used, but with the following important modifications:—(1) a minimum of 50 randomised borings are taken for areas of between one-half acre and two acres; (2) 250 grams form the flotation unit instead of 50 grams; two separate units are examined and both viable and non-viable cysts are recorded; (3) the cyst numbers are recorded as of (*a*) *H. rostochiensis*, (*b*) *H. punctata* and (*c*) lemon-shaped cysts; (4) the presence of a single spherical cyst, whether viable or not, in the soil unit is sufficient to disqualify the field from growing seed-potatoes whether for export or for S.S. certification. This British sampling system, which is accepted by U.S.A., Canada, and certain other countries, has been recommended for use in all countries by the quarantine working party appointed by the newly formed European Plant Protection Organisation (1951).

Seed suspected of carrying cysts may be fumigated in the chitting (sprouting) house *before any sprouting occurs* by means of sulphur dioxide (Fenwick, 1942); one sulphur candle per 1000 cub. ft. of space being burned in an atmosphere made thoroughly damp by spraying water over both tubers and walls. It is said that, under such conditions, every larva is killed without damage to the tubers; any developing sprouts, however, are also destroyed. Franklin (1939) obtained efficient destruction of cysts by immersing the seed-tubers in cold 5 per cent. formalin for five to six hours ; or in one per cent. formalin at 125° F. for twenty minutes. She recommended that the operation should be carried out not later than January to avoid damage to the tubers. When small quantities only of seed-tubers are involved it *may* be sufficient to wash them and brush thoroughly in water, though in U.S.A., where the method is tested annually, no more than from 80 to 89 per cent. reduction can be expected (Anon, 1946, 1948).

(2) ELIMINATION OF EELWORM FROM THE SOIL.—Once land has become infested there is no final remedy except by the breeding of potato varieties immune from attack, or by the total destruction of larvæ in the soil.

(a) *Breeding for Immunity.*—This is by no means an impossible ideal although no practical advance along these lines can, as yet, be reported. No cultivated variety is immune or shows resistance of such a nature as to provide a basis for breeding. A search among South American species of tuber-bearing *Solanum* is, however, yielding promising material in two directions. Thus Ellenby (1945*c*) states that in testing 40 such species in soil infested with *H. rostochiensis* no cysts at all developed on the roots of *Solanum pampasense* and very light infestations occurred on many others as compared with the potato variety Great Scot as a standard. *S. Ballsii* likewise resisted all first attempts to induce cyst formation on its roots (Hawkes, 1947) though later (Ellenby, 1948) it was classed as " exceptionally resistant " but not truly immune. On the other hand, of the common non-tuber bearing Solanums, only *S. dulcamara* (bitter-sweet) appeared to be capable of developing cysts on the root system (Mai and Lownsbery, 1948). Many species have been tested to ascertain if their root excretions stimulate hatching from the cyst of *H. rostochiensis* ; the assumption being that, while such stimulation need not necessarily imply susceptibility to attack (*vide* certain grasses), the absence of stimulation would encourage the hope that the *Solanum* possessed inherent powers of resisting attack. Ellenby (1945*c*) immersed cysts first in root excretions from each of many South American species of *Solanum* and then transferred them to the root excretions from the potato Great Scot. He found that this pre-treatment in nearly all cases prevented all but a few cysts from hatching, and that none at all hatched after preliminary immersion in the root excretions from two species ; afterwards stated to be *S. depexum* and *S. Fendleri* (Hawkes, 1945). There was other evidence also that *S. Calcense* gave little or no stimulation to hatching.

(b) *Resistance of Commercial Varieties to Attack.*—From immunity we must turn, for the present, to the discovery of resistant varieties—at best a palliative. First Early varieties suffer less than main crop varieties in some districts (Ayrshire according to O'Brien and Prentice, 1930, 1931) and in Eire (Dublin) as reported by Carroll and McMahon (1935). But these cases appear to be a matter of the plants escaping severe infection owing to soil conditions retarding cyst hatching ; when an attack occurs before full development of the root system even the early varieties are badly affected. Nevertheless, there is evidence of a definite difference in the power of varieties to resist infestation. Thus, Gemmell (1943) compared the cysts on four varieties and found that not only had Epicure only ⅓ the number of cysts as compared with Golden Wonder, but that the cysts which did develop had a significantly smaller diameter. The cysts on Majestic and Doon Star were intermediate in number but were even smaller than those on Epicure. In hatching experiments, fewer larvæ emerged from the cysts on Epicure and Doon Star than in the case of the other two varieties, and about 20 per cent. of the cysts liberated no larvæ at all as compared with only one to two per cent. in Majestic and Golden Wonder. These results were confirmed and extended by Ellenby (1946*b*), who found that cysts—under similar conditions—from the roots of Arran Banner, Doon Star, Redskin and Kerr's Pink, differed both in cyst-type and in their reaction to root excretions (though there was no correlation between these two factors). The largest number of cysts hatched from Arran Banner and the fewest from Doon Star. During the first autumn only 31 larvæ hatched from 9 of the 200 cysts obtained from Doon Star, and in the following spring the remaining cysts hatched on the average 70 larvæ each, as contrasted with 253 from Redskin and 168 from the Arran Banner cysts. Again, hatching began in seven days in cysts from the two latter varieties and only on the eleventh day in the case of those from Doon Star. When the small size and less viable larvæ from the variety Doon Star are also taken into account, Ellenby considered he had evidence of metabolic differences in the host plant which inhibited full development of the parasite. Similarly, Robertson (1939) found Epicure to give the heaviest yields in infested soils although cysts were as numerous on the roots as in other early varieties; among the main-crop varieties Kerr's Pink was better than Golden Wonder. Under New York conditions, Chitwood and Buhrer (1946*a* and *b*) believed that varietal resistance was correlated with the ability of the host to produce roots at temperatures below that at which heavy eelworm attack occurs. Thus the relatively resistant variety Irish Cobbler shows root growth at 45° F. to 58° F., while the more susceptible Green Mountain variety has an optimum range of 54° F. to 58° F. for root development. They recorded little nematode invasion at 51° F. to 52° F. but there was mass invasion of the roots at 60° F. to 61° F. Mai and Lownsbery (1948), however, have been unable to find any appreciable difference in the resistance shown by 34 varieties of potato in U.S.A., or in 43 varieties of tomato, but state that tomatoes were less strongly attacked than were potatoes.

(c) *Elimination of Larvæ by Biological Methods*.—It has already been mentioned that Triffitt (1929, 1930) obtained promising results in pot experiments in which white mustard seedlings were broken into infested soil in which potatoes were growing (a reduction of 60 per cent. being effected in the cyst population of the roots). Mustard root excretions intensified this effect and it was shown to be due to a neutralisation of the potato-root excretions; field experiments, however, gave disappointing results. O'Brien and Prentice (1930, 1931) were unable to confirm Triffitt's results, nor were they able to effect any reduction in cyst population by growing chicory on infested land. Ellenby (1945*a*) compared the rate of hatching of cysts in potato-root excretion with that obtained when immersed in root excretions from white mustard, black mustard, turnip, rape, cress, brussels sprouts and lettuce. A marked but temporary effect was obtained with black mustard and a slighter one with white mustard and cress; in each case the normal rate of emergence was resumed when the cysts were transferred to potato-root excretion. A somewhat different approach was made by Reinmuth (1929) by first digging in the fragmented potato-tops as soon as the crop was lifted and at once seeding down with either sweet clover (*Melilotus alba*) or with lupins (*Lupinus luteus*) as a catch-crop, which was ploughed in early in September. Later in the month the land was top-dressed with "stinking animal oil" at the rate of 6 cwt. per acre; the oil being absorbed in sawdust for convenience in handling. The object, of course, was to stimulate hatching of larvæ by the animal oil, which then became a lethal agent and destroyed them; a method which did, in fact, greatly reduce the cyst content of the soil and led to a marked increase in yield of potatoes in the following year. The effect on hatching was confirmed by O'Brien and Prentice, but not the reduction in cyst content. A method of "trap-cropping" was suggested by Kühn as long ago as 1891 as a means of controlling beet eelworm, which involved the taking of a susceptible catch-crop immediately after harvesting the sugar-beet; a method which failed because the crop actually used proved to be immune from attack by the eelworm. The principle, however, was adopted by O'Brien and Prentice who advocated the broadcasting of the "chats" or "thirds" from the newly lifted potato crop and ploughing them in. After about fifty days' growth it was assumed that full infestation would have occurred but that no new cysts would have formed; at this stage, therefore, the trap-crop was to be grubbed up and gathered into a large heap to rot. They do not appear to have tested the method on a field scale, but Carroll and McMahon (1939) obtained promising results from small plots in which two successive trap-crops were grown and lifted by the end of May. They reported that while all rhizomes must be removed, any broken roots left in the soil were harmless. Unfortunately, later work on a larger scale by these authors (1944) gave disappointing results due, it was believed, to the failure of the trap-crop of potatoes to hatch out a high proportion of the cysts. The stimulation of root development by the application of heavy dressings of farmyard manure was another method adopted by O'Brien and Prentice (1930, 1931) and was found to increase the yield of potatoes from 1 ton 11 cwt. to 6 tons 3 cwt. per acre; it did not, however, reduce the cyst content of the soil. In general it must be admitted that biological methods for solving the problem of eelworm elimination have not, as yet, led to any marked practical results.

(d) *Elimination of Eelworm by Chemical Means.*—The occurrence of potato-sickness in lime-deficient soils in Lincolnshire, and the fact that, while numerous cysts were found in soil with a *p*H value of 6·0, there were few at a *p*H of 6·7, led Peters (1926) to conclude that a real relationship existed between soil acidity and cyst formation, and to suggest that lime dressings would be found useful as a means of controlling potato-sickness; later, Morgan and Peters (1929) gave a *p*H value of 6·25 as the optimum soil reaction for cyst production. It is now known that if any such correlation does exist it is largely obscured by other factors, and the application of lime has not proved to lead to any direct benefit in eradicating eelworm. Smith (1929) demonstrated that a negative correlation existed between cyst counts and soil *p*H in 53 samples of peaty soils in which the *p*H value varied from 5·0 to 6·2; but found no correlation in 25 peaty-sands with *p*H values from 4·2 to 5·0. In field trials, however, in which these soils received heavy dressings of calcium carbonate, Smith and Miles (1929) found that, although there was some indication of a fall in cyst count as the lime dressing increased, the most obvious relationship was between cyst count and increase in yield; with few exceptions the cyst count increased when the yield exceeded 50 cwt. per acre, and decreased at yields below that very low figure. O'Brien and Prentice (1930, 1931) failed to confirm the existence of any relationship between soil reaction and cyst counts, and stated that, in Ayrshire, applications of lime which raised the *p*H value to over 6·0 had not increased the yield nor brought about any marked reduction in cyst content of the soil. They did, in fact, find evidence that plants growing in soil with a *p*H value between 4·2 and 5·0 tended to suffer less than those on soils outside those limits, but concluded that the soil reaction influenced the growth of the potato plant rather than the activity of the eelworm since, even when eelworms were absent, potatoes grown in soil of *p*H 4·0 or less failed completely. Some approach to harmonising these apparently conflicting results may be found in Ellenby's (1946) experiments on rates of hatchings from eelworm cysts. He demonstrated that maximum hatching occurred at a *p*H value of 6·0 and decreased when the *p*H exceeded 7·0; the numbers emerging also steadily decreased as the *p*H value fell from 6·0 to 4·0, below which the cyst contents appeared to have been killed.

Morgan (1925) reported a significant increase in crop yield, accompanied by a reduction in the cyst population of the roots, by the application of carbon disulphide or calcium cyanide to the soil. This was followed by evidence from the work of many investigators that increases in yield were obtained by the use of naphthalene (Roebuck, 1928; Buckhurst and Fryer, 1931); "drained" creosote salts (Edwards, 1929); calcium cyanide (O'Brien and Prentice, 1930, 1931); calcium cyanamide (Hurst and Franklin, 1938*a* and *b*); bleaching powder (Molz, 1932; Smedley, 1936); calcium chloroacetate (O'Brien *et al.*, 1939; Edwards, 1939; Gemmell, 1944). All, however, proved very expensive to apply and, in most cases the data recorded were either incomplete or conflicting. Thus, Edwards (1939) obtained increases in yield, by the use of calcium chloroacetate, of from 17 cwt. to 3 tons despite an actual increase in the number of cysts in treated soil. On the other hand, Gemmell (1944) found no increase in yield after using this substance, but reported that root infestations, though high, ranged only from 20 to 38 per cent. as compared with 67 per cent. in the controls.

Meanwhile there was a growing recognition of the complexity of the factors involved in chemical control measures, and of the need for detailed laboratory and pot experiments before field tests were undertaken. How complex is the problem has recently been shown by Chitwood and Feldmesser (1948) in a study of soil and plant populations of cysts, based on the wet sieving of a weighed amount of dry soil, and the counting only of cysts found viable on dissection. Analysis of the soil volume occupied by one potato plant yielded an average of 31,000 new cysts and 277,000 old ones (mostly empty). There was evidence of a 50 per cent. sex-ratio, and the rate of population increase was greatest in the less-populated soils; the increase was 23-fold with an original cyst content of 10, and was only increased by 0·5 times in a population of 12,000. A heavily infested soil may contain 2,000,000 female larvæ for each potato plant though such a plant can only support about 40,000. Hence there must be an enormous natural mortality, and the addition of a chemical of only moderate killing power can have little effect on the number of cysts developing on the roots. Indeed, in one test, a 76 per cent. reduction in the viable cysts in the soil (by the use of a one per cent. ammonia fumigant) was followed by a reduction of only 4 per cent. in the number of cysts developing on the subsequently planted potatoes. It is important to realise that these two criteria of control (*i.e.* reduction in soil cysts and reduction in root cysts) will only approximate when the destruction of cysts in the soil equals 98 per cent. or more.

Promising results have been obtained by the use of various Isothiocyanates, and Smedley (1939) who used a number of them found Phenyl Isothiocyanate to be the most effective. Cysts were killed by twenty-four hours' exposure to a 0·001 per cent. solution, and pot experiments in which the chemical was used at the rate of 2 cwt. per acre, gave complete control; the same dressing applied on a field scale gave significant increases in yield, but control of the cyst population could not be demonstrated. Ellenby (1945*a* and *b*) worked with the volatile oil from black mustard (Allyl Isothiocyanate) and obtained complete inhibition of cyst hatchings at a concentration of 1 in 2000, and much reduced hatching at a strength of only 1 in 20,000. When applied at the rate of 0·1 cwt. (11 to 12 lb.) per acre on small field plots 100 per cent. increase in yield was obtained; the application being made in the drills at the time of planting.

The most recent trials have been carried out with the proprietary substance known as D-D, which is a mixture of 1-3-dichloropropylene, 1-2-dichloropropane, with traces of higher chlorides. In Long Island, U.S.A., Chitwood (1946) applied the chemical by hand, and by machine, at the rates of 450, 850 and 1700 lb. per acre, and obtained control measured as an efficiency of 0·999. Counts of 15,255 cysts were found on the control plants and only 953 on plants in treated soil. Quite similar results have been recorded by the U.S.A. Department of Agriculture (Bureau of Plant Industry, Soils and Agricultural Engineering) in the annual reports of the last few years, but a note of caution is found necessary. Thus the 1946 report states that in some cases as many as 2839 cysts per plant were counted in treated soil, from which a heavy soil infestation could soon develop. In this country, Peters (1948, 1949) has compared the effects of D-D with those due to steam sterilisation, using the height of the tallest shoot and the total weight of tubers produced as criteria of crop improvement. As in the trials of Buckhurst and Fryer (1931), Peters found in pot experiments, in which D-D was injected into the soil at the rate of 1460 lb./acre, that eelworm infestation had no significant effect on the first year's crop. Steam had the expected and large beneficial effect on yield, but so also had D-D for, in the absence of eelworm, D-D had a soil-amendment effect amounting to 28 per cent. of the improvement effected by steam sterilisation. The nematocidal action of D-D was very great in the first year and persisted to a considerable degree into the second season. As a result of comprehensive trials on seven 2-acre sites, however, in which D-D was injected at 4 and 8 in. depth and at rates of 0, 200, 400 and 800 lb. per acre, Peters and Fenwick (1949) have concluded that the immediate prospects for controlling *Heterodera rostochiensis* on a field scale by injecting D-D are not promising. At the most responsive of the centres they found that the higher the dose, the higher the yield, the better the kill, and the *higher the final eelworm count* in the soil. This increased soil population of eelworms is understandable under favourable conditions (*e.g.* on sand or silt as opposed to blackland), for although an increase of 50 per cent. in yield could be expected from an application of 800 lb. per acre of D-D, there was a kill of only 50 per cent. of eelworms some four weeks after treatment (*cf.* Chitwood and Feldmesser, 1948—above). Such a reduction would merely facilitate the early establishment of the plant, and bring into effect the operative law of—the better the plant, the more the cysts. Peters and Fenwick (1949) also report that although the nematocidal effect of autumn application of D-D continues for many weeks, so also do the adverse effects on plant growth which, indeed, may be evident six months after soil treatment ; necessitating thorough aeration of the soil in spring. They likewise found that when potatoes are planted within a month of injecting D-D at 400 lb. per acre, a taint may be produced in the tubers which is objectionable to a " fair proportion " of people ; at some interval, from one to seven months, between injecting and planting, the taint ceases to be detectable.

On the credit side, Grainger (1949, 1950*b*) believes that, under Ayrshire conditions, the control effected by an application of D-D at the rate of from 200-400 lb./acre may be the answer to the problem of controlling losses due to root-eelworm. The treatment is carried out in July or immediately after the early crop is lifted, so that seven to eight months elapse before the next potato crop is planted, even when no rotation is practised. His results over the period 1947-50 (Grainger, *in litt.*) show, under these conditions, that D-D consistently reduced the number of cysts per inch of root in the following year, and increased the yield by an amount which, in value, exceeded the cost of treatment. Grainger's counts of root-cysts are made on 12 plants taken at random in each unit plot, involving 160 ft. length of drill; the cysts being counted on measured lengths on several parts of the root system. Although the method is open to criticism it has the big advantage that it measures directly the disease-producing capacity of the cyst population. Contrary to the generally accepted view that D-D retards the hatching of the eelworm egg, Grainger believes the effect is to stimulate hatching for, five months after treatment, he finds only a small (6 per cent.) reduction in the number of eggs but an 87 per cent. *increase* in the number of free larvæ; most of which die before the next potato crop is planted. Hence the reduction in the number of root-cysts, rather than the cyst population of the soil, is the better measure of the potency of the treatment. Grainger agrees with Peters (1949), however, that some lethal factor other than D-D operated in both their trials, since not only did the number of cysts/inch of root fall in the treated soils from 2·75 in 1948 to 0·8 in 1950, but a quite similar trend was observed in the *control* series, where the number fell from 6·25 (1948) to 2·3 in 1950. That this inhibiting factor directly affected plant growth rather than eelworm activity is suggested by the fact that in the same years the yields in both treated and control series also fell steadily from 7·43 tons/acre to 5·2 in the treated plots, and from 6·51 to 5·04 in the controls. Also, it should be mentioned that, in Martin's (1947) view, although D-D is too expensive for general recommendation as a soil fumigant, it not only gives a 95 per cent. kill of eelworms under favourable conditions, but is also effective against weeds, wireworms, cutworms and centipedes. Nevertheless, the disastrous results from an ultimate increase in eelworm population following treatment with D-D, outweigh any of the more immediate advantages, and further work—particularly on dosage—is urgently required. Thorne and Jensen (1946, 1947), for instance, have reported complete failure of sugar-beet from

Heterodera schachtii, on land which had given a good crop the previous year in response to D-D injection ; while Simon's (1949) trials with D-D at the rate of 800 kg. per acre gave a kill of not more than 82 per cent. of *H. schachtii*, and sugar-beet growing in treated clay soils showed signs of phytotoxicity and the roots were distorted. Encouraging preliminary results have been obtained by Staniland (1950) in the treatment of root-eelworm infested soil with Chlorphenol dust. The "chlorphenol" contains both orthochlorphenol and 2-4 dichlorphenol in the proportions of 70 and 30 per cent. respectively, together with 6 per cent. of water and ¼ per cent. of free hydrochloric acid. The "dust" used consisted of an inert carrier incorporating 15 per cent. by weight of chlorophenol. The best results were obtained with a rate of application of 1½ lb. of dust to 9 ft. of drill in a strip one foot wide ; the treatment increasing the yield to 1½ times that of the control. With an application at the rate of 1000 lb./acre growth was good, no root injury occurred and there was no tainting of tubers. As with D-D, however, both cyst and egg counts showed an increase in both control and treated plots.

(3) SUMMARY OF CONTROL MEASURES.—(a) *Clean Seed.*—From 1950 onwards no potato crop will be inspected in Great Britain and N. Ireland for a stock-seed certificate unless the land has previously been certified to be free from eelworm. Administrative difficulties prevent the extension of this safeguard, at present, to other grades of seed so that the ware-grower is dependent on the recognition by the seed-grower and the seedsmen that both duty and self-interest demand that seed from contaminated land should be kept off the market. The risk of contamination by purchasing such stocks from reputable firms is probably not a serious one at present and it should not therefore be necessary for the ware-grower to attempt to eliminate this risk—and any eelworms—by sulphuring the boxed seed in the chitting house, or by washing and brushing the seed before boxing. The onus of taking such precautions in cases where contamination may have occurred rests with the seed-grower and his seedsman.

(b) *Initial and Light Infestation.*—"Eternal vigilance is the price of freedom"—from eelworm—and an inspection of the roots of newly lifted plants for the presence of cysts should be regarded as an essential routine measure. Control begins as soon as root infestation is discovered for it is vital to prevent any " build-up " of the population to the point at which the crop suffers. The long-term benefit obtainable would probably justify an immediate raising of the crop and the destruction of the roots or, failing this drastic measure, the same object might be achieved by sowing " thirds " or " chats " the following spring and lifting (and destroying) the whole crop after time has been allowed for it to become infested without the production of a new lot of cysts (say from forty to fifty days' growth). It is in the initial stages of infestation that the greatest confidence can be felt in an application of D-D in autumn at the rate of 800 lb. per acre ; the few survivors from this treatment are unlikely to remain viable until the next potato crop is taken, particularly if a somewhat longer ley is included in the rotation.

(c) *Old and Heavy Infestations.*—From the earlier discussion it will be evident that the eradication of eelworm in heavily infested land is a most difficult undertaking. Leiper and Trifitt (1934) record that in certain areas in Lincolnshire a profitable crop (although some 1 to 3 tons per acre less than would be expected from clean land) may be obtained by heavy manuring after a four-years' rest from potatoes ; obviously a policy of despair since the only certain effect would be to increase the eelworm population. Lengthening the rotation in itself is not a complete answer, for viable cysts can be found in land ten years after the last crop of potatoes has been taken (Triffitt, 1932), and exceptional cases of crop failure have been recorded following a seven to eight years' interval between potatoes (Wood, 1946). Miles and Miles (1942) also showed that a single seven-year period of rest is not sufficient since, in one case, when potatoes were again taken after a further three-years' rest the cyst population was restored at once to that found before the original seven-year rest period. In Germany during the 1939-1945 war total prohibition of potato planting was enforced on heavily infested land (Ext and Goffart, 1942), but in the post-war years this has been relaxed and Goffart (1949) suggests that an enforced five-years' rest in which potatoes are replaced by other crops, excluding brassicæ, should give reasonable control. Certainly there seems no reason why sugar-beet, other conditions being favourable, should not replace potatoes in one, or even two, rotations. In any case, whatever minimum period of rest from potatoes is adopted, its effectiveness can be increased by ruthless destruction of susceptible plants such as potato "self-setts" or *Solanum nigrum* (black nightshade), and by the inclusion in the grass ley of what would normally be an excessive amount of such grasses as cocksfoot or the meadow-grasses which, while being themselves immune from attack, stimulate the hatching of the remaining cysts in the soil. An autumn application of D-D at the time the ley is ploughed and before potatoes are again taken after a long rest, should give the maximum beneficial effect in eelworm reduction. Finally, it may be worth while when taking the first potato crop to select a variety such as Epicure which, apparently, will return a minimum of viable larvæ to the soil.

Tuber Eelworms

Two distinct species of eelworm are now known to attack potato tubers, i.e. *Ditylenchus dipsaci* and *Ditylenchus destructor*. To British farmers the latter is of more immediate importance since it is now considered to be the species responsible for a rot of tubers in this country as well as in North America. In Holland, however, *both* species cause serious tuber-rots and this fact cannot be ignored by the British grower; the more so as *D. dipsaci* comprises many "races" with varying, and overlapping, ranges of host-plants, and that many of these races are serious pests on agricultural and horticultural crops in this country. It would be rash to assume that none of the three races, known in Holland to attack potato tubers, is to be found in Britain, or that a re-distribution of host-plants or a change of environment may not lead to some other race establishing itself on the potato crop. It seems advisable therefore to discuss fully the problems presented by *D. dipsaci* although this species is not at present known to occur on British potato crops.

(1) POTATO STEM EELWORM

Ditylenchus (*Anguillulina*) *dipsaci* (Kühn, 1857) Filipjev, 1936

Identity of the Potato Stem Eelworm.—The eelworm attacking stem structures in many plants, including the potato, was long known as *Tylenchus dipsaci*, Gerv. and v. Ben, 1859, until it was referred on grounds of priority of name (Goodey, 1932; Anon, 1932) to the genus *Anguillulina*, and designated

Anguillulina dipsaci (Kühn, 1857) Gerv. and v. Ben, 1859. In a recent paper of considerable taxonomic importance, however, Thorne (1949) has shown, *inter alia*, that the morphological characters of this species are those of the genus *Ditylenchus* Filipjev, 1934, and that the Stem-Eelworm should therefore be known as *Ditylenchus dipsaci* (Kühn, 1857) Filipjev, 1936.

NATURE AND EXTENT OF DAMAGE.—The segregation of a new species, *Ditylenchus destructor*, from the well-known and widely distributed *D. dipsaci* will, of course, necessitate a re-examination of the distribution of each species in relation to tuber-rots. Both are definitely known to occur in Holland and, doubtless, in other parts of the continent of Europe, but present estimates of the distribution of *D. dipsaci* are no longer valid. It is, for instance, uncertain to which species Belova (1939) was referring in stating that *D. dipsaci* is widespread on tubers in the Ukraine where, although the degree of infestation is usually not more than 3 per cent., it occasionally rises to as much as 24 per cent. The symptoms ascribed to *D. dipsaci* in continental potato crops differ to a marked degree from those found in Britain. Quanjer (1927) emphasises the ability of the Dutch form of the eelworm to attack the foliage and haulm; the latter becomes brittle and thickened, and carries curled and wrinkled leaves which may also show yellowish-brown spots. Diseased leaves or lateral shoots may be bent downwards and galls are formed, usually at the nodes of the haulm or on the mid-rib on the lower surface of the leaf, but such galls soon shrivel. Galls may also be found on the sprouts as soon as they emerge above ground, but affected sprouts usually die early. Invasion of the stolons occurs through the lenticels which, in consequence, become much enlarged; the stolons also become swollen and curved, and galls are developed. Entry into the tuber appears to be either through a lenticel or at an "eyebrow"; in either case small galls form and quickly increase in size. An early stage of infection of the tuber shows as a small discoloured patch of skin which enlarges as new tissues are invaded by the eelworm. The underlying tissue becomes greyish-brown and mealy as the intercellular spaces enlarge and the middle lamellæ are destroyed. On cutting an affected tuber a brown, well defined line is seen to delimit the diseased zone and, outside this, a thin, transparent line indicates the position of a cork-cambium formed by the healthy tissue to cut off the diseased area. The older-infected tissue loses its starch contents, turns a deeper brown and may become necrotic. Meanwhile the skin darkens to a blackish-grey and peels off to reveal large irregular surfaces of the brown, mealy, underlying tissue. Quanjer (1927) lays special emphasis upon the rapidity and extent of tuber-rotting during storage; the flesh being reduced finally to a blackened putrefying mass in which a few eelworms have managed to survive.

LIFE-HISTORY AND BIONOMICS OF *DITYLENCHUS DIPSACI*.—The genus includes non-parasitic, free-living, species as well as some which are among the most important of plant-parasitic nematodes. In Holland, the potato malady with which we are concerned is ascribed to *Ditylenchus dipsaci* which, as has already been mentioned, occurs in a number of distinct races. The form attacking potato is of less economic importance than those which attack other crops and, in consequence, the life-history of the species has been studied almost exclusively on such crops and not on potato. No doubt the main stages of development are identical on all the host plants, but it would be most unwise to assume that important differences of detail will not become evident when a full study is made on the potato race or races. All available evidence suggests that the species *D. dipsaci* cannot exist as an active organism apart from a living host-plant (*i.e.* it is an obligate parasite), so that its persistence depends largely on the discovery and infection of suitable host-plants. Eggs are laid at any time in the year within the tissues of the living plant and, after hatching, the larvæ develop without any well-defined "second-stage" such as that described earlier for *Heterodera*, until a "pre-adult" stage is reached in which the sexes become differentiated; all stages from the egg to the mature adult being found in the same tissues. Goodey (1932) states that the time required for the complete life-cycle (in clover) is from twenty-four to thirty days, and that in all probability more than one generation occurs within one year.

As the eelworm continues to feed, the plant tissues die and putrifaction usually sets in; this causes a movement of the eelworms to new tissues for, if trapped within the putrifying mass, the toxins produced are sufficiently potent to kill them in a matter of a few hours—although non-parasitic species continue to flourish (Hodson, 1926). If the infested plant tissues dry up instead of putrifying, the eelworm coils up like a watch-spring and, as Goodey (1923) has shown, it can then lie quiescent for a period of at least six and a half years; awaiting only moisture to regain its full activity. However, Hastings (1942) has stated that longevity under such conditions of desiccation depends upon the type of host-tissue; thus the eelworm can persist for nine years in dried oats or teasel, seven years in garlic, six in plantain leaves, five in alfalfa (lucerne) and for only four years in narcissus.

Eventually most of the eelworms are released into the moist soil but it is not known for how long a period they can then survive until a suitable host becomes available. Goodey (1932) has pointed out that not only is the "pre-adult" larva the infective stage of the eelworm but that it also is the one provided with most fatty reserve-food, and is therefore best adapted to survive for a long period in the absence of a suitable host-plant. The work of Robertson (1935) is of interest in this connection since he was able to demonstrate in pot experiments that the *oat-strain* of *D. dipsaci* could survive, and cause infection, after a period of three years under grass. Nevertheless, the possibility must be borne in mind that each generation of eelworm might have obtained sustenance from some grass or weed plant, for Hodson (1926) is of the opinion that the oat-strain of the eelworm is equally at home on cocksfoot. Staniland (1945) has found affected weed-plants in an infested oat crop and, from the weeds *Gallium aparine* (cleavers or goosegrass), *Stellaria media* (chickweed), *Cerastium arvense* (field mouse-ear chickweed) and *Arenaria serpyllifolia* (thyme-leaved sandwort), he has successfully infected oats and—in the case of the two chickweeds—has again transferred the eelworm back to the original hosts.

These facts are of the utmost importance in considering the potato stem-eelworm problem, for until we know the host range of the potato-strain we cannot gauge the effect of the various crops taken in a rotation. *Ditylenchus dipsaci*, in its many strains, can attack cereals, peas, beans, clovers, onions, beet and mangold, as well as potato and a large number of flower-crops. But some strains, in the course of time, have become highly specialised and appear to be unable to transfer to less congenial hosts which, in turn, are preferred by other strains of the eelworm. So arise what are known as "biological strains" or "races" which, to quote Goodey (1931), "represent a present adaptation such that, the longer a parasite attacks a particular host, the higher the degree of specialisation becomes, and the less able it becomes to attack other plants." Thus, the same authority (1947, 1950) regards the races attacking oats, onions, field-beans, parsnips and rhubarb, as belonging to the same biological race, and believes that it is distinct from the one found on clovers for, while clovers can be artificially infested from any of these plants, the eelworm fails to mature sexually and the clovers are not successfully parasitised. The continental race of *D. dipsaci* which attacks potato foliage as well as the tuber is stated by Quanjer (1927) to be capable also of parasitising oats, peas, beans, cabbage and mangold, and "many other plants," and is to be regarded therefore as a generalised, rather than specialised, feeder. The wide range of crop plants liable to attack from the forms of *D. dipsaci* found in potato greatly complicates the possibility of control by any modification of the rotation. Further, as has already been said, there can be no guarantee that, at any time, some other strain of *D. dipsaci* will not adapt itself to the potato, and possibly reproduce in this country the serious continental malady of potatoes referred to by Quanjer (1927).

CONTROL MEASURES.—It is probable that contaminated, or slightly infected, seed-tubers serve as a means of introducing the pest to clean land; any tubers suspected of contact with infected material should therefore be fumigated or treated with 5 per cent. formalin as suggested in the case of the Root-Eelworm (page 220), although there is less likelihood of complete success since eelworms already within the potato "flesh" will probably escape the treatment. Certainly all tubers with brown, mealy flesh and discoloured areas on the skin should be burned or otherwise destroyed; they should not be thrown on the manure heap, nor fed to stock without first being boiled.

Little experimental work on a field scale has been done to test varietal reaction in potatoes to infestation, and most workers would wish for more conclusive evidence on which to express an opinion. Belova (1939) reports that in the Ukraine the most susceptible varieties are Early Rose and Epicure, while Voltman and Parnassia show most resistance.

In potted plants, artificially infested with the eelworm, Hastings (1940) found that only one American variety (Netted Gem) remained free out of twelve tested. Some encouragement from long-term breeding work for immunity is afforded by the results of Seinhorst and Dunlop (1945). These authors found that, while *Solanum demissum*, *S. antipoviczii* and *S. andigenum* were all susceptible, they obtained no infection in the case of *S. chacoense*. Chitwood and Chitwood (1940) have recorded some success by the application of a number of chemical substances to the soil; but many factors beyond the control of the experimenters appear to be operating, and further trials are necessary. Goodey (1945) has found that neither calomel, nor its decomposition products in moist soil, has any effect upon the larvæ of *D. dipsaci*.

(2) POTATO-ROT EELWORM
(*Ditylenchus destructor* Thorne, 1945)

IDENTITY OF THE POTATO TUBER-ROT EELWORM.—A destructive rot of potato tubers, believed to be due to *Tylenchus* (*Ditylenchus*) *dipsaci*, was first reported in the British Isles by Theobald (1909). It was again found by Goodey (1923) who surmised that it was probably old-established but that the symptoms might often have been confused with Blight (page 334). Since then it has been recorded from many counties in Great Britain, especially in the east, but, apart from an occasional severe attack, it has never assumed serious economic proportions. In 1945, Thorne described a new species, *Ditylenchus destructor*, as responsible for a serious rot of tubers in Idaho, and its occurrence was quickly confirmed in Canada (Prince Edward Island) by Baker (1946), and in Holland by McCubbin *et al.* (1946) and by Seinhorst (1949). A re-examination of British material also disclosed that the tuber-rot was due to this species (Goodey and Goodey, 1949), and it must now be accepted that there is no authentic record of the occurrence of *Ditylenchus dipsaci* on potatoes in this country. This statement is by no means equivalent to a denial of its existence, for the morphological differences between the two species are small and require expert observation. The most important of these differences are (1) the rounded tail-tip of *D. destructor* as opposed to the pointed or conical tail-tip of *D. dipsaci* (Thorne, 1945; Goodey, 1951) and (2) the occurrence of four longitudinal striations, or incisures, marking, in *D. dipsaci*, the thickened lateral parts of the body known as the " lateral fields " ; there being six such incisures in the case of *D. destructor* (Thorne, 1945 ; Goodey and Goodey, 1949).

NATURE AND EXTENT OF DAMAGE.—There is nothing in the appearance of the foliage to indicate the presence of the eelworm, but an early stage of an attack is disclosed in the tuber by the small, discoloured areas of the skin, under which the flesh may be white and glistening, contrasting in its mealy texture with the firm, compact, flesh of the rest of the tuber. This stage is short, however, and the affected tissue soon darkens to a rusty brown and is soft and spongy to the touch. Goodey attributes the characteristic glistening of affected tissues to the development of " air-pockets " as the intercellular eelworm destroys the middle lamellæ which, otherwise, would bind the cells together. As in the case of *D. dipsaci*, the eelworm continues to invade new tissues with the consequent extension of both external and internal symptoms ; the affected zones dry up and the outside of the tuber becomes traversed by deep, irregular cracks with outwardly curling margins (*cf.* Figs. 34 and 35). As compared with Blight, the affected areas are slightly sunken, softer to the touch, and frequently develop large internal cavities. J. B. Goodey has recently (1951) shown that, although the eelworm is principally found in the tuber, it also occurs in lesions on the underground parts of the haulm. In the same paper he describes experimental infections as occurring generally through the lenticels, though occasionally entry was effected at an " eye-brow " ; with heavy infections most of the tuber rotted away. Apart from the potato, *D. destructor* has been described on only a few host-plants. McCubbin *et al.* (1946) reported it on the dandelion (*Taraxacum officinale* Weber) in Idaho, and Hurst (1948) found it in Canada on the rhizomes of corn-mint (*Mentha arvensis* L). Goodey and Goodey (1949) confirmed the occurrence of this species on corn-mint and on corn-sowthistle (*Sonchus arvensis* L) from the fens of East Anglia, and J. B. Goodey (1950, 1951) has shown that the form attacking bulbous irises from English, Dutch, and Guernsey sources is also *D. destructor* ; narcissus, on the other hand, although commonly parasitised by *D. dipsaci*, gave negative results when experimentally inoculated with *D. destructor*.

COMPARISON OF THE TWO TUBER-ROTTING SPECIES.—As a preliminary to a consideration of control measures suitable for *D. destructor*, it will be as well to summarise the main differences between the two species.

TABLE XIII

Comparison of D. dipsaci (*potato strain*) *and* D. destructor

D. dipsaci.	*D. destructor.*
1. Tail-tip pointed or conical (Filipjev and Stekhoven, 1941 ; Thorne, 1945).	1. Tail-tip rounded (Thorne, 1945 ; 1945 ; Goodey, J. B., 1951).
2. Four incisures on lateral fields (Thorne, 1945 ; Goodey and Goodey, 1949).	2. Six incisures on lateral fields (Thorne, 1945 ; Goodey and Goodey, 1949).
3. Experimentally transmitted to oats, wheat, rye, peas, beans, clover, onion, cabbage, turnip and mangold (Quanjer, 1927).	3. Negative on all crop plants used in Quanjer's trials (Goodey, 1935). Negative on oats and clover (Edwards, 1936). Negative on narcissus (Goodey, J. B., 1951).
4. Recorded on *Cardamine pratense*, *Trifolium repens* and *Ranuncalus repens* (Quanjer, 1927).	4. Recorded on dandelion (McCubbin *et al.*, 1946) ; corn-mint (Hurst, 1946 ; Goodey and Goodey, 1949) ; corn-sowthistle (Goodey and Goodey, 1949) ; bulbous iris (Goodey, 1950, 1951).
5. On potato it attacks aerial parts, with formation of galls (Quanjer, 1927).	5. Appears to attack only underground organs ; the only exception noted being in dandelion, where it is ectoparasitic between the leaves of the rosette. (McCubbin *et al.*, 1946 ; Goodey, 1951). No galls formed.
6. Gall formation on stolons and tuber. On tuber, large irregular areas of blackish-grey skin peel off to expose brown, mealy, infected tissue underneath (Quanjer, 1927).	6. No galls formed on stolons or tubers. Early stage shows skin discolouration on tuber, below which affected flesh is white, glistening and mealy ; later becoming rusty brown. Skin surface sinks slightly in affected areas and conspicuous, and deep, cracks develop (Goodey, 1923).
7. In some hosts at least, *e.g.* teasel, narcissus, unfavourable conditions following heavy infection cause "clumping" of pre-adult larvæ to form "eelworm wool" (Goodey, J. B., 1951).	7. "Eelworm wool" never found in potato or bulbous iris. Even if host was completely rotted the population was a mixture of eggs, larvæ and adults ; there were no quiescent, highly resistant, pre-adult larvæ (Seinhorst, 1949 ; Goodey, J. B., 1951).

CONTROL OF *Ditylenchus Destructor.*—It seems unlikely that this pest will assume serious economic proportions for, although it has been known for some fifty years, there is no evidence of any increase either in infested localities or in the severity of attack. Indeed, Goodey (1935) found that successive cropping of infested land with potatoes tended to reduce, rather than to increase, the degree of infestation. This rather surprising result was probably due in the main to (i) the fact that on lifting the crop most of the eelworms were also removed; a probability which Goodey (1929) had already established in field trials. These showed that King Edward potatoes planted on land which in the previous year had carried a heavily infected crop, yielded only six infected tubers out of a total of 1551 lifted, (ii) the few surviving eelworms presumably contained no resistant, quiescent, pre-adult forms, such as might be found in the " eelworm wool " of *D. dipsaci*, and (iii) the extremely restricted host-range of *D. destructor* would provide little opportunity for survival until the next potato crop was taken; a handicap to survival which would be increased in proportion to the care taken to avoid " self-setts " or " ground-keepers."

Little or no work has been reported on breeding for resistance to the tuber-rot eelworm. As regards varietal differences in this respect, Goodey (1929) advised caution in accepting, without further trials, the indications given in his own trials that, of the main-crop varieties tested, only Arran Chief was severely attacked, while among " earlies " Epicure suffered badly. Edwards (1936) found the variety King Edward decidedly less severely attacked than others tested, and Seinhorst (1949) regards Red Star as fairly resistant. Goodey did not include Red Star in his trials but he obtained no evidence that any variety was resistant to a marked degree. It is unlikely that chemical means of eradicating the eelworm from the soil will prove necessary for, in Goodey's opinion, there should be no great risk involved in taking potatoes even as often as once in every three years where, for other valid reasons, such a short rotation is practised. Precautions to avoid the introduction of the pest to clean land should, of course, include the discarding of any seed-tubers showing a tendency to cracking; the use of manure from stock which may have been fed on infected tubers should be avoided, and care taken to prevent the mechanical transport of contaminated soil on boots or implements.

CHAPTER XVII

MOLLUSCA (SLUGS) AND MYRIAPODA (CENTIPEDES AND MILLEPEDES)

SLUGS

THE *Mollusca* to which belong the oyster, whelk, mussel and limpet, are soft-bodied (invertebrate) animals usually protected by a shell and adapted for life in water. Snails and slugs are also molluscs but, in the course of evolution, they have lost their gills and have replaced them with a form of " lung " known as a " pulmonary chamber " which enables them to exist under land conditions. Nevertheless, the very high water-content of their bodies (more than 80 per cent. is water) is in constant need of replenishment and hence they can live only in moist surroundings. Although certain snails sometimes cause damage to upland pastures and to sainfoin and clovers, they do not share the unenviable reputation of slugs as destroyers of farm crops, and will not be referred to further in this account of *Mollusca*.

STRUCTURE OF SLUGS.—For all practical purposes the slug is unprotected by a shell although a vestigial one is buried near the hind end of the body, just below a fold of the skin known as the shield or mantle. Close to the right-hand margin of the mantle is the respiratory pore leading to the pulmonary chamber which, by the stretching and contraction of the body, is alternately filled and depleted of air. The greater part of the body consists of the flat, so-called " foot," which is a muscular organ of locomotion. Movement by means of the foot is helped, as well as protection afforded to the slug, by the excretion of large quantities of mucus-slime from a pore placed just behind the mouth, and from numerous small glands on the surface of the body. When it comes into contact with some irritant substance the slug frees itself by casting off the covering of slime, and replacing it with a further excretion. This process cannot be carried on indefinitely, and after two or three successive sheddings of mucus the slug is much weakened and may die. The blunt head of the slug carries the mouth, furnished with a strong upper lip below which is the chitinous, file-like tongue or radula; the forward and backward movement of which enables the slug to rasp away the plant tissues forming its food.

Immediately above the mouth are two pairs of "horns" or tentacles serving as delicate organs of touch. The eyes are borne laterally on the rear pair of tentacles and, although according to Cooke (1895), their structure is far from primitive, the slug is unable to see at a distance of 1 to 2 cm. (*e.g.* less than 1 in.). There can be no doubt that the sense of smell is extremely well developed, though the location of the olfactory organs has been variously placed on the side of the tentacles (Moquin-Tandon, 1851), at the forward end of the foot (Sochaczewer, 1881) and, by Simroth (1882) as quoted by Cooke (1895), as a general function of the integument or skin, though concentrated in the tentacles and near the respiratory pore. The extraordinarily acute sense of smell shown by slugs was demonstrated by Bartsch of the Smithsonian Institute (quoted by Buller, 1920), who proved that *Limax maximus* was sensitive to mustard gas at a dilution of 1 in 10,000,000 and gave some indication, by the nature of its response, of the degree of dilution; whereas man reacts only to a dilution of 1 in 4,000,000. Although this slug was at once enlisted to serve on the western front in the first world war as a detector of gas attacks, this sensitivity to gas exhalations does not seem to have been fully appreciated by scientific workers in searching for "baits" with which to destroy the slug. Thus Buller (1920) found that the smell of the fungus known as the "Stink-horn" (*Phallus impudicus*) and even the far less potent *Russula heterophylla* and *R. nigricans* served to attract slugs in the open at a distance of from 10 to 21 ft.; yet the best "bait" at present in use (metaldehyde and bran) is only effective, according to Thomas (1944), at a distance of 4½ ft. on finely worked soil, and at 3½ ft. on rather coarse soil.

The slug is hermaphrodite (*i.e.* both male and female genital organs develop in each individual). Self-fertilisation, however, is extremely rare, since normally the ovaries of the female organs do not mature until the production of spermatozoa by the male organ has ceased; each functional female is therefore fertilised by a functionally younger male, and upwards of 1000 eggs are laid during the season.

Species of Slugs causing Damage to Potatoes.—The herbivorous slugs with which we are concerned are grouped into three families :—(i) the Milacidæ, with the respiratory pore *behind* the centre line of the mantle, and a strongly marked " keel " or dorsal ridge extending backwards from the mantle to the tail. The Milacidæ include *Milax sowerbyi* Fér. ; *M. gracilis* Leyd. and *M. gagates* Drap. ; (ii) the Limacidæ, with the pore as in Milacidæ, but keeled only (and that less conspicuously) at the tail-end. It includes *Agriolimax reticulatus* Müll. ; (iii) the Arionidæ, with the respiratory pore in *front* of the centre line of the mantle, and a complete absence of a keel except in some very young individuals. The genus *Arion* includes *A. ater* L. ; *A. subfuscus* Drap. ; *A. hortensis* Fér., and *A. circumscriptus* Johnst. Barnes (1949), in addition to giving a " Key " to the identification of slugs, notes that the Milicidæ are the toughest to the touch and the stickiest, the Arionidæ are less tough but rather sticky and the Limacidæ are the softest and most slimy (*cf.* Fig. 36). Our knowledge of the life-history and bionomics of the various common species of slug is far from complete, but much that is available has been brought together and extended by Miles, Wood and Thomas (1931), Carrick (1942) and Barnes (1944). Potatoes are liable to attack by slugs either during growth or in storage, and it is therefore necessary to know something of the habits of the various species which may be involved in the damage. Although they will all feed, on occasion, either on or under the surface of the soil, the different species exhibit definite preferences which may be important. Thus the Grey Field Slug (*Agriolimax reticulatus*) is probably the most widely distributed and, of all species, most responsible for crop damage, yet because it is partial to leafy tissue and normally feeds on the surface of the soil, it is likely to be less important as a pest of growing potatoes than species of other genera which, as in the case of *Arion* spp., feed at or just below the ground surface, or as in *Milax* spp., which feed almost wholly below the surface. Nevertheless, Carrick (1942) states that the population of the grey field slug may increase from 30,000 per acre to 500,000 in a potato field, and that when the number reaches 100,000 per acre severe damage to the crop will result. This author, however, mentions that *Arion*

FIG. 36.—Species of Slugs (page 240).

M. gracilis *A. reticulatus*
A. hortensis *M. Sowerbyi*
M. gracilis *M. Sowerbyi*

circumscriptus, an underground feeder, was also present though rarely trapped, and it may be that the fluctuating numbers of the grey field slug merely served as an index to a similar fluctuation in the underground population of *A. circumscriptus*. Certainly this latter species is regarded by Esslemont (1938) as the chief culprit in the same area of south-eastern Scotland as that investigated by Carrick. Thomas (1947) states that most damage in south-western England is caused by *Arion hortensis* and by *Milax* spp.

Agriolimax reticulatus Müll is a large slug, variable in colour, but usually a mottled grey with a reddish or yellowish tinge ; there are no longitudinal markings along its back or sides, and the respiratory pore is visible near the rear of the right-hand side of the mantle. According to Miles *et al.* (1931), mating takes place on the surface of the ground in warm, moist weather, and is followed by three weeks' quiescence before the eggs are laid in clusters of from 8 to 60 and embedded in a jelly-like mucus. The eggs are translucent, spherical, and about $\frac{1}{12}$ in. in diameter. A few days before hatching the young slug becomes active, eventually ruptures the egg membrane, and reaches any available food-supply of organic matter. Conditions of temperature and food-supply determine the length of time required to attain maturity, but this is usually not more than six to eight months. Mating and egg-laying take place at intervals throughout the year, but eggs laid in late autumn may not hatch until the following spring ; those which *do* hatch, however, are hardy and continue to feed at temperatures only a few degrees above freezing.

Arion spp., " The Garden or Black-Field Slugs." The best known species is *A. ater* L., the large black slug common in moist ditches or hedges, which when extended may be 2 or 3 in. long, but which assumes an almost spherical shape when contracted ; the straw-coloured young forms may easily be thought to be a distinct species (Barnes and Weil, 1944). It rarely causes serious damage to cultivated crops. *A. subfuscus* Drap., is smaller than the last species and never assumes a similar semi-spherical shape. It is coffee-brown in colour, and the body has definite longitudinal dark bands along the sides and back ; like other species of this genus it has a characteristic yellowish foot, a very tough skin and the mucus-slime is yellow to brown. The species is recorded as common in East Lancashire on clays underlying grass, newly broken-up grassland, or near stacked turf. *A. hortensis* Fér. is smaller than the last species, and the longitudinal bands are more distinct on the brown to black body; during the survey made by Miles *et al.* (1931) in East Lancashire, it was reported, together with the grey field slug, as generally distributed on many soils from sands to peat, and clay. *A. circumscriptus* Johnst., on the other hand, is only locally abundant and is rarely taken on pastures in south-east Scotland according to Carrick (1942). The species is grey in colour and the body has a somewhat flattened appearance; the chief characteristic is the prominent white foot which has given it the common name of the " white-soled " slug.

The life-history of *Arion subfuscus* has been described by Miles *et al.* (1931). The eggs are laid in soil or decaying vegetation in clusters of from 20 to more than 30, held together by a translucent slimy mucus; each egg is almost spherical in shape and from 2·5 to 2·8 mm. in diameter. Incubation takes about one month and, when hatched, the young slug has a semi-translucent, long and tapering body with eyes and shell clearly visible. Within three days from hatching the young slug is able to turn its attention from decaying vegetable matter to unbroken leaves on which it feeds voraciously; notwithstanding this, its rate of growth is definitely slower than in the case of the grey field slug.

The species of *Milax* are known as " keeled " slugs because the body is acutely keeled from just behind the mantle to the end of the " tail." They are subterranean feeders and are probably the cause of most of the slug damage to potato tubers in the ground. A common species is *M. sowerbyi* Fér., particularly on stiff land. About 4 ins. long, it is dark brown or dark grey in colour, acutely keeled, with a lenticular (*i.e.* lip-shaped) groove and a respiratory pore placed just behind the centre of the right side of the mantle; the keel is lighter in colour than the rest of the body, often orange-coloured, while the foot is an apricot-yellow. An even more common species in some parts of the country, at any rate as a potato pest, is *M. gracilis* Leyd. (Barnes, *in litt.*) which is smaller (3 ins.) than *M. sowerbyi*, and has a characteristically grey foot, along the centre of which is a dark longitudinal band. In winter *M. sowerbyi* can be found congregated in numbers under stones or rubbish, but the gregarious habit does not extend to feeding and is probably associated only with hibernation. Contrary to *Agriolimax*, which normally feeds but little during the day, *M. sowerbyi* continues to feed below the surface of the ground throughout the day, and may be found feeding within a quarter of an inch of the surface on hot, sunny days in mid-summer (Miles *et al.*, 1931). Mating is most readily observed in autumn or late summer when the slugs congregate, but is probably not confined to this period. The eggs are transparent, somewhat ovoid, and comparatively large, being 4 to 5 mm. long and 3 mm. wide. They are laid below the surface of the soil in small clusters of from 4 to 12 held together by a transparent mucus. Incubation requires about four weeks. On hatching, the young slug is creamy-white and measures 4·5 mm. in length and 1 mm. in width. After two or three weeks the colour becomes dull grey and gradually the slug assumes the adult coloration.

CONDITIONS AFFECTING SLUG POPULATION.—It is generally agreed that soil reaction has little or no effect upon slug population. Thus Miles *et al.* (1931) found heavy infestations in East Lancashire soils with *p*H values of 6·0 to 6·5, and also at *p*H 4·5, while in other cases peaty soils with *p*H 4·5 were relatively free from slugs. Carrick (1942) believes he has evidence that the white-soled slug is more tolerant than some other species to acid conditions.

Moisture is one of the most important factors determining slug population ; which is not surprising when one remembers that slugs have no mechanism, apart from excretion of slime, by which to accommodate their bodies to changes of humidity. It is probably this fact which results in the nocturnal feeding habit, for it is then that the relative humidity of the air is likely to be high. Activity is greatest under moist conditions but, as the atmosphere dries, the rate of movement is reduced from the normal 10 ft. to 1 ft. per hour by the loss of water by evaporation from the mucus slime. Hence there must be constant excretion of fresh slime, leading to exhaustion and finally death. During dry seasons, therefore, crop injury by slugs is at a minimum and is largely restricted to below ground level but, with the return of wet conditions, there is an immediate increase in serious damage. According to Carrick (1942) eggs are not laid in soils with a moisture content of less than 10 per cent., nor do they develop or hatch unless the soil is from 40 to 80 per cent. of saturation. Breeding also is determined by soil water-content; a summer drought persisting throughout August reduces breeding to a minimum but, with a high rainfall in August, there will be large numbers of young slugs inflicting damage during late September and October; an average of 200-300 may easily be picked up in a single half-hour (Barnes and Weil, 1944).

Temperature is important, but less so than moisture. Carrick (1942) states that eggs soon succumb to freezing and that ovi-positing and hatching require a minimum temperature of 5° C. (41° F.). Incubation varies with the temperature; at 5° C., although all eggs may be expected to survive, the time required for hatching is 105 days, whereas with a rise in temperature, the mortality also rises until, at 20° C. (68° F.) 37 per cent. fail to hatch; the remainder, however, only require eighteen days incubation. For adult slugs, Miles *et al.* (1931) found the lethal temperature to be −1° C. to −2° C.; both the grey field slug and *Milax sowerbyi* continued to feed throughout the winter except at temperatures below freezing point, the latter species being more susceptible to frost than the former. The seasonal activity of slugs, as might be expected, appears to vary with the species. Barnes (1944) and Barnes and Weil (1944, 1945) made a hand collection over two years from some 50 gardens, and found that *Arion subfuscus* was the first to reach maximum activity in what is usually the dry, warm weather of June. This was followed from June to September by *Agriolimax reticulatus*, and by *Milax sowerbyi* in September. It was not until October to December that *M. gracilis* and *Arion hortensis* reached their peak activity; these last two species being trapped far less often in summer.

Cultivation affects the slug population in various ways. Thus the addition of large amounts of undecomposed organic matter increases the water-holding capacity of the soil and also provides an abundance of food in the absence of growing crops. Morris (1927) reported an increase from 13,500 per acre to 33,700 at Rothamsted following an application of farmyard manure on land previously unmanured. An improvement in drainage, in so far as it is effective in reducing the water-content of the soil, will tend to reduce the slug population but, as pointed out by Miles *et al.* (1931), would also raise the temperature at certain times in the year, and would allow slugs greater freedom of movement and a wider range of activity.

CONTROL MEASURES.—(a) *Natural Enemies.*—Although slugs are eaten by many birds as, for instance, rooks, starlings, blackbirds, thrushes and ducks, their nocturnal habits probably prevent any large scale reduction in numbers. Nor does the activity of moles, toads, shrews and certain carnivorous beetles, all of which are said by Theobald (1905) and quoted by Miles *et al.* (1931), to devour slugs appear to have much effect.

(b) *Hand Trapping.*—This method of eradication by means of cut potatoes, fruit-skins, or cabbage leaves, is of some value in gardens, but the effect is probably only temporary; the available evidence, showing considerable stability in slug population from year to year, suggests that localised trapping merely results in a movement of slugs from over-populated areas into the depleted ones.

(c) *Chemical Means.*—Chemicals are used either as "repellents" or as "baits." Repellents are often, but not necessarily, toxic to the slug which, in any case, is averse to crossing areas dressed with these substances. Thus common salt induces copious excretion of slime and this, if repeated several times, leads to weakness and death. It is similarly known that slugs avoid traversing soil treated with lime or soot. Washing soda, crude naphthalene, aluminium sulphate, copper sulphate and dry Bordeaux powder, have also been used with success when applied along rows of seedlings. Some difference in response by different species to these substances is suggested by the fact that while Hodson (1924) found aluminium sulphate lethal to *Agriolimax reticulatus*, Miles *et al.* (1931) reported that *Milax sowerbyi* easily cast off this substance in the slime.

Other attempts have been more successful by the use of toxic substances which either themselves attract the slug or do so after being mixed with a suitable food such as bran. Of these, "Meta-Fuel" has largely replaced the older bait of "Paris Green," both because it is usually more efficient and, although dangerous to the health of human beings if eaten in quantity, is much less poisonous than the Paris Green. The active constituent of this proprietary substance is metaldehyde, which is a compound crystallising in colourless needles, and is produced by the action of acids on acetaldehyde at low temperatures—and which, despite its name, is not really an aldehyde. In preparing " Meta " for use, the sticks or bars, in which form it is sold, are ground to a uniform powder and mixed in the proportion of 1 oz. of meta-fuel to 3 lb. of bran (or the bran may be replaced by waste material such as sawdust or tea-leaves, if bran is unobtainable). This quantity is sufficient for one rod, and ½ lb. of the meta mixed with 25 lb. of bran can be broadcast per acre. Many of these chemicals, including meta-fuel, rapidly lose their efficiency when wet, and it is therefore convenient to use the meta in small heaps under some form of cover to protect it against rain and birds. A mild evening when the soil is moist should be chosen ; dry or frosty conditions are not suitable. Thomas (1948) states that one part meta in thirty parts of bran by volume is the minimum effective concentration for obtaining an economic kill of slugs under average weather conditions. For use against *Milax gracilis* Leydig, heaps of bait should not, normally, be spaced more than two yards apart and, against *A. hortensis*, not more than one yard apart ; the mortality obtained depending on the drying properties of the soil and atmosphere around the bait. He found that D.D.T. " flea-beetle dust " and powdered pyrethrum flowers, when mixed with bran, were sufficiently distasteful to prevent slugs from consuming a lethal dose of the poison, while the addition of 10 per cent. (by volume) of dried blood to meta-bran bait increased the catch but did not increase the mortality. The addition of 10 per cent. (by volume) of dextrose increased the mortality obtained by meta but, on the other hand, did not increase the number attracted to the bait. A meta-bran bait, compacted in biscuit form with anhydrous calcium sulphate, caught more slugs than the ordinary meta bait but almost completely neutralised the effect of the meta. A meta-bran-casein glue bait in biscuit form increased the catch and kill of *M. gracilis* and *A. reticulatus*, but not of *Arion hortensis*. When this complex bait is broadcast in broken biscuit form it remains effective over a long period, thus producing a greater kill of slugs than is obtained from broadcasting an ordinary meta-bran bait. It appears to be still uncertain whether " mets " acts as a contact or a stomach poison and, unfortunately, it seems to be specific to molluscs such as snails and slugs; it is quite ineffective against soil insects (wireworms or leather-jackets) or woodlice (Gimingham, 1940).

(d) *Artificial Fertilisers*.—From what has already been said it is clear that the substitution of artificial fertilisers in place of heavy dressings of organic manure, should prove of value when the slug population is very high. This is particularly true of market gardens where the soils are normally maintained at a very high level of organic matter content.

(e) *Potato Varietal Reaction*.—There is a general belief that some varieties of potato are more readily attacked than others, but precise evidence is scanty. Thomas (1947) has pointed out that the results of field trials should, wherever possible, be related to the species of slug involved. Thus some species (*Arion hortensis*, *Milax gracilis*, *M. sowerbyi* and *M. gagates*) could be regarded as causing primary damage since they attack unbruised tubers, whereas *Agriolimax reticulatus*, *Arion circumscriptus*, *A. intermedius*, *A. subfuscus* and *A. ater* rarely do so although they may eat their way into any cut or damaged tuber. This author found that, of three varieties of potato tested in land infested with *Arion hortensis* and *Milax gracilis*, Arran Banner was most severely damaged, Arran Peak the least, while Majestic occupied an intermediate position. These varietal differences were associated with differences in times of tuber maturation and little damage occurred in any variety prior to this date. He quotes Fox-Wilson as recording in November 1943 the apparent immunity of Arran Peak from attack by *Milax* spp. when growing alongside Dunbar Standard, Red King and Golden Wonder, which suffered badly. On the other hand Carrol and Deasy (1947), while recognising that the damage to any variety tends to increase from mid-August onwards and that it is therefore unwise to plant late-maturing sorts in infested land, put forward the view that the intensity of slug attack is correlated with the skin-colour of the tuber. Generally speaking, the white-skinned, or pale-yellow varieties tested (Epicure, Spry's Abundance, British Queen, Up-to-Date, Dunbar Rover and Arran Banner) suffered least damage, while pink or pink-splashed ones suffered worst (*i.e.* Kerr's Pink, King Edward and Gladstone); although the russett-skinned Golden Wonder and the purple Arran Victory were also rather badly attacked.

It seems clear from all these results that other factors are involved in addition to skin colour and date of maturation (of which simple palatability may well be one), but any such factors still remain to be demonstrated. For the present we can say no more than to recommend that lifting should be done without delay after maturation, and that heavily infested land should preferably be cropped with first or second-early varieties.

Centipedes and Millepedes

The *Myriapoda*, which include the centipedes and millepedes, are elongated, " worm-like " animals with a distinct head and segmented tubular body. They are frequently called " false wireworms " through confusion with the larvæ of certain click beetles (page 269) to which the name of wireworm should be restricted, and from which they can readily be distinguished by the fact that the *Myriapoda* possess many more than the three pairs of legs to be found on a wireworm. The *Myriapoda* closely resemble the primitive insects known as the *Thysanura* or " bristle-tails " (to which belongs the " silver-fish " so destructive of old books) and the *Collembola* or " springtails " and, through them, are allied to the winged insects. Their internal structure is very similar, while externally they are alike in possessing a single pair of jointed feelers or antennæ, and in the structure of their biting mouth-parts, the cutting or masticatory organs of which (the mandibles) are hinged to operate from side to side, and not vertically. The eyes, however, unlike those of most adult insects, are not compound but consist merely of two groups of " eye-spots " or ocelli, in which respect also the *Myriapoda* resemble adult *Collembola* and the larvæ of most other insects.

A clear distinction should be drawn between the centipedes which belong to the Class *Chilopoda*, and the millepedes or *Diplopoda*, for the former are carnivorous and live mostly on small insects and slugs, whereas the latter are vegetarian, and at least extend the damage begun by other plant pests such as slugs and wireworms. The most obvious differences lie in the rather flat body of the centipede as contrasted with the cylindrical form of most millepedes, and in the fact that the former possess only one pair of clawed and jointed legs on each of the many segments of the body (*cf.* Fig. 37), whereas the millepedes have two pairs on each segment except the first three (*cf.* Fig. 38). This curious doubling is also true of the respiratory, circulatory and excretory systems, and is really due to the fact that each segment represents two incompletely separated segments. There are other points of difference also, of which perhaps the most important is the possession by the centipedes of sharply toothed, cutting mandibles, and two pairs of outer jaws, or maxillæ as they are called, furnished with sensory appendages or "palps," and with the addition of a fourth pair of organs which are really legs modified to serve as "poison-claws." The mouth-parts of millepeder have a pair of blunt masticating mandibles and only one pair of maxillæ; they have no poison-claws.

LIFE-HISTORY OF MILLEPEDES.—The millepedes breed from May to July, the fertilised female burrowing into the soil and laying from 60 to 100 eggs inside a spherical nest formed of grains of soil glued together with saliva. After about a fortnight the eggs hatch and the young millepedes find their way into the soil. At first the body has only a few segments and only three pairs of legs, which are found on the first three segments. Growth takes place by the addition of new segments between the last two segments and the animal sheds its skin, or "moults," several times before the adult size is reached. Millepedes are somewhat lethargic in movement and, when disturbed, coil up in the form of a watch-spring; whereas centipedes are very active and usually make good their escape when disturbed. Millepedes seldom cause primary damage to potatoes, but their attempts to eat through the tuber-skin to reach the succulent inner tissues may produce superficial injury easily confused with Common or Superficial Scab (page 375). Once this outer barrier of skin is broken, however, the millepede can greatly extend the damage, and is often the forerunner of rots due to bacteria and semi-parasitic fungi.

COMMON SPECIES OF MILLEPEDES.—As a class the millepedes are divided into groups, of which two are most often associated with damage to plant tissues in this country. The more important of these two groups is characterised by possessing a smooth cylindrical body of thirty or more segments, in contrast to the other group which has a flatter body consisting of only twenty segments. To the former group belongs the so-called " Spotted Snake-Millepede " (*Blanjulus guttulatus*, or *Jules pulchellus* as it is often called), probably the species most commonly found in partially eaten potato tubers. It is small, slender, and about one-eighth of an inch long when full grown. This species can always be recognised by its creamy-pink colour and the occurrence of a row of crimson spots along each side of the body. Perhaps the commonest member of the second group is *Polydesmus complanatus* which, when fully grown, is about an inch long and varies in colour from a pale purplish-white to a dull red or brown.

CONTROL.—On a farm scale the damage done is not sufficient to justify special methods of control. In badly infested gardens the millepede population can be reduced by (1) attention to general garden sanitation, for the millepede abounds in decaying vegetable refuse ; (2) hand-trapping in hollowed-out roots such as beet or turnip which, of course, must frequently be inspected and the millepedes destroyed ; (3) by the application of certain chemicals. Thus, crude naphthalene applied at the rate of 2 to 3 oz. per square yard, and worked into the top few inches of soil, or the thorough incorporation into the soil of a heavy dressing of ground quicklime, will serve as a repellent and so help to protect the crop. The proprietary substance known as " meta-fuel " so commonly used against slugs has little or no effect on the *Myriapoda* (Gimingham, 1940).

CHAPTER XVIII

INSECTA

Collembola, Thysanoptera and Hemiptera

I. COLLEMBOLA OR SPRINGTAILS

THE *Collembola* or Springtails are primitive insects belonging to the *Apterygota* (pages 201-202); one species commonly occurring on the potato. Indeed, this species (*Bourletiella lutea* Lubbock) is one of the most common of insects to be found on potato foliage and it is for this reason, as well as the possibility of confusing *Bourletiella* with aphides—particularly *Aphis* (*Doralis*) *rhamni* Boyer (page 261)—that some brief description of its appearance must be given. *Bourletiella lutea* is a very small (about $\frac{1}{20}$ in.), orange-yellow and globular insect with large black "eye-spots," frequently found in colonies on the underside of potato foliage, to which it clings by means of a small bi-lobed "sucker" on the first segment of the abdomen. The mouthparts are adapted for chewing, and considerable damage is sometimes done to mangolds and sugar-beet by other species; on potatoes, however, the injury is negligible, nor is there any record of its being implicated in the spread of any virus disease. The merest touch results in the insect making a spasmodic spring, which is perhaps the easiest way of distinguishing *Collembola* from the aphides. This leap is made possible by means of a two-pronged "spring" on the underside of the abdomen, which is pointed forward when at rest and is held back by a trigger-like hair. When the "trigger" is released the spring strikes the soil or leaf surface violently and the insect is "flicked" into the air.

II. THYSANOPTERA OR THRIPS

The *Thysanoptera* or Thrips are also primitive insects belonging, however, to the *Exopterygota* (pages 201-202). They are minute (usually less than $\frac{1}{25}$ in. long), generally with two pairs of long narrow wings, so heavily fringed with long hairs as to resemble delicate feathers. The mouthparts are adapted for piercing and sucking plant juices; they are characteristically "lop-sided" in appearance and consist of a bristle-like stylet encased within a cone-shaped structure. The protective cuticle of the leaf epidermis is first broken by "pick-axe" jabs from the mouth-cone and the stylet then sucks up the juices. Externally the damage appears as silvery patches on the leaf and, according to Wardle and Simpson (1927), there is no evidence that the saliva of the thrips is toxic to the plant cells. Thrips are rarely reported as occurring on potatoes in the field though *Thrips tabaci* Lindeman, the onion thrips, is known to breed on potato and tomato (Morison, 1943). This fact is of some interest since the species actively transmits several viruses of Solanaceous plants (page 554) and has been given by K. M. Smith (1937) as a possible vector of potato virus "X" (page 554). According to Morison (1943) there are two generations each year in north-east Scotland and probably three in southern England. Hibernation is probably in the adult stage and fertile females deposit eggs on many succulent kinds of plants during April and May; larvæ (nymphs) appear in June, and become adult in July when males also appear in the progeny. After mating, a second generation develops which is mature by October, the males disappear and the females pass into hibernation. In this country the species is associated essentially with plants belonging to the *Compositæ* but occurs on many other types. Morison believes that it may be the thorough destruction of suitable food weed-plants on cultivated land which drives the insect to attack the crop. The purely superficial feeding by thrips would appear to preclude them from acting as vectors of viruses associated with the deeper plant tissues, *e.g.* potato leaf roll or curly-top of sugar beet, while at the same time apparently fitting them to spread such mechanically transmitted viruses as potato virus "X" (page 501). Nevertheless, no conclusive evidence has been advanced to support this possibility, and it may be significant that, in transmitting the virus of tomato "spotted wilt," the role of thrips is essentially biological rather than mechanical. Thus Bald and Samuel (1931) have pointed out that the ability to pick up the virus is restricted to the larval stage although the infective larva continues to spread the virus after reaching adult life. Mechanical transmission is ruled out also by the fact that a latent or "incubation" period of from five to nine days must elapse between the feeding of the insect on an infected plant and any successful transmission of the virus to a healthy plant.

III. HEMIPTERA

(Plant-Bugs, Jassids, Psyllids and Aphides)

INTRODUCTION.—Although the *Hemiptera* include some serious pests of a number of crops, their importance to the potato grower is chiefly indirect in the fact that these insects include the most active means by which viruses are spread in the field (page 554). Apart from this, many *Hemiptera* inflict direct injury to plant tissues, which may be killed by toxins present in the insect saliva. The mouthparts are adapted both for piercing and sucking, and the brief description of the mouthparts of aphides given on page 557 may be taken as applying, with small modifications, to other members of the *Hemiptera*. Both apterous (wingless) and alate (winged) adults occur ; the latter possessing two pairs of wings of which the hind pair is wholly membraneous, while the forewings may, or may not, be horny near the point of attachment to the thorax. Metamorphosis is both gradual and incomplete.

(A) Sub-Order *Heteroptera*. This includes all forms in which the forewings are horny at the base, of which the "plant-bugs" are typical. Those attacking the potato are grouped in the family *Miridæ* (*Capsidæ*) or Capsid-Bugs, many of which cause serious injury to fruit and other crops as well as to potatoes. They are extremely active insects and can run with great agility. When at rest the wings are laid flat over the back with the rear parts overlapping. Three species are found on potato :—

(1) The Potato-Bug *Calocoris norvegicus* (Gmel) (*bipunctatus* Fab), which is rather less than ⅓ in. long and the largest of the three species. It is a green insect covered with short black hairs and usually with two black spots on the head.

(2) The Common Green Capsid-Bug *Lygus pabulinus* L., an almost entirely green species about ¼ in. long.

(3) The Tarnished Plant-Bug *Lygus pratensis* L., is also about ¼ in. long, but is brown in colour with shades of yellow ; there may be black spots on the body.

All over-winter in the egg stage though *L. pratensis*, according to Smith (1931), and possibly the other species, can also persist through the winter in the adult form, even out of doors. In early summer the first brood of adults can be found on their many hosts, of which the most important are the potato and the stinging nettle. The immediate effect of the puncturing of the leaf by the insect's stylet and the injection of toxic saliva is to produce a red spot which, as the cells die, turns brown and may fall out to give a " shot-hole " effect. A heavy attack results in the death of so much leaf tissue that the continued growth of the remainder causes considerable puckering and distortion of the lamina. In late summer eggs are laid on the food plant and a second brood of adults appears which, in turn, oviposit in the woody hedgerow plants in which the eggs pass the winter (*see* Pethybridge *et al.*, 1922; Smith, K. M., 1920, 1925; Butler, E. A., 1923; Petherbridge and Thorpe, 1928). *C. norvegicus* and *L. pratense* have been implicated (on rather slender evidence) in the transmission of some potato viruses (Murphy, 1923; Elze, 1927).

(B) Sub-Order *Homoptera*, *i.e.* those *Hemiptera* in which all four wings are entirely membraneous. The group includes the Jassids (leaf-hoppers), the Psyllids (jumping plant-lice), the Aphides (greenfly), Scale insects and " White-Flies." Of these, only the first three are normally found on potatoes.

(1) *Jassids or Leaf-Hoppers.*—This group also includes the tiny " Frog-Hoppers " which excrete a frothy liquid suggestive of " spittle." The leaf-hoppers can readily be distinguished from other groups by the angular shape of the longest of the leg-joints (the tibia), the rear pair of legs having a row of spines down each angle of the tibia. The adults are winged and, when at rest, carry the wings sloping upwards like a roof over the back. When disturbed the insect leaps a considerable distance into the air and takes to flight. The two species found on potatoes are :—

(i) *Chlorita viridula* Fall, which is barely $\frac{1}{10}$ in. in length, green and with almost white markings on the head; and (ii) *Eupteryx auratus* Liv., an insect about $\frac{1}{8}$ in. long with the fore part of the body greenish-yellow and the abdomen black; the legs and forewings are yellow. According to Smith (1931) there are probably two or three broods per year; hibernation

FIG. 37.—Centipede (*Geophilus* sp.) (p. 250).

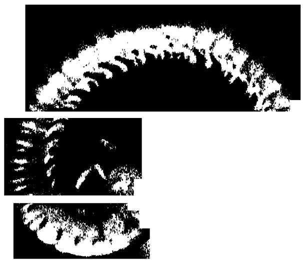

FIG. 38.—Spotted Millipede (page 250).

FIG. 39.—Tuber-Moth; Caterpillar on tuber (page 263).

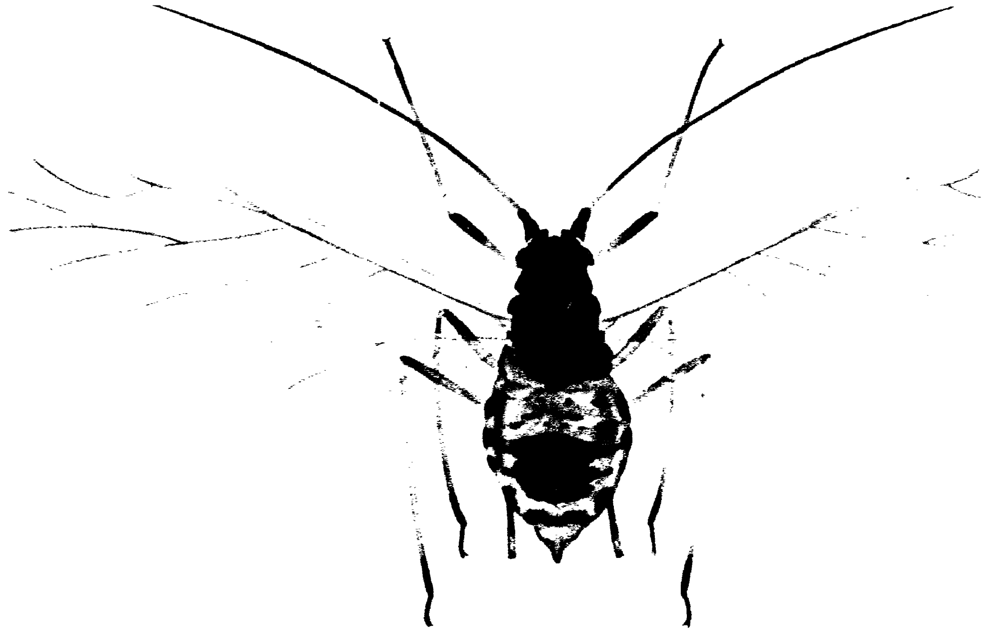

FIG. 40.—*Myzus persicæ* Sulz, alate form (page 260).

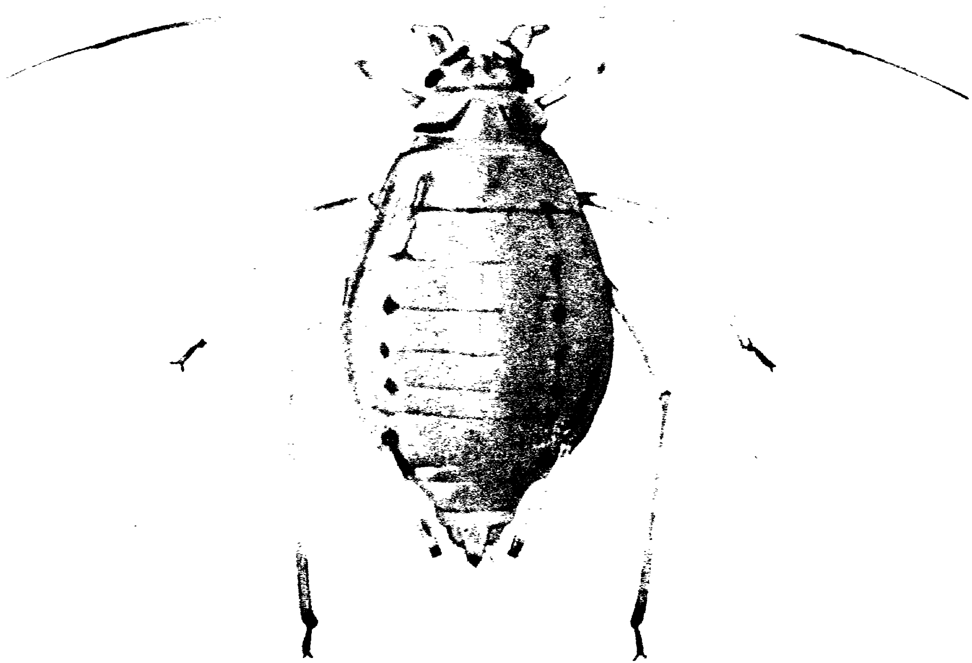

FIG. 41.—*Myzus persicæ* Sulz, apterous form (page 260).

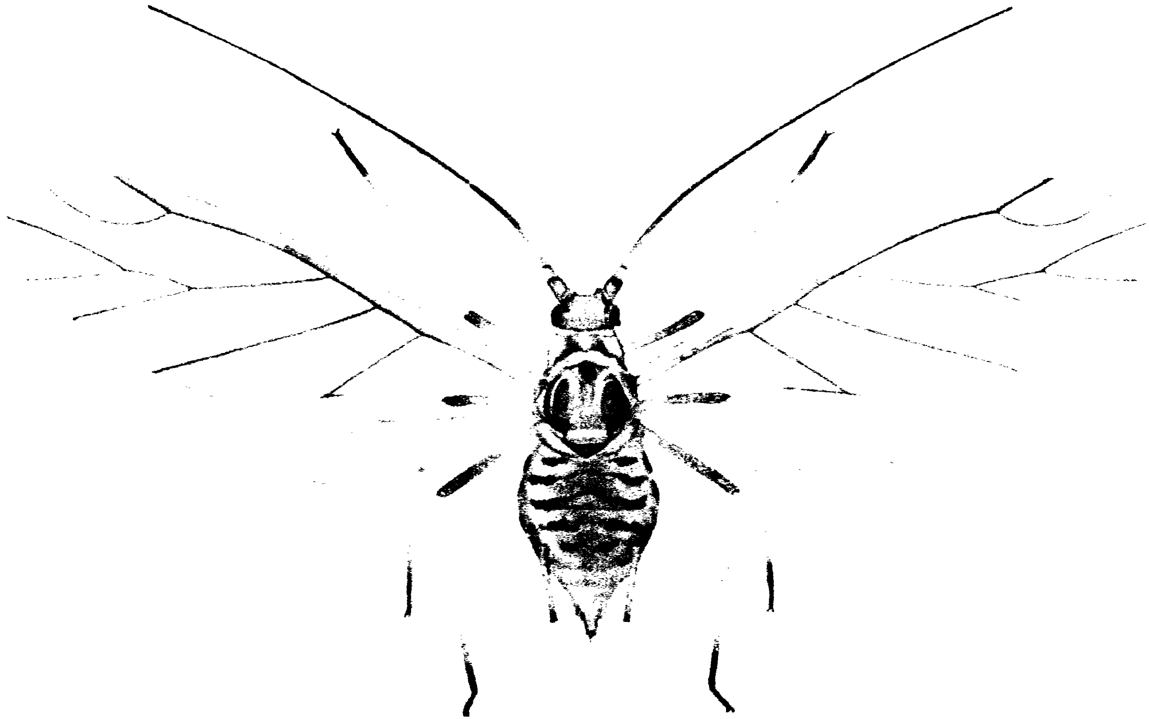

FIG. 42.—*Aulacorthum solani* Kalt, alate form (page 260).

FIG. 43.—*Aulacorthum solani* Kalt, apterous form (page 260).

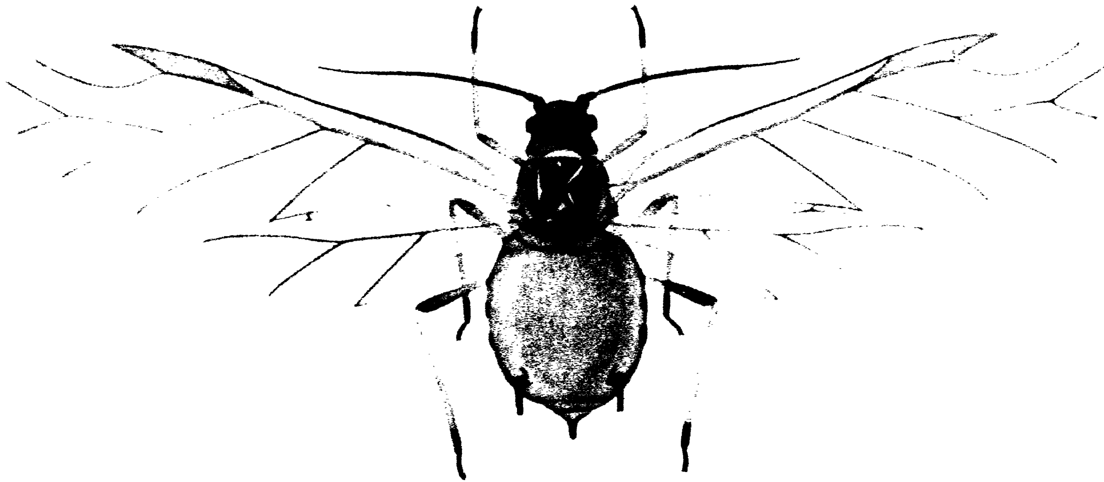

FIG. 44.—*Aphis nasturtii* Kalt, alate form (page 261).

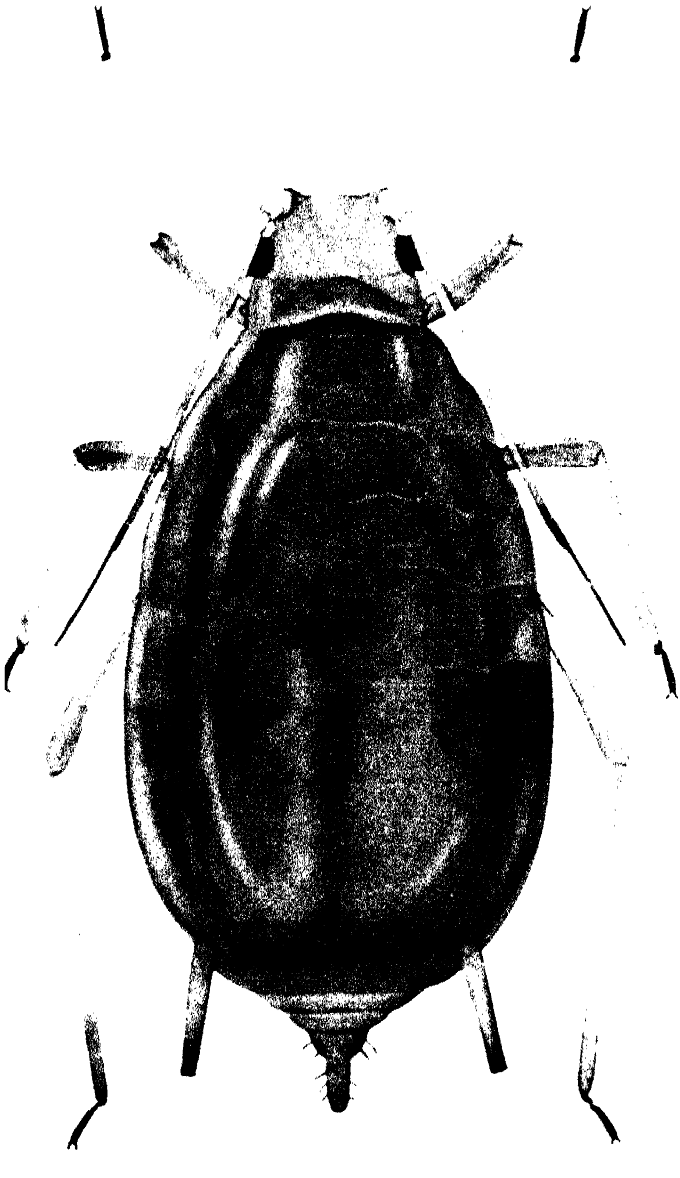

FIG. 45.—*Aphis nasturtii* Kalt, apterous form (page 261).
This species is confused in current literature with *Doralis Aphis rhamni* (Fonsc) *cf.* p. 261.

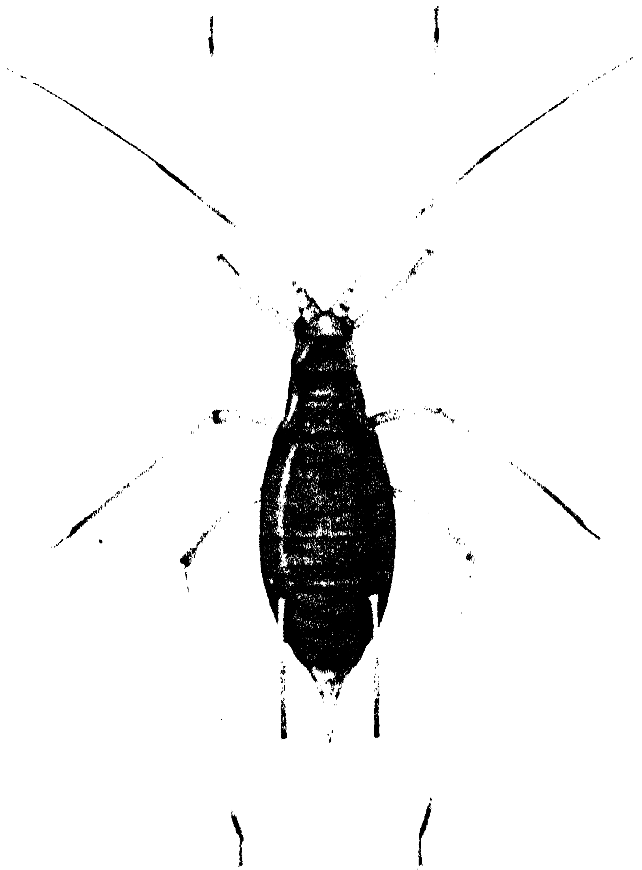

FIG. 40.—*Macrosiphum euphorbiae* (Thos), apterous form (page 261).

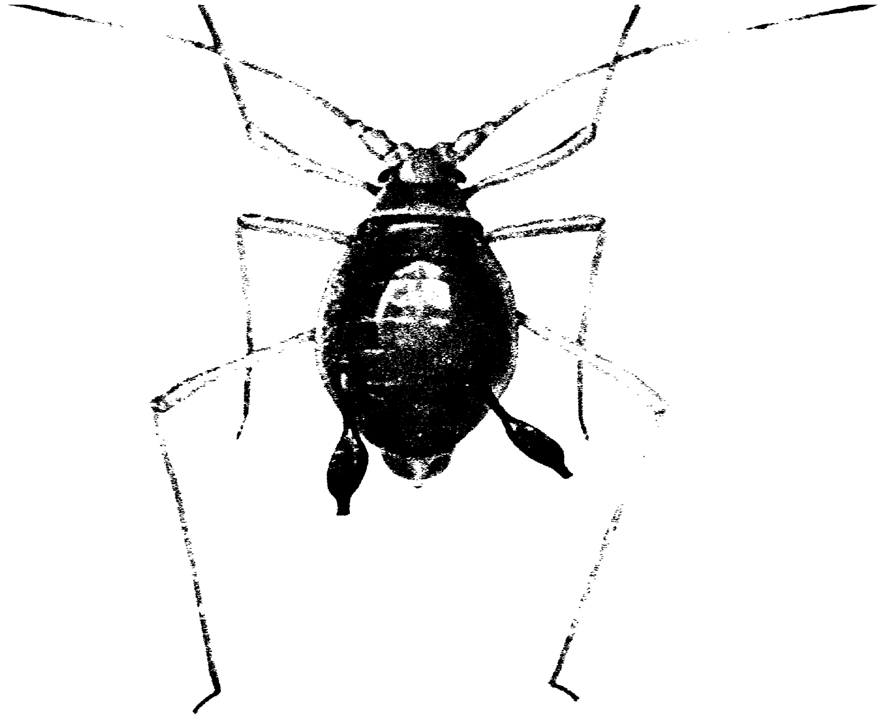

FIG. 47.—*Rhopalosiphoninus latysiphon* (Davidson), apterous form (page 571).

in the egg stage is the most likely though *Eupteryx* may also be capable of hibernating as an adult. The damage caused by these Jassids in this country is small, and is characterised by the bleaching of cells around the puncture to form a white spot (not red as in capsid-bug damage), many of which may ultimately coalesce.

As in the case of plant-bugs, interest in leaf-hoppers in this country centres around the possibility of some of them acting as virus disease vectors (page 554). This is also true of Northern America, where, in addition to this problem, there is an interesting condition of potato foliage known as " Hopper-Burn " which may have serious effects and is regarded as the direct result of the feeding of the potato leaf-hopper *Empoasca fabæ* Harris. It is distinguished from " Tip-Burn," due to excessive loss of water from the leaves, by the fact that instead of a drying out of the tissue between the leaf veins, as occurs with tip-burn, the leaf-hopper effect starts first in the veins and only later spreads to the inter-veinal tissue. Externally there is first a marked retardation of growth, a shortening of the petioles and crowding of leaflets which may turn yellowish or red. Internally the phlœm elements are clogged and disorganised, and there is an accumulation of starch and sugars in the affected leaves (see also leaf-roll, page 440). These observations by Granovsky (1930) were confirmed by Smith and Poos (1931) and by Johnson (1934) but these authors rejected Granovsky's conclusion that the effects were due to the toxic nature of the insect's saliva. Leach (1940), however, points out that Johnson failed to reproduce the effects by repeated puncturing of the phlœm tissues by means of a fine glass needle, and concludes therefore that the initial effects, at least, must be due to the injection of a salivary toxin. *Empoasca fabæ* is believed to be the only species which feeds almost entirely in the phlœm tissues ; it does not appear to have been recorded in this country.

(2) *Psyllids or Jumping Plant-Lice*.—These are very small ($\frac{1}{10}$ in.) insects which, although possessing wings, are incapable of any prolonged flight, and progress by means of short, " flying " jumps aided by their powerful hind legs. They can be recognised by their 9 to 10 jointed antennæ and the swollen femur (the " thigh " or first long joint of the leg). The larva or nymph has a flattened body and prominent wing-buds ;

it is the feeding by the larvæ which is responsible for injury to plant tissue.

Several psyllids cause damage to various crops but none appears to attack the potato in this country. In U.S.A., however, the "potato and tomato" psyllid *Paratrioza cockerelli* Sulc is closely associated with an interesting condition of potato foliage known as "Psyllid Yellows." The symptoms, which vary with the number of feeding insects, include a marginal yellowing and upward rolling of the basal portions of the leaflets, the terminal leaves of some varieties turn bright red or purple in colour and in late stages the older leaves are necrotic. Affected plants are stunted, with swollen nodes and axillary buds which may either develop into aerial tubers or become short shoots with swollen bases and small distorted leaves. When young plants are attacked there may be little or no tuber formation but, instead, secondary aerial shoots may arise on the stolons.

It is still an open question whether the symptoms represent the effect of a virus (*cf.* page 471), as claimed among others by Binkley (1929), Shapovalof (1929) and Smith (1937), or are directly due to the toxic saliva of the psyllid, which is the view expressed by Leach (1940) and by Richards and Blood (1933), although the latter do not exclude the possibility of a virus being concerned—as, indeed, is very strongly suggested by the systemic nature of the symptoms. The adult psyllid hibernates in warm, dry situations and begins to feed in early spring before migrating to potatoes; no symptoms being produced on potatoes by the adult. The eggs are laid on the young, apical leaves of the potato and, within five days, the larvæ hatch out and start feeding by puncturing the phlœm tissue with their stylets; the symptoms produced vary to some extent with the light intensity as well as with the number of larvæ involved.

(3) *Aphides or "Greenfly."*—Under somewhat exceptional conditions of warmth and shelter the aphid infestation of potatoes may be so great as to cause serious direct injury by the withdrawal of sap from the leaves. Following on this there may be still further injury, or death, if the heavily infested plants are sprayed with a copper compound to control Blight, by the penetration of the spray *via* the numerous punctures made by the aphid stylets. The economic importance

of aphides, however, is almost wholly due to the essential role played by many of them in the spread of viruses, including several of the most destructive viruses of the potato (page 554). Questions of the breeding, feeding, movement and over-wintering of aphides in this country are discussed on page 570 *et seq.*, and the structure of the mouthparts on page 557.

(a) *Outline of the Aphid Life-History.*—An aphid may be found in nature in any one of six well-defined forms. (1) The *egg* is deposited by the fertilised female on the winter host plant which, in many cases, is an entirely different kind from the summer food plant. With the advent of warmer days, usually in March, the egg hatches to give rise to (2) the Fundatrix or *Stem-Mother*. This is a large apterous (*i.e.* wingless) aphid which, under suitable conditions, rapidly produces a succession of living larvæ without the aid of a male. (3) These larvæ pass through four stages or " instars " before attaining the fifth or mature stage (the adult louse), the skin being shed by a process known as ecdysis at the end of each of the first four instar stages. The adult is capable of an extraordinarily rapid production of living larvæ (a process known as vivipary). Occasionally in early summer, but rising to a maximum (usually) in August, the young so produced differ from ordinary larvæ in the possession of wing-buds, and are then more correctly called nymphs. Given suitable conditions, the nymphs develop complete wings and become (4) alate (*i.e.* winged) females which usually migrate in autumn to some winter host plant on which they may deposit larvæ as described under (3), or may produce the normal sexual individuals of which (5) the female is apterous, whilst (6) the male may be either apterous or alate. After pairing, the females deposit eggs on the winter host plant and so complete the life-cycle of the species.

(b) *Species Involved.*—Five species of aphides have been recorded as vectors of potato viruses. The typical aphid (in the apterous condition) has an oval-shaped body as viewed from above, green in colour, and like all insects is provided with three pairs of many-jointed legs. The head bears a pair of long flexible jointed antennæ, or feelers, and a conspicuous pair of compound eyes. At the rear end of the body are two prominent cornicles or " horns " whose function appears to be to secrete a waxy substance, not " honey-dew " as is popularly supposed. The important genus *Myzus* can usually be recognised by the occurrence of a prominent protuberance on the inner surface of the base of each antenna, the pair being known as the "frontal lobes." Apart from this diagnostic feature, the chief characters of the apterous form of the five vector species are briefly described below; but it often happens that other species find temporary shelter on potatoes, *e.g.* the plum leaf-curling aphid (*Anuraphis helichrysi* Kalt), and it should be understood that identification of a species is really a specialist's work and usually requires microscopical examination of the insect.

(i) *Myzus persicæ* Sulz. has a pinkish or yellow-green oval-shaped body, about $\frac{1}{10}$ in. long and somewhat pointed in rear. The antennæ are slightly shorter than the body, and the frontal lobes are very conspicuous. The cornicles converge and are slightly swollen midway to give a spindle effect. The insect has a very wide range of summer food plants and, on the potato, is to be found mainly on the middle and lower leaves. As will be seen later, it over-winters as apterous "lice" on brassicæ out of doors and on many glasshouse plants; it is common on boxed seed potatoes in spring. The egg stage is passed on peaches and nectarines in particular, but also on cherry and *Daphne* (*cf.* Figs. 40, 41).

(ii) *Myzus pseudosolani* Theob. = *Macrosiphum* (*Aulacorthum*) *solani* Kalt. The species is of similar size and appearance to *M. persicæ* but can be distinguished by the occurrence of dark green patches on the body immediately in front of the cornicles; these organs are themselves shorter, pale, cylindrical and more widely flared at the tips than in the former species. It is less common on potato than is *M. persicæ*, but when present the distribution on the plant is much the same. The egg stage is known to occur on foxglove, but, according to Ris Lambers (1938), this is only one of the many plants on which oviposition takes place (*cf.* Figs. 42, 43).

(iii) *Aulacorthum circumflexum* (*Myzus circumflexus*) Buckt.—Typical specimens are easily recognised by the occurrence of two large black patches on the back of the body, the front one being shaped like an irregular horseshoe. The shape and size are much the same as in the two former species. *A. circumflexum* is a glasshouse species particularly common on Arum Lily, but will breed readily on many plants out of doors in summer. It is most unlikely that it will be found on field potatoes unless in the vicinity of glass, or possibly of outdoor greater-periwinkle plants.

(iv) *Macrosiphum solanifolii* Ashm.—According to Ris Lambers (1938), the species is more correctly named *M. euphorbiæ* Thomas, and it is certainly distinct from *M. gei* with which it is commonly confused. It is the largest aphid occurring on potato (⅛ in. long), with an elongated body widening towards the rear; the antennæ are as long as or longer than the body. The species usually forms the bulk of the aphid population on potatoes, and although it most commonly occurs on middle and lower leaves, it is quite frequently found on the upper foliage and the flower-stalks. Before the segregation of the species from *Macrosiphum gei* Koch by Ris Lambers, it was assumed to pass the egg stage on roses, but with its separation has come uncertainty in this respect, and further work is necessary before the range of the winter host plants can be determined (*cf.* Fig. 46).

(v) *Aphis (Doralis) rhamni* (Fonsc.).—This is the smallest species ($\frac{1}{20}$ in. long) occurring on potato, is almost circular as viewed from above, and has a characteristic golden-yellow colour which contrasts sharply with the short dark cornicles. It is found on a number of summer food-plants, including the potato. On this latter plant, however, its occurrence is spasmodic and localised, but when present it usually forms large compact colonies restricted to the lowest leaves (*cf.* Figs. 44, 45). The egg stage is passed on the buckthorns (*Rhamnus cathartica* and *R. frangula*).

The name of this aphid should be altered to *Aphis nasturtii* Kaltenbach. The true *Aphis rhamni* of Fonscolombe was refound a few years ago; it is an altogether different insect, which does not live on potatoes (Hille Ris Lambers, *in litt.*).

CHAPTER XIX

INSECTA

LEPIDOPTERA (BUTTERFLIES AND MOTHS), COLEOPTERA (BEETLES) AND DIPTERA (FLIES)

IV. LEPIDOPTERA

THE *Lepidoptera*, with few exceptions, possess two pairs of membraneous wings which are covered with opaque, overlapping scales; the varied colours of which are usually due either to the presence of pigments in the scales or to the spectrum effect of light refracted from them. The adult mouthparts are adapted for sucking only and not for piercing, whereas the larvæ (caterpillars) possess biting mouthparts. The characters relied upon to distinguish between butterflies and moths are not very satisfactory but, for our purpose, it can be assumed that butterflies have antennæ ending in a swollen club and, when at rest, keep their wings erect. Moths, on the other hand, rarely have clubbed antennæ, which instead are of varied shape of which feathery or saw-like ends are the most common; the wings when at rest are usually laid flat over the back. Butterflies cause no damage to potatoes but certain moths may be of considerable importance to the crop.

(1) The Rosy Rustic Moth, *Hydræcia* (*Gortya*) *micacea* Esp.—This moth has a wing-span of from 1 to 1½ in. and owes its common name to the pink or reddish-brown colour of the forewings, the margins of which, however, have a broad grey "hem." The rear wings are entirely grey but a dark line delimits a similar "hem" corresponding to that of the fore-wings. The moth emerges from the pupal case at any time from August to early October and proceeds to deposit eggs on the underside of the potato leaves. From these eggs emerge the larvæ, which have reddish-brown heads and pink or flesh-coloured bodies with a reddish stripe on the back. Each segment of the body bears dark brown wart-like spots surmounted by bristles.

The larva enters the potato haulm, or shaw, and burrows

FIG. 48.—Turnip Moth (page 264).

FIG. 49.—"Cutworm" (p. 264).

FIG. 50.—Yellow Underwing Moth (page 264).

upwards, hollowing it so completely that the plant wilts and dies. Later, the larva leaves the plant and, forming an earthen cell in the soil, pupates in July until some five weeks later when the winged moth emerges. In addition to the potato the moth can be found on other solanaceous plants, on hops, and on such wild host plants as couch grass, plantains, docks and sedges. The only control that can be suggested is to burn infested plants.

(2) The Potato Tuber Moth, *Phthorimæa operculella* Zell.—This moth is believed to be of Central American origin but has now become widely distributed with potatoes and occurs in the southern states of U.S.A., Australasia, Hawaii, India, North and South Africa, and the Atlantic Islands ; spreading in the early years of this century into Italy, Spain and Southern France. It has not yet been recorded in the British Isles but infested consignments of potatoes have been successfully intercepted on several occasions from overseas, *e.g.* from S. Africa, the Canary Islands, Egypt, Cyprus, Malta and Portugal (Fryer *et al.*, 1928-31 and 1932-34). The official view of the serious effects of its introduction may be judged from the fact that it shares with the Colorado Beetle the doubtful honour of being the only insect pest of potatoes named under the Destructive Insect and Pest Acts (Importation of Plants Orders, 1939 to 1945) ; imported stocks suspected of being infested must either be re-exported or destroyed.

This moth is a small grey insect with a silvery body and minute dark specks on the forewings. Like many moths it flies only at night and lays upwards of 300 oval, pearly eggs on the stems and leaves of the host plants. Of these, the potato is the most important but many others of the Solanaceæ, including the tomato, are infested. Incubation in the egg may be only a few days in warm weather and, according to Essig (1912, 1926), there may be from four to six overlapping generations per year ; breeding apparently occurring throughout the winter. It is said to be unable to survive in areas with severe winters. The larva (caterpillar) which is a little less than $\frac{1}{2}$ in. in length, has a dark brown (or black) head and a body which may be white, yellow, pink or green. The damage is caused by the larval burrowings in leaf, stem or tuber ; most being done on tubers in storage (*cf.* Fig. 39). The effect on the tuber is the thorough, though at first superficial, tunnelling of the flesh ; these burrows are partially blocked by white, mealy debris and, being usually superficial, they are outlined as irregular channels by the sinking of the discoloured skin over them. When full grown the larva pupates in a silken cocoon in the soil, in sacks, or in the potato storage bins. According to Essig (1926) the deep planting of clean seed, thorough earthing up, avoiding exposure of tubers in the field overnight at lifting, and taking care not to cover the tubers with potato tops are effective in controlling the pest. Fumigating infested tubers with carbon-disulphide at the rate of 2 lb. per 1000 cub. ft. of air-space in an enclosed compartment is effective in killing eggs and caterpillars, while storing tubers at a temperature not exceeding 40° F. will prevent their further development. Effective protection of stored potatoes against the Potato Tuber Moth by means of derris dust is reported from Queensland (Brimblecombe and Cannon, 1949). Wardle (1929) quotes Picard's view that there is little risk of the moth becoming established in Northern Europe so long as certain precautions are carried out. These include destruction of infested plants, storage of sound potatoes under a layer of sand, and disinfection of infested premises with petroleum or petroleum emulsion. Biological control by means of the Californian Braconid fly *Habrobracon johanseni* Vier. is regarded as promising in view of the fact that the larval moth is not only parasitised by the fly maggot but also serves as food for the adult.

(3) " Cutworms " or " Surface Caterpillars."—These common names are correctly applied to the larvæ of certain Noctuid moths which include :—

(*a*) The Turnip Moth, *Agrotis* (*Euxoa*) *segetum* Schiff., with a wing-span of rather more than 1 in., greyish-brown forewings carrying dark to black markings, and rear wings which are pearly white (*cf.* Fig. 48).

(*b*) The Heart and Dart Moth, *Agrotis* (*Feltia*) *exclamationis* L., with a wing-span of 1 to 1¼ in., brown and black markings on the brown forewings and rearwings which are pearly white in the male and brown in the female.

(*c*) The Yellow Underwing, *Triphæna pronuba* L., having forewings varying from brown to umber in colour and a wavy line forming a " hem " to the rear margin ; the hindwings being yellow with a narrow black border. The wing-span may be as much as 1½ in. (*cf.* Fig. 50).

(*d*) The Silver Y Moth, *Plusia* (*Phtometra*) *gamma* L., with a wing-span of from 1½ to 1¾ in., marbled silvery to reddish-grey forewings, glistening like velvet, and hindwings brownish in colour with a dark border.

In all these species the actively parasitic stage is the larva which superficially resembles a leather-jacket, but can at once be distinguished by the presence, in the moth larva, of four pairs of " prolegs " on the middle segments of the body (two only in the case of the last species) in addition to a single pair on the last segment and the normal three pairs of true legs on the first three segments. The larvæ are smoky or greenish grey in colour and from 1 to 1½ in. long (*cf.* Fig. 49). The first two species have rows of dark spots along the sides, and the last two rather pronounced yellowish or greenish lines running lengthwise along the back and sides.

The adult moths appear from the beginning of June to the end of July, and lay eggs on many common weeds and cultivated plants. Caterpillars hatch out within a fortnight and attack the underground parts of the food plants. In the case of potatoes, rootlets may be eaten through but most damage is caused by the hollowing out of the tubers. In warm seasons some of the caterpillars pupate at the end of July, or in August, so that a second brood of moths appears in the following month ; from these arise a second lot of caterpillars which begin feeding by September. Feeding continues throughout the winter but, in April, pupation begins in earthen cells in the soil. Damage is said to be worst on weedy land, and after potatoes or any root crops have been badly attacked there is risk of great damage to the succeeding corn crop unless the infestation has been reduced. Baiting with a poison consisting of moist bran and Paris Green is, however, less effective for this purpose when, as with potatoes, the caterpillars are feeding well underground. In gardens, hand-picking or running poultry over infested land will greatly reduce the number of cutworms.

V. COLEOPTERA (BEETLES)

This is one of the most numerous of all insect groups. Metamorphosis is complete and both larva and adult possess biting mouthparts. Two pairs of wings, or none, are present; the forewings (elytra) are always horny and form wing-covers for the membraneous hindwings when the insect is at rest. These forewings meet down the middle of the back and may give the impression that the insect is wingless.

(*a*) The Potato Flea Beetle, *Psylliodes affinis* Payk.—This beetle is about $\frac{1}{10}$ in. long, oval in shape and yellowish-brown in colour; the head is dark brown. The wing-covers have rows of large punctures becoming smaller towards the rear of the body. The eggs are laid in the soil near the solanaceous host plant and hatch in about a week, after which the larvæ tunnel for some weeks in the roots before pupating and, later, emerging as an adult beetle to feed on the foliage. The damage done to potato foliage is usually negligible and the insect is only referred to because it has been cited as a vector of potato viruses (page 553).

(*b*) The Colorado Beetle, *Leptinotarsa decemlineata* Say.—The fully grown adult is rather less than half an inch long or slightly larger than the "seven-spotted" Ladybird with which it is most frequently confused. It is the horny wing-covers (elytra) protecting the rose coloured, membraneous hindwings, which afford the best means of identification. In the Colorado Beetle the head and thorax are polished-brown with irregular black markings, and the wing-covers are clay-yellow in colour with ten conspicuous black stripes running longitudinally down the back (*cf.* Fig. 52). On the other hand, the seven-spotted Ladybird *Coccinella septumpunctata* and the two-spotted Ladybird *Adalia bipunctata*, have red wing-covers on which are seven or two black spots respectively. Ladybirds also differ of course in being carnivorous, and indeed they afford one of the best means of reducing aphid or other small insect infestation of potato foliage.

From the end of June onwards the female beetle lays clusters of orange-coloured eggs, in groups of ten or more, on the underside of the food plant—usually potato or other solanaceous host—and these hatch out in a few days as dark-red, hump-backed larvæ which, as they feed, change gradually

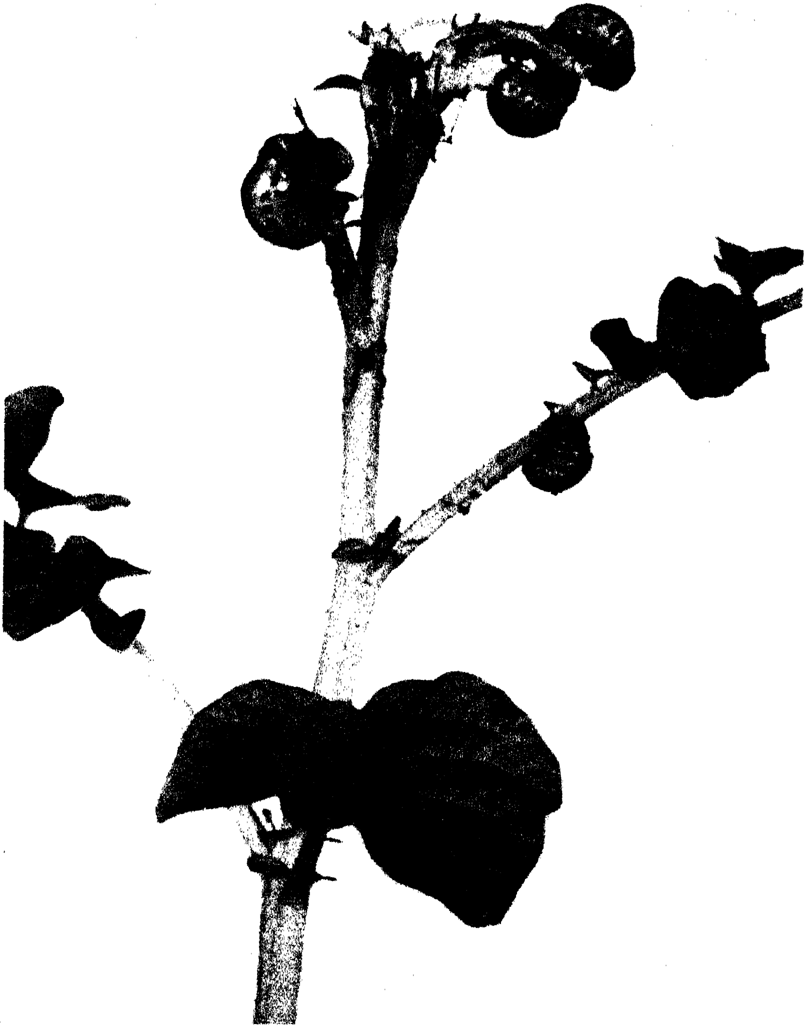

FIG. 51.—Colorado Beetle; Larvæ (p. 266).

FIG. 52.—Colorado Beetle, Adults (page 266).

to a pink or orange colour, with two rows of black spots along each side of the body (*cf.* Fig. 51). It is of interest to note that the yellow colour is the result of the absorption of the yellow carotin constituent of the chlorophyll from the leaf (Palmer and Knight, 1924*a* and *b*), quoted by Imms (1924). Ladybird larvæ are narrow and flatter than those of the Colorado Beetle and, although they have orange spots on their backs, they are otherwise almost black and are commonly known as " niggers."

After feeding on the potato foliage for two or three weeks, the larva of the Colorado Beetle forms a pupa which falls to the ground—differing in this respect also from the Ladybird larva which remains hanging by the " tail-end " to the potato leaf. The adult beetle is fully formed after ten to fifteen days pupation, emerges on the surface of the ground, and starts to feed. Under the most favourable conditions these beetles lay eggs which mature into a second brood of adults in September. This appears to be usual in western U.S.A. and possibly also in many European areas but, although this possibility must always be present, there is no evidence of a second brood occurring in this country, even in 1947 when conditions appeared to be exceptionally favourable. In autumn the beetle burrows some 10 to 12 in. into the soil and hibernates until the late spring, when it again reaches the surface ready to fly considerable distances, if necessary, to reach the nearest potato crop.

The Colorado Beetle was discovered in the Rocky Mountain region of the Upper Missouri River in 1823, but was of no economic importance until the middle of the century when the early settlers arrived with a new food plant, the potato, which proved more satisfying to the beetle than the native wild host plant *Solanum rostratum* Dunal. Within thirty years the beetle had successfully colonised most of the U.S.A. and, three years after its arrival on the American Atlantic seaboard, a single specimen was found in Liverpool Docks. Subsequently, several attempts at colonisation in Europe were frustrated until, in 1920, a number succeeded in establishing themselves on potatoes in the neighbourhood of Bordeaux. The relaxation of control during the war years of 1939 to 1945 resulted in a great extension in the area colonised, and in the post-war period Belgium, Holland, Germany, Poland and

Denmark have been invaded. The beetle had also become established in the Channel Islands and it is evident that the resumption of seaborne and air traffic between the continent and this country has greatly increased the danger to our potato crops. Dunn (1949) has shown that Colorado Beetles can survive up to ten days in sea-water and still be capable of flying when the temperature reaches 80° F. (26·67° C.). The 1947 and 1948 invasions of the Channel Islands occurred as a result of migrant beetles from the Cherbourg peninsula surviving forced " landings " on the sea ; a total distance of some 30 miles. Since the second world war, therefore, the most determined efforts have been made both in the Channel Islands and in this country to eliminate every beetle arriving from the continent. In 1947 for instance the cost of spraying all potatoes in Jersey amounted to £50,000, or nearly £1 per head of the population (Small, 1948). During this year there was also a heavy infestation on the northern seaboard of the continent and some 224 beetles were discovered in this country with every evidence of their transport by boat on imported produce. In 1948 the continental infestation was phenomenal and by the co-operative efforts of the countries concerned, including Great Britain, a million acres were sprayed or dusted.

In this country the Colorado Beetle is a notifiable pest and the occupier of land known or suspected of being infested is required to inform the Ministry of Agriculture, London, or the Department of Agriculture, Edinburgh, according to the location of the site. No other steps are to be taken except to forward, in a securely sealed tin box, a specimen of the suspected insect together with a piece of potato leaf. Unauthorised spraying may cause the dispersion of the pest. Arrangements for destroying the beetle then devolve on the Government scientific staffs who carry out (*a*) *emergency* treatment with an insecticide (D.D.T., *i.e.* dichloro-diphenyl-trichloroethane, is at present used as a 5 per cent. dust, coupled with injection of carbon disulphide in the soil) ; and (*b*) *protective* treatment of neighbouring crops. As a further precaution potatoes are always grown on suspected land in the following year and examined for the emergence of beetles which may have over-wintered (Gimingham and Thomas, 1948). So far, the main potato growing areas in this country have been kept free, and the strenuous efforts made here and in the

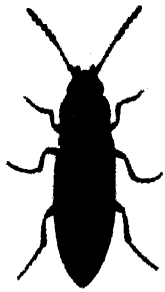

FIG. 53.—Adult Click Beetle (page 269).
(enlarged)

FIG. 54.—"Wireworms"; larvæ of Click Beetle.
(enlarged)

Channel Islands give reasonable grounds for the belief that, even with the exceptionally favourable conditions in 1947 and 1948, the imminent danger of the beetle becoming established has been averted. In the meantime search is being continued among native South American species of *Solanum* with a view to the selection of suitable parents for use in crossing with *S. tuberosa* to produce hybrids resistant to Colorado Beetle attacks. Several are known belonging to different groups, but only those in the *Commersoniana* group hybridise with *S. tuberosa* and, of these, *S. chacoense* (*sensu latiore*) has been chiefly used in breeding for Colorado Beetle resistance (Hawkes, 1947).

(*c*) " Wireworms."—These are the larvæ of certain species of " Click " beetles or " Skip-Jacks " as they are sometimes called. Both common names are descriptive of the manner in which the adult beetle is able, when lying on its back, to somersault into the air, and alight again on its feet with the accompaniment of a loud " click." The most common and destructive are the three species of *Agriotes* ; *A. obscurus* L., *A. lineatus* L., and *A. sputator* L., but other genera are sometimes implicated, e.g. *Athous*, *Corymbites* and *Hypnoidus*.

All agree in general characters. That is, the adult is a dull brown or black beetle, narrowly rectangular in shape and rather more than one-third of an inch in length. The wing covers (elytra) are coarsely pitted, the lines of pits in *A. lineatus* being so well marked as to give a striped effect. In front of the elytra is a prominent horny shield, covering the pro-thorax region and with the rear corners prolonged backwards. The legs are brown or yellow and somewhat slender. The gymnastic prowess is due to the beetle engaging a springy, and backward-directed, spine on the underside of the pro-thorax with a notch in the next segment or meso-thorax ; a sudden pressure then forcibly disengages the spine and the insect is " flicked " into the air (*cf.* Fig. 53).

The female beetle lays her eggs during summer in clusters of from 40 to 100 in damp, shady, spots such as beneath tufts of rough grass, for direct sunlight or drought will quickly kill both eggs and larvæ. Each egg is only $\frac{1}{50}$ in. in diameter and takes about five or six weeks to hatch into a whitish larva, which at once begins to feed on decaying vegetable matter. Later in its first year of growth it turns to the roots of growing plants as food, and thereafter during a period of five years (possibly even six in some cases) it continues to feed voraciously; being apparently directed in its search for food by a reaction to certain chemical compounds secreted in small amounts by the growing roots (Crombie and Darrah, 1947). Evans (1944) confirmed Evans and Gough (1942) that growth depends largely on the type of food; it was greatest with wheat and carrots, less when the food was grass and clover, while with mustard and potatoes the larva only just maintained its weight —or even lost weight when fed on flax. In the first year there is only one moult, but in each succeeding year the skin is cast twice until full growth is attained with a length of ¾ to 1 in.; the larva gradually assuming at the same time the well-known appearance of a "wireworm," *i.e.* a thin caterpillar-like shape, yellowish-brown in colour and with a very tough, shiny skin. According to Lees (1943*a* and *b*) the wireworm is provided with sensory organs on the head by means of which it avoids dry air and is led to the moist conditions under which it tends to congregate. The same author states that the wireworms feed more actively at low, than at high, temperatures, and Falconer (1945*a*) has shown that they can withstand 18° of frost (14° F.) unless this temperature is reached suddenly. The wireworm possesses very short antennæ and powerful jaws on the head, and three pairs of legs only on the three segments of the thorax; although the last, pointed, abdominal segment is provided with a spine or "anal-foot" on which the long body rests like an aeroplane fuselage on its tail wheel (*cf.* Fig. 54). In the genus *Athous*, which is perhaps next in abundance to *Agriotes*, the last segment is not pointed and carries two anal spines.

When the larva is full grown it burrows to a depth of 8 to 10 in. in the soil and, remaining upright, spins round until a smooth cylindrical cell has been formed. In this it pupates, and the pupa undergoes complete metamorphosis until, in about three weeks, the adult beetle is fully formed. Such young beetles can be found in the cell during September, and there most of them remain until the following spring unless they are disturbed, when they seek shelter in the bottom of hedges and ditches. The beetles normally emerge from the soil from March onwards with, according to Brian (1947), the males predominating at first; also at any one time, Brian's traps of *A. obscurus* contained more males than was the case with *A. lineatus*, and these latter had a greater number of males than had *A. sputator*. The click beetle feeds on vegetable matter and, according to the unconfirmed report of Mesnil (1930), on small insects. The most congenial habitat appears to be under old tufts of grass during the day (Miles and Cohen, 1938-1941). Brian (1947) states that the female lays more eggs on the three grasses *Lolium perenne*, *Agrostis tenuis* and *Festuca ovina*, than on mustard, wheat, flax, clover and potato; the more prolific females have the greater longevity, and the males usually have a shorter life than the females. All observers are agreed that the beetle has a relatively sedentary habit of life and, in this country at least, it is reluctant to take to flight (Cohen, 1942). On the ground also it displays little mobility though Gough and Evans (1942) have trapped adult *A. sputator* some thirty yards away from the point of liberation. The greatest activity is shown from the late afternoon to early morning and, according to Roebuck *et al.* (1947), who used a trap of a 3 in. layer of hay overlying closely clipped grass, activity reached a maximum in late May and early June. Brian (1947) followed the movements of the beetle by means of an electronic detection method, and he found a positive correlation between movements at night and temperature. This was also the case with early morning activity but, in addition, there was a negative correlation with hours of sunshine. The sedentary habits of the beetles are believed, partly at least, to explain the wide variation in numbers within a species as well as in the proportion of one species to another in nearby areas (Gough and Evans, 1942; Brian, 1947). Thus the latter worker found very different numbers of all three species in areas only some fifteen yards apart, while Gough and Evans report that the ratio of *A. obscurus* adults to those of *A. sputator* varied from 1 to 62 in one of two nearby fields and nearly 3 to 1 in the other.

It is, of course, the larva or "wireworm" which is so destructive of crops, but many factors, in addition to numbers per acre, are involved in determining the risk of cropping any particular field. These factors as well as the position in respect of modern means of controlling the pests are discussed in detail in Bulletin No. 128 issued by the Ministry of Agriculture, which summarises the findings of a Survey of

England and Wales carried out by Advisory Entomologists during the period 1939-1942; still more recent information has been summarised by Thomas (1949). The following points drawn from both these sources are of direct importance to the potato grower.

(1) DISTRIBUTION IN RELATION TO LOCALITY AND SOIL TYPE.—The three species of *Agriotes* formed the bulk of wireworm samples taken over England and Wales although serious damage was recorded from species of *Athous* and *Corymbites*, especially in Derbyshire, North Wales, Lancashire and Cheshire. The total wireworm population under grass showed a gradient from a high level around 700,000 per acre in Eastern England, during 1940-1942, to less than 200,000 per acre in Western England and Wales. In areas of high population of wireworms the greatest infestation occurred on heavy land and in alluvial, fen, or estuarine soils; and the lowest on lighter and drier land. This relation of infestation to soil type, however, disappeared in areas where the average wireworm count was low. High moisture content (especially summer wetness) and acidity in soils showed a tendency to support a higher wireworm population. Wales appears to be much less seriously affected by wireworms than eastern England. Data from 1871 fields in Mid- and West Wales showed an average infestation of 218,000/acre, with 117 fields giving from 600,000 to 999,000/acre and only 28 having a total elaterid beetle population of one million or more (Erichsen Jones, 1944). There was little apparent relation between this total population and altitude, though a gradient of genera and species could be detected. Thus, in passing from lowland conditions to altitudes of 1000 ft. or more the proportion of the genus *Agriotes* to the total elaterid population fell from 95·4 per cent. to 62·8 per cent.; being replaced largely by *Corymbites* (especially *C. cupreus*). Within the genus *Agriotes*, *A. obscurus* was dominant at all altitudes while *A. sputator* appeared to be a lowland species, becoming rare above 600 ft. and absent above 1000 ft. Erichsen Jones concludes that growing crops at high altitudes affords no measure of escape from wireworms, but rather the reverse, for with increased altitude the smaller *A. sputator* tends to be replaced by the larger *A. obscurus* and this, in turn, by the still larger and more voracious *Corymbites*. He also states that, irrespective

of altitude, fields of high total population tend to be grouped together. Edwards and Evans (1950) consider that, of the three genera, *Agriotes*, *Athous* and *Corymbites*, the last named is much the most injurious to potatoes, wheat, oats, barley and other cultivated crops, but because it is restricted to comparatively high altitudes, it is seldom that *Corymbites* becomes a pest of major importance.

These estimates of population may be assumed to be reasonably valid on a comparative basis, but new methods have supplanted the hand-sorting technique used in the Survey of 1939-1942, and it is now certain that the estimates then made were far too low in many cases. Thus Salt and Hollick (1944) proved, by means of a mechanical method of analysis, that approximately 60 per cent. of wireworms in grassland are larvæ less than ¼ in. long, mostly not recoverable by the older technique, and that the total population in some fields reached 10 millions per acre and, in exceptional cases, even 20 millions. These workers (1946) found that over a period of three years some spots in a field were consistently three to four times as heavily infected as other spots only four yards away; the most important factor determining the distribution being the amount of soil moisture at a depth of 3 in., although the nitrogen and organic matter content, the abundance of certain grasses, and of some other insects, also played a part. In their more recent work Salt and Hollick (1949) have found that the number of wireworms recorded on successive occasions from five Cambridgeshire fields declined during the first year of cultivation to 25 per cent. of the number present before the old leys were ploughed up. This reduction was accompanied by a change in the composition of the larval population; the larger individuals which, under grass, formed only a small proportion of the numbers of wireworms, withstood the changed condition better than the smaller ones until their numbers ultimately equalled these of the smaller size-groups. Salt and Hollick found that many wireworms were destroyed by the actual process of cultivation and that, under cultivation, the wireworm population fails to replenish itself; they believe also that the physical condition of the cultivated soil adversely affects the number of wireworms.

(2) Effect of Cropping on Population and Damage Due to Wireworms.—The Survey showed that the wireworm

population was usually highest on good pastures, less on rough grazing, and lowest on arable land after several years cultivation. Really serious loss occurs as a rule in the first two arable crops taken after breaking up old grass, for the great regenerative power of grasses prevents any noticeable loss even from high wireworm counts and the number normally falls below the danger-line after two years intensive cultivation of crops. More recently an exhaustive study has been made at Cambridge on wireworm populations in relation to crop production (*cf.* Ross *et al.*, 1947, 1948, Cockbill *et al.*, 1947, and Stapley *et al.*, 1947). Thus the work of Stapley *et al.* (1947) fully confirmed the general view that a bare fallow greatly reduces the numbers of wireworms and the subsequent damage to crops; the reduction being greater in fields ploughed in February and March than if ploughed in May. There are important qualifications to be made, however, to the accepted view that crop damage varies with the wireworm population. Thus crops grown on heavy land with a high wireworm count often suffer less than on light land carrying a much smaller population, possibly due to the greater consolidation of the heavier land. Ross *et al.* (1948) agree that wireworm-damaged areas did not always have the higher population, but the greatest damage was found on soil with the highest calcium carbonate content and the lowest sand content. With equal numbers of wireworms there is less risk of crop failure on land of high fertility than on poor soil; a result to be expected since a good "stand" of well-grown, vigorous plants, will outgrow all but the most severe root damage. Finally, there is some difference in the degree of tolerance shown by various crops, apart from that already mentioned as exhibited by grasses. Cereals perhaps suffer the worst damage, whereas flax (linseed), beans, and—to a less extent peas—show comparatively little injury. This is not necessarily an effect of population, for there is no reduction in wireworm counts recorded under peas, though it has been known to under occur flax and, under beans, the reduction has sometimes been spectacular. Rothamsted, for instance, reported a reduction of two-thirds in wireworm population in 1942 following beans; there being no fall in numbers under other crops in the same field. Potatoes are often severely attacked, gapping occurring when seed-tubers are planted in heavily infested land. The damage to the new crop cannot be estimated in terms of loss in yield, but rather as a percentage of the total tubers rendered unsaleable by "holing" or tunnelling. That this is frequently serious, even with very low wireworm infestation, can be seen from the following Table XIV, compiled from data in Bulletin 128.

TABLE XIV

Wireworms (1000 per acre).	Per cent. Tubers Injured.	
	Cheshire (1938-41).	Flintshire (1942).
Less than 100	15	—
100-200	23	—
150	—	45 (20) *
200-300	30	—
Above 300	44	—
850	—	99 (68) *

— = No record. * Figures in brackets = per cent. severe injury.

There is no conclusive evidence of any appreciable difference in the reaction of potato varieties to wireworm attack, and insufficient data on which to base a definite opinion as to the differential effect on early and late maturing sorts respectively. What evidence is available, however, supports the view that the length of exposure to attack may be as important as the number of wireworms per acre. Thus, of eight potato crops sampled in South-western England on two or three occasions in September and early October during the 1942 survey, seven showed an increase in the proportion of damaged tubers of the order of 1 per cent. for each day's delay in lifting; an increase which appeared to bear no relation to the number of wireworms present per acre.

(3) CONTROL MEASURES.—(a) *Safety Margin for Potatoes.*—Other things being equal, the risk of damage increases with the number of wireworms per acre. The first step, therefore, should be to obtain through the medium of the County or District Agricultural Advisory Officer, an estimate of the wireworm population in the fields intended for potatoes; the counting being carried out by a Specialist Officer. On light land, using the hand-sorting technique, a count of 250,000 per acre should certainly be regarded as the upper limit, though a liberal dressing of farmyard manure will reduce the risk. On light to medium loams the crop may suffer little damage with a

population of up to 450,000 per acre, but if this count approaches 600,000 per acre potatoes are not advisable except on heavy land, and the crop should be lifted not later than the middle of September.

(b) *Place of Potatoes in Rotation.*—It has been mentioned that the highest wireworm counts are usually found on old grass, *i.e.* land under grass for ten or more years, and there is some evidence that "hay" grass tends to support a higher population than pastures. Where possible, therefore, potatoes should not be taken during the first two years after breaking up old grassland. A selection can, instead, be made from crops tolerant to wireworm attack; among these are beans, peas and mustard or, if a cereal is taken, oats will probably be the most tolerant and a mixture of oats and peas still better. Virgin moorland often gives a low wireworm count and the same is true of short (two to three years) leys unless they have followed too closely (*e.g.* two or three years) upon an earlier breaking up of permanent grass; potatoes in such cases therefore can form the first arable crop provided the safety margins described under (a) are maintained. When a cereal is the first crop, thorough consolidation of the soil to the full ploughing depth should be ensured by the use of a heavy disc, followed as soon as practicable by persistent rolling.

(c) *Chemical Treatment to Reduce Wireworm Population.*—It is only with the introduction of the newer insecticides that real hope has been aroused of the possibility of reducing wireworm numbers by soil treatment. There has been ample confirmation of the results of the extensive experiments of Jameson *et al.* (1947, 1951) showing that Benzene hexachloride (the B.H.C. of commerce), which contains 13 per cent. of the insecticidally active "gamma isomer" known as Gammexane, effected a significant reduction in the wireworm count of fields with over one million per acre, and gave a very considerable increase in yield of cereals. The effect varied with the method of application. Thus, when broadcast as a 2 per cent. dust at the rate of 3 cwt. per acre there was a reduction of one-third in the wireworm population, while a fall to one-half the original number followed on combine drilling of the same dust at the rate of only 1 cwt. per acre. When the cereal seed was dressed before sowing at a rate equivalent to rather less than the dosage given in combine drilling there was a reduction of one-quarter in the wireworm population. A comparison of this B.H.C. treatment with equivalent dressings of D.D.T. (Dichloro-diphenyl-trichlorethane) brought out the interesting fact that, although the reduction in wireworm count was of the same order in the two treatments, the B.H.C. was followed by a much greater improvement in yield of the crop. This increased protection, it is suggested, may have been due to the repellent action upon, or partial paralysis of, many more wireworms than were actually killed by the B.H.C. Horber (1948), reporting on Swiss experiments, states that "complete" mortality of wireworms to a depth of 10 ins. in heavily infested grassland was obtained when B.H.C. was applied at the rate of 9 lb./acre, as a suspension in liquid manure during September. Tests of B.H.C. and D.D.T., both as soil and tuber dressings for the control of wireworm damage due, mainly, to *Ctenicera* (*Corymbites*) *aeripennis destructor* Brown, were carried out in Canada by Arnason *et al.* (1948). As a soil treatment, B.H.C. was highly effective and D.D.T. less so, but neither material afforded any satisfactory protection when applied as a tuber dressing, and sprouting was both reduced and delayed by the B.H.C. In addition to B.H.C. very promising results have been obtained by Jameson *et al.* (1947) by the use of Ethelyne dibromide. Unfortunately B.H.C. insecticides are not without their disadvantages, and the Ministry of Agriculture do not at present recommend their use on soils to be cropped in the same year, or either of the two following years, with potatoes, onions, carrots and other root vegetables for human consumption, because of the risk that flavour may be affected (Thomas, 1949). The recent work of Jameson and Tanner (1951) has shown that the degree of taint produced in potatoes is a function of the amount of crude B.H.C. applied per acre and the time lapse after treatment. After four years' trials they conclude that treatment with 4 lb. B.H.C./acre will induce a taint if planting occurs within eighteen months from the date of application, but that after a three-year lapse the crop should be free from taint. Nevertheless, on present records, the B.H.C. insecticides represent a very great advance in the use of chemicals for the control of wireworms.

VI. DIPTERA (Flies)

"Flies" are of no particular importance in potato culture, with the interesting exception of the "Seed-Corn" Maggot *Delia* (*Hylemyia*) *cilicrura* Rond (*Phorbia fusciceps* Zett). This insect causes no direct injury to potatoes, but the larva or "maggot" has been shown to be capable of transmitting the bacterial "Blackleg" disease to healthy potato plants in U.S.A. In the British Isles *Delia cilicrura* is known as the "Bean-Seed" fly and, curiously enough, although it is common and widely distributed its larvæ have not, as yet, been found infesting potatoes (Mrs M. Miles *in litt.*); it is a close relative of the onion fly (*Delia antiqua* Meig) and of the cabbage-root fly (*Delia* (*Erioischia*) *brassicæ* Bouché).

The fly is smaller than a house-fly and light-grey in colour; the single pair of wings being almost transparent. The adult fly emerges from the pupal case in the soil during early summer, and at once begins to lay the minute ($\frac{1}{25}$ in.) white eggs (which are covered with a sticky adhesive gum), near to newly planted potato tubers. In a few days the whitish, transparent maggot is hatched; this being little bigger than the egg but is easily visible to the naked eye. With its claw-like mouthparts the maggot soon penetrates to the inner tissues of the tuber, where it reaches its maximum size of about $\frac{1}{3}$ in.; after this it leaves the tuber to undergo a fortnight of pupation in the soil. Two broods thus occur in the year; the second lot of eggs often being deposited, according to Leach (1940) near, or on, the stems of plants already infected with Blackleg.

Our knowledge of the association between the insect and bacteria, and of the role played by the fly in disseminating the Blackleg disease, is due to the work of Leach (1926, 1930) in Minnesota. Pathogenic and putrifactive bacteria are said to be normally present on the outside of both the egg and maggot, and in the intestinal tissues of maggot, pupa and adult fly; the causal organism of potato Blackleg being usually, but not invariably present. According to Leach the bacteria serve an essential function in rendering the vegetable matter more digestible for the maggot; for sterile maggots, hatched from surface-sterilised eggs, were not able to develop normally on sterilised potato until the potato was inoculated with the bacteria usually associated with the insect. As though in return for this service the insect (*a*) serves as an active means of inoculating the tuber in which both maggot and bacteria feed, (*b*) ensures the survival of the bacteria in the hibernating pupa and (*c*) secures the surface contamination of the eggs as these pass between the anal appendages of the female fly during oviposition. Finally, the emerging maggot is assumed to pick up the bacteria from the contaminated egg-shell, or from the soil or infected seed tubers, and is thus fully charged with inoculum when feeding on a healthy tuber. The cogency of this argument in its relation to the spread of Blackleg is examined further on page 398, but there can be no doubt that this American work opens up a new field for research on the relationship between soil fauna in general and the spread of plant diseases.

CHAPTER XX

THE CHIEF DISEASES OF THE POTATO

INTRODUCTION

SOMEWHAT cynically it has been said that the potato crop only becomes profitable when half the produce is rotting in the pit or clamp. This was, of course, true in pre-war years and reflected the dependence of prices on supply and demand. As prices are now regulated, however, it no longer holds and, quite apart from the urgent need to increase production, it is in the grower's interests to restrict losses through disease. Much of the rotting, as well as other forms of loss, can be checked or even eliminated altogether, and the grower who succeeds in keeping his produce healthy in times of shortage is amply repaid for his care and foresight.

The main causes of loss in the potato crop are the various diseases and, to a less extent, the pests to which it is liable, and these too often vitiate all the care exercised by the grower in ensuring both good soil conditions and the best cultural practice. In approaching the question of prevention or eradication of a disease the grower must first learn the characters by which each disease can be recognised. With the help of the KEY on pages 282-285 this should not prove too difficult a task, and attention can then be focused on obtaining sufficient acquaintance with the conditions under which the disease occurs, and spreads, to enable him to grasp the principles on which control measures are based. The descriptions of diseases which follow have been written mainly with this object in view, although for the benefit of those who wish to extend their knowledge beyond this point, details are added which may not be of immediate interest to the practical grower. The rapidity with which information on disease control is being accumulated makes it impossible for any grower to keep abreast of modern developments. It is therefore strongly suggested that he should seek the advice of his county agricultural officers and, through them, the specialist advisory officers of the National Agricultural Advisory Service in

England and Wales or those attached to most of the agricultural colleges in Scotland and Ireland. Advice so obtained is free, and it is in the best interests of the grower to co-operate with these officers in eradicating disease and so raising the productivity of the crop. Although every effort has been made to ensure that the information presented in this book is both accurate and as complete as space will permit, it should not be regarded as replacing the expert local advice so readily obtainable by the grower. It will, indeed, fail in its object if it does not increase the call made upon the Advisory Service, for the reader will note not only those facts about a disease which appear to be fully established, but also those about which we are still in some doubt. Co-operation between the growers themselves is just as essential, for if all available information was passed on from one grower to another, and acted upon, many diseases would quickly cease to be a menace to the potato crop.

How to Identify a Disease

The identification of diseases by the grower must depend upon such differences in the affected plant as can be recognised by the naked eye, with in some cases the assistance of a hand-lens. Diseases may, for instance, be divided into groups of which those in one group attack only the tuber (Powdery Scab, Common Scab, Dry Rot, Pink Rot, Skin Spot, etc.); a second group in which definite symptoms show only in the parts above ground (Botrytis disease and many virus diseases); and a third which affects both tubers and aerial parts alike. The diseases within any one group can then be distinguished from each other by smaller, but easily recognisable, differences in their effects on the plant.

The Key (Table XV) which follows is an attempt to direct the attention of the grower to just those differences in the appearance of the affected plant which will lead him finally to a correct identification of the disease. In using the Key the grower must *always* begin with the alternatives presented in 1 and reach a decision as to whether the disease occurred during the growing season or only in the late autumn on dead or dying haulms, or possibly was only noticed on the tubers in storage. If the first, he will refer to 2; if the second, he must

TABLE XV

Key to Diseases, Pests and Some Conditions of the Potato

			Key No.
1.	Noted during growing season		2
	Noted on dying and dead haulms		39
	Noted in tubers only		40
2.	Plants of at least normal size		3
	Plants definitely stunted in growth		25
	Plants failed		28
3.	Foliage wilted		4
	Foliage not wilted		11
4.	Affected haulms broken or injured		5
	Affected haulms with no sign of injury		7
5.	White mould around base of haulm		6
	No white mould, but caterpillar damage in hollowed base of haulm	*Rosy Rustic Moth* (p. 262)	
	Neither mould nor sign of caterpillar damage	*Mechanical Damage*	
6.	White mould is fluffy	*Stalk-Break* (p. 305)	
	White crusted mould sheathing base of haulm	*Stem Canker* (p. 295)	
7.	Foliage normal green, leaves carrying tiny green wingless insects	*Aphides* (p. 258)	
	Foliage wholly or partly blackened		8
	Foliage yellow and erect		9
8.	Disease begins at leaf-tip, grey mould covering black areas	*Botrytis* (p. 307)	
	Sparse grey mould on lower surface only and at junction of healthy and black areas	*Blight* (p. 334)	
9.	Base of haulm black and rotten, brown stains in flesh when haulm is cut across	*Blackleg* (p. 393)	
	Base of haulm not black and rotten		10
10.	White mould around base of haulm		6
	Without mould. Root fibres with tiny white or brown bladders (cysts)	*Root Eelworm* (p. 205)	
	Neither mould on haulm nor cysts on roots. Tuber may show brown ring internally	*Verticillium Wilt* (p. 314)	
11.	Plant with abnormally strong coarse haulms; tubers few and large	*Bolter* (p. 74)	
	Plant with many thin wiry haulms; tubers many and all small	*Wilding* (p. 75)	
	Plant with haulms of normal vigour		12
12.	White mould around base of haulm		6
	Without mould around base of haulm		13
13.	Plant with white or brown bladders (cysts) on root fibres	*Root Eelworm* (p. 205)	
	Plant without cysts on root fibres		14
14.	Foliage normal green, leaves carrying tiny green wingless insects	*Aphides* (p. 258)	
	Foliage wholly or partly blackened		15
	Foliage not blackened		16

15.	Foliage dry and withered	*Drought or Wind Damage*	
	Foliage not withered, affected leaves black and water-soaked		8
16.	Leaves with bright yellow spots	*Aucuba or Frost* (p. 449)	
	Leaves without yellow spots		17
17.	Leaf margins curled up or down		18
	Leaf margins smooth or, at most, wavy		21
18.	Leaf margins curled down, surface bronzed	*Rust or Potash Shortage* (p. 420)	
	Leaf margins curled upward		19
19.	Only leaves touching ground with slight curling	*Varietal Character or Damage* (p. 439)	
	Definite curl upward in leaves clear of ground		20
20.	Leaf mottled, margins pale, undulating and curled	*Marginal Leafrolling Mosaic* (p. 457)	
	Leaf stiffly rolled ; may show necrosis or reddish colour	*Leaf Roll* (p. 437)	
21.	Leaf mottling faint or absent		22
	Leaf mottling very obvious		23
22.	Mottling seen only against white background, no necrosis or deformity	*Mild Mosaic* (p. 451)	
	Mottling more evident ; foliage and haulms necrotic, leaves fall prematurely	*Streak* (p. 461)	
	Leaf puckered with insect punctures		24
23.	Little or no necrosis or leaf deformity	*Mosaic* (p. 451)	
	Leaves blistered and deformed		24
24.	Leaf margins wavy, pale and curled upward (spoonlike)	*Marginal Leafrolling Mosaic* (p. 457)	
	Leaf margins wavy, not pale ; leaves blistered and tend to fall	*Crinkle* (p. 459)	
	Leaf puckered and mottled around insect punctures	*Capsid Bug Damage* (p. 256)	
25.	Leaf margins rolled upward		19
	Leaf margins not rolled upward		26
	Leaves carrying tiny green wingless insects	*Aphides* (p. 258)	
26.	Plant dwarfed and trailing, leaflets tiny and compact	*Curly Dwarf* (p. 466)	
	Plant dwarfed but not trailing, leaflets normal in size		27
	Plant dwarfed, leaves carrying tiny green wingless insects	*Aphides* (p. 258)	
27.	Roots with numerous tiny white or brown bladders (cysts)	*Root Eelworm* (p. 205)	
	Roots without cysts, leaves mottled		21
28.	Seed sett riddled with holes		29
	Seed sett without holes		30
29.	Holes small, tunnels penetrating deeply, tuber-flesh dry	*Wireworm damage* (p. 269)	
	Holes small, tunnels superficial ; contain black-headed caterpillar or mealy debris	*Tuber Moth* (p. 263)	
	Holes large and irregular ; flesh with milky iridescent slime	*Slug damage* (p. 240)	
30.	Seed sett shows definite signs of growth		31
	Seed sett has not grown since planting		32
31.	Sett with black, plate-like sclerotia ; sprouts brown or rotting with brown fungus	*Rhizoctonia* (p. 295)	
	Sprouts brown and dead, no sign of fungus on sett or sprouts	*Frost or Mechanical Damage*	
	Small tubers developing around dead sprouts	*"Little Potato"* (p. 418)	

TABLE XV (*continued*)

			Key No.
32.	Sett shrivelled in concentric rings		33
	Sett not dried and shrivelled		34
33.	Bluish-white or pinkish fungal pads on shrunken parts	*Dry-Rot* (p. 319)	
	Numerous tiny black " pin-heads " visible on shallow circular depressions	*Gangrene* (p. 328)	
34.	Sett scabbed		46
	Sett not scabbed		35
35.	Skin of sett raised in pimples, especially around eyes	*Skin Spot* (p. 309)	
	Sett without pimples		36
36.	Sett with dark water-soaked areas on skin, flesh below stained brown		37
	Sett outwardly normal ; black ring internally, especially near heel end	*Blackleg* (p. 393)	
37.	Tuber with large cracks bursting outwards ; flesh " mealy "	*Tuber-Rot Eelworm* (p. 236)	
	Tuber skin with extensive " peeling," flesh mealy, galls on tuber and stolons	*Stem Eelworm* (p. 231)	
	Tuber without cracks, galls or extensive peeling		38
38.	Tuber-flesh turns salmon pink when exposed to air	*Pink Rot* (p. 351)	
	Tuber-flesh does not turn pink	*Blight* (p. 334)	
39.	Black plate-like sclerotia on haulms above ground	*Grey Mould* (p. 307)	
	Black spiny sclerotia on all parts below ground and inside haulm	*Black Dot* (p. 331)	
	Black sclerotia, pea-sized, inside and outside haulm above ground	*Stalk-Break* (p. 305)	
40.	Noted during, or shortly after lifting crop		41
	Noted at any time during storage		59
41.	Large tubers with internal cavity, no fungus seen	*Hollow Heart* (p. 415)	
	Tubers growing one from the other		42
	Tubers produced singly in usual way		43
42.	Heel end of first-formed tuber (proliferating tuber) with no sign of rotting	*Second Growth* (p. 416)	
	Heel end collapsed with black rot below ; rest of flesh yellow and glassy	*Jelly-End Rot* (p. 417)	
43.	Tubers riddled with holes		44
	Tubers not riddled with holes		45
44.	Holes small, tunnels penetrating deeply, tuber-flesh dry	*Wireworm damage* (p. 269)	
	Holes small, tunnels superficial ; contain black-headed caterpillar or mealy debris	*Tuber Moth* (p. 263)	
	Holes larger and irregular ; flesh with milky, irridescent slime	*Slug damage* (p. 240)	
45.	Tubers scabbed		46
	Tubers not scabbed		49
46.	Scabs raised above surface		47
	Scabs depressed below surface		48
47.	Scab black, plate-like and easily detached	*Black Scurf* (p. 295)	
	Scabs form large outgrowths suggestive of black cauliflowers	*Wart Disease* (p. 357)	
	Scabs small and circular ; brown powder shakes out when dry	*Powdery Scab* (p. 367)	
48.	Depressions superficial, irregular in outline	*Common Scab* (p. 375)	
	Depressions deeper, regular outline with recurved margins ; powdery if dry	*Powdery Scab* (p. 367)	

49.	Tuber s	vater-soaked or discoloured areas on skin		50
	Tubers	mness, skin not water-soaked nor discoloured		54
50.	Tuber w	acks bursting outwards ; flesh discoloured and mealy	*Tuber-Rot Eelworm* (p. 23	
	Tuber s	ensive " peeling," flesh mealy, discoloured ; galls on tuber and stolons	*Stem Eelworm* (p. 231)	
	Tuber c	not discoloured ; galls absent	*Growth Cracks* (p. 415)	
	Tuber w	s, galls, or excessive peeling ; flesh discoloured		51
51.	Rot alm	preading from heel end of tuber		52
	Rot beg	y point on tuber		53
52.	Flesh tu	pink when cut and exposed to air	*Pink Rot* (p. 351)	
	Flesh ye	glassy near heel end	*Jelly-End Rot* (p. 417)	
	Flesh bl	h black ring below skin	*Blackleg* (p. 393)	
53.	Wet rot	rom wounds, black margin to diseased flesh	*Watery Wound Rot* (p. 354)	
	Wet rot	ar dead brown tissue under skin	*Blight* (p. 334)	
54.	Silvery	ng " pie-bald " appearance on skin	*Silver Scurf* (p. 312)	
	Copper-	ngal web on skin	*Violet Root Rot* (p. 302)	
	Tubers	kin		55
55.	Discolo	sh not connected to skin		56
	Discolo	sh clearly spreading from skin		58
56.	Centre	n discoloured but with no rotting	*Black Heart* (p. 406)	
	Tuber-f	own network near heel end	*Net-Necrosis* (p. 428)	
	Tuber-f	ep-seated brown dead spots		57
57.	Brown	ed in flesh, forming tiny arcs of circles	*Spraing* (p. 427)	
	Brown	ed in flesh, not forming arcs of circles	*Internal Rust Spot* (p. 425)	
58.	Flesh b	dry, brown and " mealy "	*Blight* (p. 334)	
	Tuber-f	t heel end and spreading as black ring under skin	*Blackleg* (p. 393)	
59.	Tubers	ng storage		60
	Tubers	during storage		62
60.	Rot de	denly after severe cold weather	*Frost Injury* (p. 423)	
	Rot de	nout relation to weather conditions		61
61.	Tuber-s	aked or discoloured ; not shrivelled		50
	Tuber-s	d more or less concentrically		33
62.	Tubers			46
	Tubers			63
63.	Tuber-s	d as though with a " punch " to form pits		64
	Tuber-s	ed		65
64.	Pits ma	ular, rarely exceeding ½ in. diameter	*Pit Rot* (p. 404)	
	Pit like	b-mark ; may show tiny black " pinheads " (pycnidia)	*Gangrene* (p. 328)	
65.	Tuber-	n small pimples, especially near eyes	*Skin Spot* (p. 309)	
	Tuber	d ; no pimples, but black pycnidia near eyes	*Phoma tuberosa* (p. 330)	
	Tuber-	pimples and free from pycnidia		54

turn to 39; whilst if he first noticed the disease during storage he will consult 40. Thus, by selecting the one alternative which meets the particular case he is led ultimately to a correct identification of the disease. As an example we may take the common disease known as "Blight." The grower would almost certainly see the effects of the disease on the foliage during the growing season, in which case he refers to 2 and decides that since the plant is normal in size he must pass to 3. He is of the opinion that the foliage is wilted and therefore refers to 4 which takes him forward to 7, since there is no obvious mechanical injury. Under 7 he decides on the second alternative which takes him to 8, and the occurrence of the greyish mould around the edge of the blackened areas of the leaves finally identifies the disease as Blight. He may, however, have decided when considering the alternative under 3 that the foliage was *not* wilted. In this case he is led from 3 to 11, 12, 13, 14, 15, and so back to 8, which leaves him finally at the same disease (Blight) as before. There is still the possibility that the disease was not observed during the growing season, but only in the tubers after lifting. From 1 he will therefore pass straight to 40 and decide whether the disease was to be seen at lifting time or only developed during storage. If the former, he would be referred in turn to 41, 43, 45, 49, 50, 51, and so to 53 and "Blight." If the disease was first noted in storage, the route would depend upon whether the tuber had developed a wet rot or was still firm and hard. If the former, the route would be 1, 40, 59, 60, 61, back to 50, 51, 53, and Blight; whilst with a hard tuber the same end would be reached via 59, 62, 63, 65, back to 54, 55 to 58. More serious difficulties may be encountered if, as often happens, two diseases are present at the same time, *e.g.* Blight and Common Scab. The procedure then would be to disregard the symptoms of one disease until a decision was reached about the other. In the case quoted, for instance, when 34 was reached the grower would first identify Blight (disregarding the scabs on the tubers), and then return to 34 and pass to 46 and thence to 48 and Common Scab. The KEY is not of course infallible, but used with reasonable care it should lead to a correct identification of most potato diseases; unless, indeed, very unusual symptoms develop.

The Organisms causing Potato Diseases

The student in agricultural institutes should not only be familiar with the external symptoms of different potato diseases but also with the characteristics of the organisms responsible for them. Without some knowledge of the causal organisms, and of their interrelationships, it is impossible to appreciate fully the results of original research or to examine critically any new proposal for disease control.

The great majority of diseases of potatoes are caused by fungi, *i.e.* by primitive plants devoid of chlorophyll and hence compelled to acquire their organic food from either living plants or decomposing organic matter. The vegetative body of a typical fungus is known as a mycelium and consists of branching, threadlike tubes or hyphæ, some of which serve mainly to distribute the fungus throughout the substratum, which may be a living potato plant. Other hyphæ sometimes act as special absorbing organs analogous to root-hairs in the higher plants. These penetrate through the cell-walls of attacked plants and absorb nutriment, during which process the cell protoplasm may be killed ; they are known as haustoria and occur only in those fungi in which the main hyphæ are confined to the intercellular spaces of the plant. Still other hyphæ give rise to the reproductive spores, which develop either within the plant tissues or on the surface. The spores are very diverse in shape and structure, but all differ from the seed of higher plants in that they contain nothing comparable to the embryo plant found in all true seeds ; when they germinate they either divide internally to form a number of motile bodies, known as zoospores because of their active movement, or grow directly into a tubular hypha ; in the former case they are really sporangia, though under some conditions of temperature and moisture the sporangia may act like true spores in producing a hyphal germ tube instead of forming zoospores. Spores are sometimes produced sexually by the union of male and female nuclei, the spores so formed being named oospores, ascospores or basidiospores according to important differences in the sexual process. The sexual spores are frequently enclosed in "fruit bodies," which also have distinctive names and which form an important basis for classifying the fungi. Other spores, known for the most part as conidia, are not sexual in origin, but represent the swollen tips of vegetative hyphæ from which they are ultimately "nipped" off. These conidia also are sometimes borne within so-called fruit bodies, known as pycnidia if they form closed structures, or acervuli if they are open and disc-like in form.

No matter how they are formed the function of the spores is to distribute the fungus in a compact form from which the vegetative growth can begin again. Oospores and the "fruit bodies" containing either the sexually produced ascospores or the non-sexual conidia are very resistant to weathering effects, and so serve to maintain the fungus in a dormant condition until circumstances are favourable for the development of the more easily destroyed vegetative mycelium. Sometimes, however, the mycelium itself passes into a dormant state as a closely wefted mass of hyphæ in which the outer ones afford protection to the innermost ones; these resting masses of mycelium are known as sclerotia when they are capable of prolonged existence apart from the ordinary vegetative hyphæ.

Classification of the fungi depends in the first instance upon the existence or absence of cross walls (septations or septa) in the hyphæ, those possessing septa being grouped as the Mycomycetes and those devoid of them as Phycomycetes. The former group is again subdivided according to whether the sexual spore is an ascospore (Ascomycetes) or a basidiospore (Basidiomycetes). Many fungi have apparently lost the power to produce sexual spores, and in these cases it is impossible to be certain as to their relationship with any of the above groups. They are therefore grouped together as Fungi Imperfecti and are themselves arranged into subgroups according to the presence or absence of "fruit bodies" and the characters of the non-sexual conidia. The Scheme (Table XVI) shows in graphic form the various groups of fungi and the way in which the groups are apparently related to each other, the fungi being represented by the name of the disease they cause rather than their own scientific designation. It will be observed that other organisms responsible for potato diseases referred to as Actinomycetes, Bacteria and Viruses. Bacteria are extremely minute single-celled organisms, usually globular or rod-like, which reproduce by dividing into two individuals at a rate which may be as frequent as every half-hour under favourable conditions. They may also successfully withstand adverse conditions by forming spores which, in this case, are formed from an ordinary cell by extensive thickening of the wall. Actinomycetes consist of chains of cells, each of which is very similar to a bacterium, so that there is some doubt whether they should be regarded as a highly developed form of bacteria or as a somewhat peculiar group of fungi. Viruses will be discussed later in detail and it is only necessary here to note that they are so minute that the majority of viruses have never been seen, nor are likely to be seen, with any microscope at present available.

The Relative Importance of Different Diseases

To the grower the identification of a disease is simply a necessary preliminary to discovering the nature and extent of the loss in which he may be involved and, still more, whether any practicable means are known for minimising this loss or of preventing its recurrence.

It is not easy to assess the relative importance of these various diseases and pests. How, for instance, is one to compare the Blackleg disease, which usually affects only a very small percentage of any one crop but is so universal that the aggregate loss to the potato-growing community must be considerable, with a localised disease such as Spraing in which the whole crop of a small percentage of growers is rendered totally unsaleable ? Some maladies such as Blight, Dry-Rot and virus diseases are not only almost universally distributed but also have a very severe effect on the crop, so that there is no hesitation in regarding these as amongst the most important diseases to be considered. On the other hand, Common Scab is probably just as prevalent as the foregoing diseases, but the loss is measured, not by depression in yield, but in percentage of unsaleable tubers. Powdery Scab and Spraing may be sources of serious loss under certain soil conditions (heavy ill-drained in the former case, and light porous soils in the latter), and the unfortunate tenant of such soils can, as yet, do relatively little to make them suitable for potatoes ; the necessary combination of the presence of the causal organism and soil conditions suitable for its development does not, however, cover a very large total area. Wart disease is, potentially, one of the most serious of diseases in certain districts, and the fact that a complete control is found by the growing of immune varieties should not blind growers who occupy clean land to the need for constant vigilance to avoid its introduction. Amongst what may be regarded as minor diseases of the potato are Black Scurf and Skin Spot, both very generally distributed in some seasons, but which are only serious when the sprouts and tuber eyes are attacked and, as they sometimes are, killed by the fungus. The farmer who learns that the large number of misses in his potato drills are due to one or other of these diseases will not acquiesce in describing them as minor maladies. Finally, the ware grower approaches many of the problems raised by the occurrence of diseases from a different angle from that of the seed grower. Skin Spot, for instance, is a mere blemish on the ware produce and the grower is unfortunate if its occurrence affects his sales. On seed tubers, however, it is much more serious since the purchaser *may* suffer appreciable loss. The seed grower who wishes to build up a reliable trade will, therefore, cease to talk of blemishes and will recognise only two kinds of seed—perfectly sound as far as lies within his power, and diseased seed to which he will not attach his name.

It is possible to construct a rough guide to the importance of a disease to the grower by assessing them in the following ways :—

(1) *"Seed"-borne Diseases which may cause "Misses" in the Drill or cause Premature Death of Plants.*—These include the virus disease known as Leaf-Drop Streak, which cannot be identified in the tuber, and also others which usually *can* be detected if looked for at planting, *e.g.* Blight, Pink Rot, Blackleg, Dry-Rot, Skin Spot, Black Scurf and Gangrene.

(2) *Diseases causing a Marked Reduction in Weight of Saleable Crop.*—Amongst these are Blight, Wart disease, Leaf Roll, and other virus diseases, Blackleg, Dry-Rot, Pink Rot, the canker form of Powdery Scab, Gangrene and Watery Wound Rot ; to which may be added the net-necrosis in the variety Golden Wonder, if this is not regarded as caused by Leaf Roll.

(3) *Diseases producing Blemished and therefore Unsaleable Tubers.*—These include Blight, Common Scab, the mild form of Powdery Scab, Spraing and Internal Rust Spot, Dry-Rot, Wart Disease and Skin Spot.

(4) *Diseases which develop mainly in Storage.*—Examples are Dry-Rot, Blight, Pink Rot, Skin Spot, Watery Wound Rot and Gangrene.

(5) *Diseases contracted mainly or frequently from the Soil.* —These include Wart disease, Common and Powdery Scabs, Pink Rot and Watery Wound Rot, Black Scurf and Silver Scurf, Skin Spot, Internal Rust Spot and Dry-Rot.

(6) *Diseases contracted mainly or frequently from the Seed-Tuber.*—Amongst these are virus diseases, Blackleg, Common and Powdery Scabs, Skin Spot, Black Scurf, Silver Scurf and Blight.

It will be noticed that, whereas some diseases appear in most of the categories, others occur only once or twice. It therefore serves as a rapid, though rough, summary of any disease from the grower's point of view. Blight, for instance, is shown to be seed-tuber borne and in a condition in which it can be recognised by the grower in affected seed-tubers, failure to do so resulting in a risk of misses in the drill. It not only causes marked reduction in the weight of crop but induces further loss in storage. The disease may give blemished tubers which will be either unsaleable or, if the blemish is not obvious, may result in their use as " seed " with its attendant risks of a miss or the growth of a diseased plant which will become a source of infection to the new crop. The classification may thus be of some use to the grower, but should only be used as a basis for action after reading the fuller accounts of the diseases in later chapters.

The Principles of Disease Control

No doubt the breeding of potato varieties immune from diseases would provide the most satisfactory method of control, but the problems involved are complex and it is hardly surprising that the earlier discoveries in this field were fortuitous, rather than the result of a direct attack on the problems by the plant breeder. Immunity has been defined as the capacity of an organism for active defence against a pathogenic agent (Gäumann, 1950). This may take the form of preventing the entry of the pathogen, or of incompatibility of parasite and host-plant after infection has occurred ; resulting either in the death of the parasite or (if it be an " obligate " parasite) in its isolation by the death of the surrounding host tissues. In either event the parasite fails to establish itself and no disease develops in the host-plant. Very few, if any, cases are known of absolute immunity from infection. The immunity from virus " X " exhibited by U.S. seedling 41956 may be one such exception but, in the great majority of cases, the " immunity " is the expression of the action of multiple factors ; each of which contributes to the resistance of the host-plant. Even in the most familiar example of " absolute " immunity—that of wart disease immunity—Miss Glynne (1925, 1926) has shown that infection, and development of the parasite, may occur in " immune " varieties ; while Botjes (1926) has given evidence of " bud " variation in the tuber of an immune plant which thereon became susceptible to the disease. Complex as the problems are, however, progress has been definite, and even spectacular in a few diseases, since they have been systematically attacked by the plant breeder ; though it must be admitted that in many diseases they have only, as yet, succeeded in uncovering the attendant difficulties. Even relative resistance to attack has been found difficult to achieve, although here again a search amongst commercial varieties has resulted in the discovery of varieties exhibiting some degree of resistance to one or more diseases. The difficulties encountered in direct breeding for resistance are very real. Resistance, for instance, often seems to be linked with the possession of characters which are commercially undesirable. Resistance to one disease may be associated with great susceptibility to another. Further, different organs may show very different degrees of resistance to the one disease, *e.g.* Golden Wonder may suffer severely from Blight on the foliage, whereas the tubers are relatively resistant, the contrary being true of some other varieties such as Irish Chieftain. It cannot even be asserted that resistance, once demonstrated, remains reasonably constant, for soil and season often greatly modify the power of a plant to resist a disease. Finally, the issue is complicated sometimes by the existence of more than one strain of the disease, and resistance to one of these so-called physiologic strains does not necessarily imply resistance to another, *e.g.* several such strains are now known to exist in *Phytopthora infestans* causing Blight (Schick, 1932, 1939) but some comfort is to be found in the fact that the most promising

TABLE XV:

Sc Ini ip 'ween Organi ng of Potato

- *'iruses* microscopi· ·articles. (LEAF ROLL) (MOSAICS) (? SPRAING) (NET-NECROSIS) (? PSEUDO-NET-NECROSIS)
  - *Sphæropsidai* Asexual conidia f in Pycnidia (PHOMA RO·
- *Bacteria* Single cells. Nucleus fragmented or absent. Reproduction by fission of cell. (BLACKLEG) (NTERNAL RUST SPOT)
- *Actinomycetes* Vegetative body forming branched chain of bacteria-like cells. (COMMON SCAB)
- *Eumycetes (true fungi)* Vegetative body usually formed by filamentous hyphæ.
  - *Mycomycetes* Vegetative hyphæ coarse and septate.
    - *Basidiomyce·e·* Asexual conidia rare. Sexual spores in groups of 4 upon basidium. (BLACK SCURF) (VIOLET ROOT ROT)
    - *Ascomycetes* Asexual conidia. Sexual spores in groups of 8 within A· ·us. (STALK-BLEAK)
    - *Fungi imperfecti* Asexual conidia very varied. Sexual ·pores unknown.
      - *Melanconiales* Asexual spores formed in open acervulus. (BLACK DOT)
      - *Hyphomycetes* Asexual conidia free; neither pycnidia nor acervu· (DRY-ROT, VERTICILLIUM WILT, GREY MOULD) (SILVER SCURF, SKIN SPOT)
  - *Phycomycetes* Vegetative hyphæ formed of branched unseptate, tubular cell.
    - *Oomyce·es* Asexual conidia. Sexual oospores from fertilisation of female oosphere by male antheridium. (BLIGHT, PINK ROT) (WATERY WOUND ROT)
    - *Archimyc* sexual reproduction by fusion of zo· spore·
      - *Plasmodiophora·* cell-thallus naked. spores produce zoospores with unequal flagella. (POWDERY SCAB)
      - *Chytridiales* usually one-celled, which becomes sporan· or sorus of sporangi· (WART DISEASE)
- *Myxomycetes* Vegetative body a multi-nucleated, naked plasmodium. (No parasitic forms)

success is being achieved against the strain responsible for most of the loss due to Blight in this country. The problems inherent in breeding have already been discussed in Chapter VIII, and will again be referred to under the various diseases in which control has been attempted by breeding methods. The present position seems to be that, although breeding for resistance to many diseases is being pressed forward in many countries and the ultimate prospects are bright, the time is still far distant when it will be possible to obtain a high-yielding variety immune from, or even reasonably resistant to, more than one or two of the many diseases to which the potato is liable. In most cases attention is still concentrated on discovering possible correlations between some structural or physiological character of the plant and an apparent resistance to attack; *e.g.* the connection between tuber-skin thickness, or the structure of tuber-lenticels, and susceptibility to Common Scab.

It follows that in the great majority of diseases the grower must himself take the necessary steps to avert loss. It is not essential for him to acquire any profound academic knowledge of diseases in order to control them. What is required is reliable information as to the origin of the attack and its method of spread. Armed with this information, he will readily understand why spraying the foliage with a chemical is advisable against one disease and quite useless against another; he will appreciate why the utmost care in selecting healthy seed must be exercised, and the reason why this care is not always a complete prevention of loss. The principles of disease control are relatively simple, but they must be properly understood and strictly applied if they are to be successful. They can be summarised as (1) prevention is better than cure, for, apart from a few tuber-borne diseases, a cure is impossible once a plant is attacked and all that can be done is to prevent its spread; (2) strict attention to hygienic methods of production which should insist on the complete destruction of rotting tubers wherever they are found, healthy storage conditions for the produce either in clean, well-ventilated buildings, or in pits from which all diseased tubers have been excluded, and covered in some way other than by old potato haulms which may harbour disease; finally (3), by remembering that a bruised potato is well on the way to becoming a diseased one.

CHAPTER XXI

DISEASES CAUSED BY BASIDIOMYCETES AND ASCOMYCETES

(1) Black Scurf and Stem Canker (*Corticium solani* Bourd. and Galz.)

General Appearance.—The two names are used to describe the appearance of this disease on tuber and haulm respectively. Black Scurf can easily be recognised on the tuber by the small inky-black cushions, or sclerotia as they are called, which are scattered over the surface of the skin (Fig. 55). These pads of hyphæ form the resting stage of the fungus. They are readily removed by the finger nail and are loosely connected to each other by a few strands of brown hyphæ. Few growers would notice the disease in this form or, having observed it, would give it a second thought, but under certain conditions it may spread to the growing sprouts and kill them. Attacked sprouts show rusty-brown patches or cankers and die back from the tips. This induces lateral branching of the sprouts, and these in turn are liable to be attacked by the fungus. Such sprouts as survive may show severe canker lesions below ground-level, and even the roots are sometimes affected. Later in the growing season the uppermost leaves develop a characteristically soft, rolled appearance ; the leaflets being rolled tightly about the midribs and often tinged with yellow or red pigment. In the meantime the fungus produces its fruiting stage in the form of a snow-white crust around the haulm just above ground level.

Symptoms with which Black Scurf and Stem Canker may be confused.—The black sclerotia on the tuber may conceivably be mistaken for adhering soil but are readily identified when the tubers are rinsed in water. The canker stage on the sprouts and underground parts is quite frequently attributed to the action of frost, the more so that the symptoms are most serious in cold wet soil. The brown fungal strands can, however, usually be seen with the aid of a hand lens, while the fact that the branched sprouts are attacked before they reach the surface of the ground, together with the absence of symptoms on many sprouts which have been exposed, should serve to prevent any confusion. The rusty-brown threads which connect the various sclerotia may, however, be easily confused with the more abundant copper-coloured mycelium of the fungus *Rhizoctonia crocorum* causing Violet Root Rot (page 302). The white crust stage is quite distinct from any other symptoms appearing on the haulm and cannot be mistaken. Finally, although the limpness of the rolling shown by the leaves will usually serve to distinguish the disease from primary symptoms of Leaf Roll (page 437), it should be remembered that limpness or wilting is a common reaction to any cause which prevents the movement of watery salts upwards, whilst anything impeding the passage of sugars downward through the halum will induce rolling of the foliage and a tendency to form small axillary tubers above ground, *e.g.* Blackleg (page 393), Black Dot (page 331), and any mechanical injury to the haulm.

DISTRIBUTION.—The disease in all its stages is to be found wherever the potato is grown. The fungus is capable of hibernating in the soil for an indefinite period of years and is probably a normal member of the flora in most soils. It has, indeed, been found to attack potatoes when taken as a first crop in virgin soil reclaimed from the desert in Idaho (Pratt, 1916). The various strains of the fungus, or very closely related species, are able to attack many different types of farm and garden crops, a fact which no doubt helps to maintain its wide distribution.

CAUSE OF THE DISEASE.—It will have been realised that the various symptoms described are caused by one fungus. This was, however, not recognised until 1904, when the identity of the fungus on the tuber and sprout (hitherto known as *Rhizoctonia solani*) with the Basidiomycete *Corticium solani* producing the white crust on the haulm was finally established by Rolfs. It is the former which is the actively parasitic stage of the fungus. In its resting (sclerotial) condition on the tuber, however, the fungus is wholly, or almost wholly, dependent upon its own reserves of food stored up in the hyphæ, and the tuber merely serves as a support. The conditions which are suitable for sprouting of the tuber also stimulate growth of the hyphæ in the sclerotia. At first these brown vegetative hyphæ grow almost wholly in length and there is relatively little branching, but once the sprouts are reached they branch repeatedly with the lateral branch-hyphæ growing out almost at right angles before resuming a parallel direction, and exhibiting a characteristic constriction at the junction with the main hypha. The thin epidermis of the sprout is readily pierced and the hyphæ rapidly spread intracellularly until much of the cortical and vascular tissue is invaded. Externally the affected sprout shows more or less serious rusty-brown lesions which may even girdle the shoot. The effect is either to weaken or kill the sprout, and in either case the basal part of the sprout produces lateral sprouts which may also be attacked in turn by the fungus. The tuber may thus fail to grow above ground, or any growth which may appear will be weakened in proportion to the severity of the attack below ground, and will later show the typical rolled foliage symptoms of the disease. Also the haulm may become encircled by the advancing hyphæ which have now lost most of their colour and are greyish white, very closely septate, and irregular in shape. On these are formed short lateral branches which are known as basidia since each develops four minute stalked basidiospores. The ease with which these basidiospores are spread by the wind no doubt accounts to some extent for the general occurrence of the fungus in soils. The history of the spores in the soil is unknown, but it is assumed that after some vegetative growth as a saprophyte they develop the resting stage or sclerotia, in which condition they remain unaffected by temperature and other changes in the soil.

Blair (1943), has added much to our knowledge of the behaviour of the saprophytic mycelium in the soil. Given a " food-base " (which could well be a sclerotium) the mycelium grows at a rate varying with the available nutrients in the soil, but averaging just under 1 cm. per day ; in quartz sand all growth ceased at 5 cm. from the agar " food-base." Growth in soil at *p*H 7 was good but the addition of 1 per cent. fresh organic manure (*e.g.* dried grass or ground up wheat straw) depressed the rate of growth unless the *p*H was raised to 8·0. The effect of the raw organic manure is explained as stimulating competition from other micro-organisms which resulted in a local accumulation of CO_2 ; in alkaline soil, however, much of this excess CO_2 is absorbed (Garrett, 1936), and the *Rhizoctonia* makes renewed growth. Certainly it is known that, although the fungus normally thrives in moist soil which is either neutral or slightly acid, serious damage is caused to wheat in some strongly alkaline soils of South Australia (Samuel and Garrett, 1932). The need of the fungus for proper aeration was also demonstrated by Blair in the fact that he obtained best growth in soils with the lowest moisture-content (30 per cent.) and further stimulation was gained by forced aeration of the soil. An interesting negative correlation was found to exist in Australia (Bald, 1947) between the incidence of *Rhizoctonia* and *Actinomyces* (*cf.* Common Scab, page 375). He noted that a high incidence of the one usually coincided with a low incidence of the other, and that this apparent relationship was statistically significant; when "runner" hyphæ of *Rhizoctonia* reached a Scab lesion they rarely penetrated the lesion, but skirted it. In Bald's opinion these facts afford good evidence of an antagonism between these two genera of fungi such as is claimed to exist between different species of *Actinomyces* (*cf.* page 385). Richards (1921 and 1923) pointed out that, while the optimum temperature for the growth of the fungus in pure culture is 25° C. (77° F.), the best temperature for infection is 18° C. (64·4° F.) and little damage is done when the temperature approaches 24° C. (75·2° F.). Since he found this to be true in the case of plants which grow best at high soil temperatures as well as those requiring low temperatures, he considered the conditions for infection to depend more on the parasite than on the host-plant, and concluded that the enzymes or toxins necessary for infection are only produced at the lower temperatures. Generalisations, however, must be tempered with caution, particularly when, as in *Rhizoctonia*, "biological strains" are known to exist. Thus Le Clerg (1941*a* and *b*) demonstrated the existence of high and low temperature strains of *Rhizoctonia*; those pathogenic on potato having an optimum temperature for growth at 25° C., whereas the ones pathogenic on sugar-beet grew best at 30° C. and, incidentally, some of the sugar-beet strains proved much more virulent on potato than any strains he isolated from potato.

The conditions under which the saprophytic mycelium persists in the soil are obviously important and were studied by Elmer (1942) in eastern Kansas. In his view the high summer temperatures of Kansas inhibit the production of sclerotia in the soil, and persistence of the fungus therefore depends on the maintenance of the optimum conditions for the survival of the saprophytic mycelium. Elmer measured the degree of persistence, over a period of thirteen years (1928-1940) in fifteen localities, by determining percentage tuber-infection when " clean " seed was planted. The primary factor, he considered was a sufficiency of soil-moisture. From the records he obtained he established a correlation between a high incidence of Stem-Canker and the weather conditions of the previous years' July and August; a high rainfall, relatively low temperature and an absence of drying winds resulting in the following year in a high incidence of disease, whereas a low incidence followed a year in which the July and August rainfall was small with a frequency of hot, drying winds. The disease could not be correlated with the current season's weather for the crops grown from *contaminated* seed showed a high percentage infection throughout the whole survey period. In this country Small (1943 and 1945) supports Blair (1943) in demonstrating the ability of the fungus to grow well under dry soil conditions; indeed, by planting " clean " and contaminated seed in land in which the moisture content varied between 12·92 per cent. and 2·17 per cent he obtained 37 per cent. and 43 per cent. of heavily contaminated produce from " clean " and contaminated seed respectively. On the other hand it should be noted that Small's plots never had a moisture content exceeding 25·7 per cent. in 1944 or 23·3 per cent. in 1943. We have already seen that conditions for fungal growth and for infection are not necessarily the same (Richards, 1921, 1923); and it may be that in the dry conditions of Small's trials we have a partial explanation of his conclusions that the disease had little effect on the crop, either in damage to sprouts or haulm, loss in yield, or even in producing symptoms on the aerial parts.

EXTENT OF LOSS.—Reports as to the loss directly due to *Rhizoctonia solani*, the actively parasitic stage of the Stem-Canker fungus, are conflicting. There can be no doubt that many of the earlier estimates included the effects of other and more serious diseases, particularly Leaf Roll; and we may concede the correctness of the view expressed by Edson and Shapovalov (1918) that many " misses " in the drill are wrongly attributed to *Rhizoctonia* instead of to other soil-inhabiting fungi. Yet it can only be under very adverse soil conditions for the fungus that, as Small (1945) suggests, it serves as a beneficial " pruning agent " by destroying surplus sprouts ; there is, indeed, a good deal of evidence to support Appel's (1944) opinion that if conditions facilitate the infection of one sprout there is grave risk of sprouts being destroyed in succession until the vitality of the tuber is completely lost. In one such case the loss was estimated by Salmon and Ware (1935) to amount to £70 in a four-acre crop of early varieties in Kent. According to Frederiksen *et al.* (1938) the injurious effect depends partly on the depth of planting ; deep planting aggravating the loss and shallow planting reducing it. This has been confirmed by Bondartzeva-Monteverde (1946) in Russia, and by Müller (1947) in Germany. Müller showed that shallow and deep-planted plots resulted in 15 per cent. and 30 per cent. loss respectively and, in his opinion, the minimum loss due to this disease in German Pomerania with normal cool weather in May and June, is in the neighbourhood of 5 per cent.

CONTROL.—(a) *Seed Disinfection.*—There can be no doubt that, although *Rhizoctonia* appears to be widely distributed in potato soils, there may be considerable risk in planting seed-tubers carrying sclerotia of the fungus. Thus, when Sanford (1936) planted contaminated seed in British Columbia he found 42 per cent. of the sprouts developed lesions of Stem-Canker and, of these lesions, Sanford attributed 28·7 per cent. to infection from the seed-tuber and 13·3 per cent. to infection from soil-borne mycelium. Störmer and Ebell (1944) noted in German trials that contaminated seed produced 370·9 affected sprouts as against only 186·5 on " clean " seed, and an even more pronounced difference in sprout infection was reported from South Australia by Bald (1947). In this country Small (1945) found that contaminated seed gave a crop in which 65 per cent. of the tubers carried a large number of sclerotia as compared with only 7 per cent. of the crop grown from " clean " seed. Small's results have particular interest for us since, in the absence of suitable soil conditions for active parasitism, even the heaviest tuber-contamination gave very few sprout lesions and only negligible loss in yield. Nevertheless, contaminated seed should not be planted or, if this is unavoidable, the seed may be disinfected by one of the methods described in Appendix I (page 645). Formalin or one of the newer organo-mercury dips appear to give satisfactory control, and Sanford reports effective control by the use of acidulated mercuric chloride. Bald (1947) not only prevented rotting of " cut " seed tubers by dipping them in a suspension of 5 oz. zinc oxide in 1 gallon of water but also afforded the sprouts protection against attack by *Rhizoctonia*. Similarly Brown (1947) reports that proprietary dusts, in which the active principle is a chlorinated nitro-benzene, not only reduce waste by retarding sprout development in clamped " ware " tubers, but also protect these slower-growing sprouts from infection by *Rhizoctonia*.

(b) *Soil Conditions and Cultural Practice*.—We do not know how long the saprophytic mycelium can survive in the soil in the absence of a susceptible crop. Small (1945) found only a trace apparently present in soil which had been in grass for at least forty-three years, although even then some 7 per cent. of the crop developed sclerotia. Afanasiev and Morris (1948) reported no sclerotial contamination, and only slight stem-lesions, on a crop in Montana grown from clean seed on land which had not carried potatoes for twenty-five years. But again there is little comfort to be obtained from this fact since, on planting clean seed, it took only two years to build up a fungal contamination of the soil sufficient to cause serious stem-lesions in the third, fourth and fifth years, amounting to 82, 75 and 75 per cent. respectively ; while 66 per cent. of the tubers carried large numbers of sclerotia in the fourth year. It is not surprising therefore that Elmer (1942) found that land carrying an autumn crop of potatoes invariably gave a heavily diseased crop in the following year, and Sanford (1939) also concluded, in British Columbia, that one summer fallow was useless as a control of *Rhizoctonia*. Where, however, some rotation is practised so as to avoid a " build up " of soil mycelium, Richards (1923) has shown that late planting considerably reduces the amount of disease by ensuring a quicker emergence of the sprouts under warm conditions unfavourable for infection. Indeed it has long been recognised that the more severe attacks by *Rhizoctonia* occur in cold, backward springs, and this fact has led frequently to the brown, stem-lesions being wrongly attributed to frost ; recently Bondartzev and Bondartzeva-Monteverde (1946) have demonstrated in Russia that while late planting gave only 23 per cent.

stem-lesions these were increased to 46 per cent. in the early planted crops. Chamberlain (1935), in trials carried out in New Zealand, found that when potatoes were taken on contaminated land which had been in grass for one, two and three years, the crop was infected to the extent of 73, 56 and 3 per cent. respectively, while after four years under grass there was practically no infection from the soil. Goss and Afanasiev (1938) and Blodgett (1939), in Nebraska and New York respectively, also concluded that infection was markedly reduced after land had been rested for two years, but whereas in New York the further extension of the rest to five years brought no improvement in control the Nebraska workers agreed with Chamberlain that four years reduced the disease effects to negligible proportions. It would seem, therefore, that unless exceptionally favourable soil conditions occur, the normal rotations practised in this country should ensure relative freedom from the risk of infection from the soil ; while the use of clean seed, planted when the soil is warm enough to encourage sprout growth, should eliminate the disease except in very small holdings where proper rotation is difficult to achieve.

(2) VIOLET ROOT ROT (*Helicobasidium purpureum* (Tul.) Pat. or *Rhizoctonia crocorum* (Pers.) DC)

GENERAL APPEARANCE.—Some brief account of this disease must be given, although very few records exist of its occurrence on potato crops in this country. When it does attack potatoes, however, the effect is serious and may be erroneously attributed to Black Scurf. Affected tubers are covered with a fine network of hyphal threads which form a copper-coloured or purple mycelium. The conspicuous black sclerotia noted in the Black Scurf disease are absent and are replaced by very small reddish knots or cushions of hyphæ. When sprouts are attacked the symptoms are not distinguishable from those due to the Black Scurf fungus (page 295).

DISTRIBUTION.—Although rare on potatoes it may cause serious loss in many other crops, such as carrot, sugar beet, mangold, clovers, lucerne, or in bush fruit, such as currants and raspberries, and even in coniferous trees. In U.S.A. crocus suffers severely from this disease. The disease on potatoes may therefore be expected to occur when this crop is taken on land which may have been contaminated by the occurrence of the disease on such susceptible crops as those mentioned.

CAUSE OF THE DISEASE.—The active parasitic stage is *Rhizoctonia crocorum*, which, until 1927 was included in the Fungi Imperfecti. In that year Buddin and Wakefield proved the *Rhizoctonia* to be a sterile stage of the basidiomycete *Helicobasidium purpureum*. Since, however, the perfect form is itself very rare and has been found in direct association with the parasitic stage in only three instances (red clover, nettle and dog's mercury), it seems unlikely that the discovery of the fruiting stage has any practical significance.

It has already been noted that the coppery mycelium covering an affected tuber contains a number of very small knots of hyphæ, the infection cushions or *corps miliaires* as they are sometimes called. These are not merely resting bodies similar to the sclerotia associated with Black Scurf. They develop haustoria which, after penetrating through the potato skin, absorb nutriment for the benefit of the rest of the mycelium. The tuber is thus actually invaded and its tissues may become rotten in storage as a result of the action of the haustoria in reducing the vitality of the tuber and preparing the way for the entrance of putrefying organisms. Similarly, sprouts may be attacked by the growing mycelium either from the tuber or the soil, and these in turn may be damaged or killed by the infection cushions. According to Buddin and Wakefield, infection is more likely to occur in moist, well-aerated, sandy soil than in heavier land, but its occurrence is fortunately too rare to enable this belief to be tested practically. The same authors found the fungus to grow best at a temperature of about 70° F., and suggest that this need for a relatively high soil temperature may account for the rarity with which it attacks agricultural crops in this country. Garrett (1946) found that mycelial growth was less in soil than in a mixture (3 to 1) of sand and soil. It was further reduced in soil that was acid in reaction except under high moisture conditions, when soil acidity had no effect on growth.

CONTROL.—There is little possibility that infected seed will be inadvertently planted, so that the only precaution necessary is the avoidance of land for potatoes which has carried a previously diseased crop of any kind. Any such land should be put under grass for at least four years.

(3) The Honey Fungus (*Armillaria mellea* (Vahl) Fr.)

General Appearance.—The disease is identified at once by the thick brown or black strands of fungus attached to the tuber surface. They closely resemble the finer roots of a tree or, still more so, a tangled "bootlace." Below the sunken area of the part of the surface attacked the tissue is brown and develops cavities filled with either the white, rapidly growing mycelium, or brown strands similar to the external "bootlaces."

Distribution and Cause.—Although well known in many parts of the world, this disease has only once been recorded in this country, it having been identified on tubers from Midlothian in 1921 (Wilson). The causal fungus belongs to the group of the Basidiomycetes which includes the common "toadstools" and mushroom. When the disease has been identified on tubers a search should be made for the decaying stump of a tree on which, in autumn, the "toadstool" fruit bodies of *Armillaria* may be expected to develop. These are honey brown in colour and with their caps sprinkled with small blackish brown scales. They have a strong, unpleasant smell and usually occur in dense tufts. Typical "bootlaces" will be found under the bark of the stump, and it is these which are responsible for the spread of the fungus over an area centring on the stump. The "bootlaces" consist of a number of ordinary hyphæ closely wefted together, of which the outer ones have exceptionally hardened black walls which effectively protect the inner hyphæ. Technically, the entire strand is known as a rhizomorph because of its resemblance to the roots of the higher plants. It grows rapidly in length, below ground-level, and is capable of attacking the underground parts of plants it encounters.

Control.—The disease is extremely unlikely to occur except in gardens or, possibly, on the headlands of a potato field in the vicinity of felled trees. Any dead tree stump should be removed and the surrounding soil dug with a view to eradicating the "bootlaces." No chemical treatment of the soil can be relied upon to kill these rhizomorphs, but considerable success has been achieved in U.S.A. by the injection of carbon bisulphide (Thomas and Lawyer, 1939). This is most effective under dry soil conditions; holes being driven in to a depth of 8 to 10 in. by means of an iron bar, the chemical is poured in and the hole sealed up with soil (Foister, *in litt.*).

(4) SCLEROTINIA DISEASE OR STALK-BREAK (*Sclerotinia sclerotiorum*, Bref.)

GENERAL APPEARANCE.—The first indication of this disease in the field is usually the development of white, fluffy masses of hyphæ on the outside of the haulm, sometimes (but not always) near the ground-level. These should be looked for from July onwards, the earlier outbreaks occurring in seasons of heavy rainfall. Later the haulms may bend over, or even break, at the point of attack. The snow-white masses of hyphæ become more compact, darken in colour, and finally become hard, inky-black sclerotia which may reach the size of a pea, although they are often elongated. Similar black sclerotia may be found in the central cavity within the haulm. Wilting may occur during the progress of the disease, but the leaves show little or no yellowing.

SYMPTOMS WHICH MAY BE CONFUSED WITH SCLEROTINIA.—The loose, cotton-wool appearance of the hyphal outgrowths easily distinguish this disease from the white crusts of Black Scurf (page 295), whilst the shape of the mature sclerotia should prevent confusion with the flat, plate-like sclerotia of the Grey Mould disease (page 307).

DISTRIBUTION.—The disease is infrequent in Great Britain and cannot be regarded as more than a minor malady of the potato. It appears to be confined to the wetter areas of the west and north, and even in such districts serious attacks are rare except when potatoes are taken too frequently on the same land. In the west of Ireland, however, the disease is regarded as a serious menace, and in some years the loss is stated to be greater than that caused by Blight.

CAUSE OF THE DISEASE.—The causal fungus is usually known in this country as *Sclerotinia sclerotiorum*, though there seems no doubt that it is identical with the destructive species *S. libertiana* Fckl., which attacks a wide range of host plants. It is a member of the Ascomycetes group and is the only one definitely known to attack potatoes. Most of our knowledge of its life-history on this host is due to the researches of

Pethybridge in Western Ireland from 1909 to 1916. As in the two preceding diseases, the perfect sexual stage of the fungus does not develop on the growing plant, but results from the growth of the sclerotia released into the upper layers of the soil by the rotting of potato haulms. The deeper-seated sclerotia are believed to remain dormant until they, in turn, are brought near to the surface by cultivation and so exposed to winter frosts. In early summer, the sclerotia give rise to small cups or disc-like fruits which are borne on slender stalks until they just project above soil level. These fruit bodies (apothecia) are from one-quarter to half-an-inch in diameter and are pale, yellowish brown in colour. The spores (ascospores) are produced on the upper surface of the apothecia in vast numbers and are discharged like puffs of smoke through the growing crop. According to Pethybridge, these spores on germinating are unable to infect robust growing leaves, and only attack those which are over-mature and dying. From the leaves the fungal hyphæ pass through the cells into the haulm, where the wood vessels become blocked with hyphæ and so cause the foliage to wilt. The sclerotia are produced both inside the pith cavity and on the outside of the haulm by the fluffy, white mycelium gradually becoming compact and firm; colouring matter is deposited in the outermost hyphæ of the sclerotium and it assumes a black, spherical, or somewhat elongated appearance on maturing. Although this fungus rarely becomes serious in Great Britain on potatoes, it is a frequent source of heavy loss in many other (chiefly market garden) crops. Among the latter are tomato, cucumber, marrow, beans, carrots, turnips and artichokes: the disease sometimes causes much loss in storage in the last three. Sunflowers and pot plants, such as Pæony, are also attacked.

CONTROL.—The wide range of plants liable to attack points to the need for proper rotation of crops, so that no susceptible crop shall occupy the same land more frequently than once in three or four years. When the disease is noted, every effort should be made to prevent sclerotia from contaminating the ground, this being done by immediate destruction of the entire affected plant. In the west of Ireland, some success is said to be achieved by late planting of the potato crop, with the object of delaying maturation of the leaves until spore discharge from the apothecia has ceased.

CHAPTER XXII

DISEASES CAUSED BY FUNGI IMPERFECTI

(1) Grey Mould (*Botrytis cinerea* Pers.)

General Appearance.—The disease first shows as a blackening of part of a leaflet, usually at the tip, from which it spreads in a wedge-shaped area down the leaf-blade. In continuous wet weather the entire foliage may become blackened and die, whilst, if dry weather supervenes, the spread is retarded and the affected parts of the leaves dry up and wither. The dead areas become covered with a smoky-grey mould with which growers are familiar on any decaying matter in the garden. Sclerotia occur as flat, shiny, black plates on the bleached dead haulms in autumn, on which they are extremely common in the wetter areas of the country.

Symptoms with which Grey Mould may be confused.—Two diseases may easily be mistaken for Grey Mould, *i.e.* Blight (page 334) and Stalk-Break (page 305). Of these, Blight is distinguished by the sparse greyish white mould occurring mainly on the lower surface of the leaf and at the margin only of the diseased area, whereas Grey Mould shows an abundant mycelium covering both surfaces of the affected areas. The typical wedge shape of these dead areas is also characteristic of the Grey Mould disease. Stalk-Break produces no mycelium on the foliage, and is easily distinguished from Grey Mould by the spherical or raised elongated sclerotia occurring both internally and externally on the haulm.

Distribution.—As in the preceding disease, Grey Mould is only a minor ailment of the potato. It rarely causes severe damage even in the wetter parts of the country and is of no significance in the drier eastern areas.

Cause of Grey Mould.—The causal fungus *Botrytis cinerea* is classed with the Fungi Imperfecti, since no sexual stage has yet been definitely proved to occur in the form found on potato. Some strains are, however, known to be a stage in the life cycle of an Ascomycete (*Sclerotinia Fuckeliana*, de Bary), and it is possible that the fungus on potatoes is merely a strain which has lost its power of sexual propagation. On this assumption this disease is closely related to the fungus causing Stalk-Break, and in fact the two were for long believed to be identical. The smoky-grey mould developing on the dead areas of the leaves is made up of masses of hyphæ on which are borne spherical conidia in bunches, the arrangement looking exactly like a miniature bunch of grapes when examined through a hand lens. The conidia are easily detached in the wind and are blown over the crop. In damp cool weather they germinate and penetrate either through a breathing-pore (stoma) or directly through the cell walls to the interior of the leaf. The leaf cells are destroyed and on the dead area so produced is developed another crop of millions of conidia ready for further distribution of the fungus far afield. The haulms also are affected, and in autumn the hyphæ in the haulm become compact and so form the flat inky-black sclerotia. The rotting of the haulm during winter releases the sclerotia into the soil where they are weathered and, in spring, produce a new crop of spores in time to infect the potato foliage in mid-summer. Apart from one or two instances in which the fungus appears to have been recovered, there is little evidence that tubers become infected in the field in this country. Moore (1943) records the fungus on tuber lesions in Shropshire, and it has also been found on tubers in the Solway, Forth, and Clyde drainage areas in Scotland (Dennis and Foister, 1942). In U.S.A., also, Folsom (1933) has described a form of tuber rot which he ascribes to this fungus.

CONTROL.—Measures to counteract this disease are not likely to be required, except in very wet areas or where serious attacks have previously occurred. Nevertheless, it should be clear that all dead haulms bearing sclerotia are better destroyed. Pethybridge (1916*a*) states that varieties showing resistance to Blight attack are similarly resistant to Grey Mould. Close planting, or interplanting other crops such as brassicæ between potato drills, serve to keep the atmosphere moist within the crop and so ensures the most favourable conditions for this and many other fungi to cause serious damage to both crops.

(2) SKIN SPOT (*Oospora pustulans* Owen and Wakef.)

GENERAL APPEARANCE.—Skin Spot attacks the tuber alone, on which the symptoms are usually only recognised after a period of storage. These symptoms take the form of unbroken pustules on the surface of the skin which Owen (1919) separated into two distinct types. One of these types, consisting of tiny raised "pimples" from 0·5 to 1 mm. in diameter, she regards as characteristic of coarser-skinned varieties such as Arran Chief; the smooth, thinner-skinned sorts such as King Edward more commonly developing flat pustules, or "crater-like" depressions with raised centres. Millard and Burr (1923), however, consider that the depressions are simply a later development of the pimples due to shrinkage of the tissues. The pustules have the same colour as the healthy skin when dry although they have also a characteristic "sheen"; when wetted they become purplish-grey in colour. The pustules may coalesce over a great part of the tuber skin, in which case a shallow, pimpled, depression with a clearly marked margin is produced; there is no change of colour or rotting in the tuber "flesh" beneath the attacked part. The cells immediately underneath become loose and corky so that the whole pimple can be picked out with a pin, leaving behind a circular pit of white flesh. (Fig. 56.)

SYMPTOMS WITH WHICH SKIN SPOT MAY BE CONFUSED.—Usually there is no difficulty in distinguishing Skin Spot from all other diseases of the tuber. The unbroken skin prevents confusion with either Common Scab (page 375) or Powdery Scab (page 367). In severe attacks the pimples coalesce over a large part of the tuber so that the continuous marginal depression around the area gives much the same appearance as Blight (page 334). In such cases, it is only necessary to cut the tuber and note the absence of any rotting of the flesh for any doubt to be removed.

DISTRIBUTION AND EXTENT OF LOSS.—The causal fungus appears to be a common inhabitant of potato soils, and there is a record of land in Scotland carrying the fungus in an infective condition after twenty years under grass; no farmyard manure, in which the fungus might have persisted, having been applied during this period (Anon, 1932). At best the disease produces no more than a blemish on the tuber-skin but this may be sufficiently obvious as to reduce the market value of ware. It is on seed, however, that the most serious effects are found, for an aggregation of pimples in the neighbourhood of the "eyes" will almost certainly result in many of these latter being destroyed. Misses in the drill are all too common as a result of an attack of Skin Spot, and the Ministry of Agriculture (Moore, 1943) reports losses of up to 60 per cent. as a consequence of affected seed tubers failing to grow; the same writer states that the disease is seen mostly on Scotch and Irish seed and occasionally on English "once-grown," but in the present state of knowledge too much significance should not be attached to this apparent difference in distribution. Certainly, varieties are attacked to different degrees and in Scotland it is reported (Anon, 1932) that while Golden Wonder is free from the disease, others such as Kerr's Pink, Arran Chief and Arran Banner are frequently attacked, and Ally, Majestic and King Edward are particularly liable to "blindness," *i.e.* to destruction of the "eyes." Foister (1943) confirms that the last two varieties are specially liable to blindness and adds Sharpe's Express to those varieties less severely attacked but often disfigured sufficiently to affect their sale. Greeves and Muskett (1939), working in Northern Ireland, state that severe Skin Spot is usually much worse in clamp-stored tubers than in boxes.

CAUSE OF SKIN SPOT.—What appears to have been this disease was first recorded in this country by Carruthers (1904) on potatoes from Lancashire. It was noted by Pethybridge (1915) in Western Ireland in 1914, and to it the present descriptive name was then given. Owen (1919) first investigated the causal organism in detail, and her work was later confirmed by Millard and Burr (1923). There are still, however, many important details of the life of this fungus awaiting further investigation. A mature pustule of the disease on the tuber is purplish-black at the surface and brown internally to a depth of perhaps an eighth of an inch. Microscopically, the tissues of the pustule are composed of cells which are either empty or contain brown, disorganised protoplasm; the walls are brown and much thickened. Amongst the brown disorganised cells are others with clear contents and thin normal walls, these obviously having escaped direct infection by the fungus, or showing, by the disintegration of nucleus, starch grains and other contents, early stages of attack. Below the pustule is a well-marked layer of cork cells, often six or more cells thick, which localises the effect of each point of infection, and incidentally is the reason why the entire pustule is so easily lifted out with a pin. The hyphæ are closely septate and are colourless to

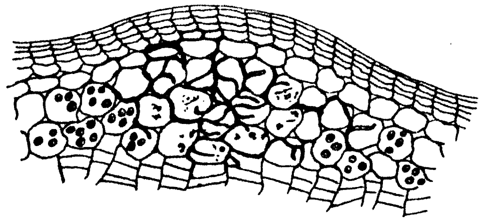

FIG. 56a.—Section of "Pimple" on Tuber caused by *Oospora pustulans*, showing mycelium destroying cells and their contents. The development of the fungus is retarded by the cells internal to the infected zone being stimulated to form a corky layer by cell-division. (*After* Owen.)

brown, the colour possibly developing relatively late in maturation. In artificial cultures on sterile potato, the hyphæ develop chains of rather elongated oval conidia, the chains being either simple or irregularly branched. Whether such conidia are often formed in nature is not known, nor is the mode of entry into the potato established, although Millard and Burr found that entry was most frequently effected at the "eyes." Growth of the fungus is most abundant at low temperatures, around 53° F., and under moist conditions. It is therefore to be expected that infection occurs in early spring or late autumn, and that further development does not occur until the tubers are exposed to cold conditions in winter. Certainly it is rarely observed in newly raised tubers but is far too frequently seen in seed in early spring. Affected "eyes" of the potato are usually either killed or weakened, with the corresponding result of a miss in the drill or the production of weak shoots. It may happen that secondary shoots arise after the death of the original eye, but these later-developed shoots will seldom be vigorous or able to yield a normal crop.

CONTROL.—Greeves and Muskett (1939) have studied methods of controlling this disease in Northern Ireland where, they state, it is much more severe in clamped than in boxed potatoes. Digging the crop unusually early effected no reduction in the amount of Skin Spot, from which it may be inferred that contamination, if not actual infection, may occur as the tuber itself develops. They showed, however, that Skin Spot is effectively controlled by immersing tubers, at lifting time, for not more than one minute in a 0·1 per cent. solution of an organic mercury compound (*cf.* Appendix I, page 649). Similar success was obtained by steeping tubers for ninety minutes in a 0·1 per cent. solution of mercuric chloride, but the treatment was unduly tedious; formalin at a strength of 1·5 per cent. gave little control and its use is not recommended. Whatever method is used there should be no delay in its application after the tubers are lifted; after a lapse of eight weeks, for instance, it is useless to attempt to control the disease, and nothing is therefore to be gained by treating possibly infected seed immediately before planting. Foister (1943) also obtained good control in Scotland by dipping the seed crop, at lifting time, in a 0·1 per cent. solution of an organo-mercurial compound for one minute; dipped stocks ultimately showing, when planted, from 0·5 to 1 per cent. of "misses" in the drill as compared with 10 per cent. of failures in the untreated seed.

(3) Silver Scurf (*Spondylocladium atrovirens* Harz)

General Appearance.—The common name well describes the typical symptoms of this disease. It shows in the form of grey or silvery patches on the tuber surface but never becomes more than a blemish. The affected area of skin is usually slightly depressed, and careful inspection will reveal that the surface is dotted over with minute black specks or sclerotia. No symptoms develop on any part of the plant other than the tuber, and even here they are easily overlooked. The disease is extremely common, especially on certain types of light soils, and is most conspicuous in early spring, particularly on "greened" tubers. If storage conditions are very unsuitable, *e.g.* unduly moist and hot, the silvery surface may be covered with black fungal growth resembling soot.

Cause of Silver Scurf.—The most complete study of the fungus on potatoes has been made by Schultz (1916) in U.S.A. According to this author the fungus over-winters on the tubers left in the field, but nothing is known as to its longevity or whether it can exist in the soil as a saprophyte. Growth is strongest at a temperature of from 70° F. to 80° F., but the fungus is not killed even at temperatures well below freezing point, *e.g.* at 14° F. Entrance is effected mostly through the lenticels (breathing pores) of the tuber and only the corky cells comprising the " skin " are invaded and destroyed by the mycelium. In this way the surface cells are loosened and may slough off. All attempts to infect the haulm, stolon or roots with the fungus have failed. Under moist conditions some of the cells of the almost colourless surface hyphæ become brown, and from them arise short, septate and dark-coloured branches (conidiophores) which bear conidia in whorls. Each conidium is from four to seven septate, club-shaped, and attached to the conidiophore by the broad end. It is the development of these dark brown conidia which gives a characteristic " sooty " appearance to affected tubers. Later, the ordinary hyphæ of the mycelium darken with age and form small " knots " or sclerotia, barely visible to the naked eye, which serve as a means of persistence throughout at least one winter. It is not known whether infection of a new crop of tubers is effected by germinating conidia or by vegetative hyphæ developed from the sclerotia.

CONTROL.—In this country the disease has never been regarded as a serious one but Kramer (1942) reports it as increasing in importance in Brazil. He states that not only does *Spondylocladium* infection result in heavy direct loss but that it paves the way for infection of tubers by secondary parasites. Kramer obtained promising control by one and a half hours' immersion of tubers in 1 per cent. mercuric chloride but, in addition, he recommends a three or four year interval between potato crops, planting in dry soils and storage of the crop in well-ventilated conditions ; timely harvesting as soon as the tubers reach maturity will, in his opinion, forestall the development of large numbers of lesions before storage. It may be noted that Schultz (1916) obtained a high, though not complete, control by steeping infected tubers in *warm* mercuric chloride (*cf.* Appendix I, page 649). Tuber disinfection for this disease is probably unnecessary in this country but obviously the use of infected tubers as seed should be avoided.

(4) VERTICILLIUM WILT (*Verticillium albo-atrum* Reinke and Berth)

GENERAL APPEARANCE.—This is another of the minor ailments of the potato crop and one that is difficult, if not impossible, to identify with certainty in the field. An affected plant is usually dwarfed and with erect leaves which give the plant a "staring" habit. The leaflet-blades become pale or yellowed, roll upward along the midrib, and finally become dry and withered. The foliage symptoms thus closely resemble those found in Blackleg (page 393) and Leaf Roll (page 437). It is separated from Blackleg by the firmness of hold, and absence of any blackening of the haulm at ground-level. Also, when the haulm is cut across, the vascular bundles at the angles are yellow, as distinct from the black vascular bundles of Blackleg. The yellow colour and "softness" of the rolling in the leaves similarly serve to distinguish this disease from Leaf Roll, as does the fact that in Verticillium Wilt most of the leaves (particularly the upper ones) show rolling, whereas typical cases of secondary Leaf Roll have only the lower leaves affected. Plants with Verticillium Wilt give a much reduced yield, but such tubers as are formed appear normal. When, however, they are cut across at the heel end they usually, though not invariably, show a brown ring below the skin.

DISTRIBUTION.—The disease was first described by Pethybridge (1916) as occurring in Western Ireland in 1909, but it was not until 1916 that it began to be recorded regularly in the British Isles. There is little doubt, however, that Verticillium Wilt had long been confused with Blackleg and other "curl" producing diseases. It is typically a light-soil and dry-weather disease, though even under the most favourable conditions an infection of 1 per cent. of the plants would be an exceptionally heavy attack.

Although it would seem, therefore, to be of little importance to the potato grower, it is well to remember that this may not always be the case. In New Zealand the disease was unknown until 1931, yet by 1935 it was stated by Chamberlain to be present in every potato-growing district of the Dominion. Some varieties showed field infections of 30 per cent. of the crop, and in one case the yield was reduced by 50 per cent.

In U.S.A., also, it is regarded as a serious menace to potato-growing.

CAUSE OF VERTICILLIUM WILT.—The causal organism (*Verticillium albo-atrum*) is closely related to, if not identical with, the one responsible for the "Sleepy" disease of the tomato. Many species of this fungus are known to occur as saprophytes in the soil, and the species affecting potatoes has been shown to hibernate in this way by McKay (1926) in U.S.A., and Chamberlain (1935) in New Zealand. The former worker traced the spread from plant to plant in the row from the root systems of affected plants, while the latter believes that late infection of tubers is due to the entrance of the fungus directly from the soil. In this country, however, the slight attacks which occur are usually attributed to the use of infected seed tubers. The mycelium is present in the vascular strands of the tuber where it sometimes, but not invariably, produces the brown ring at the heel end to which reference has already been made. During storage the fungal hyphæ may progress towards the rose end of the tuber and, according to Dale (1912), some of the "eyes" may be killed. The bases of the sprouts are invaded, and during the growing season the mycelium spreads slowly up the haulm and into both roots and stolons. The rate of spread is possibly determined by the external temperature, but in this country it is usually slow, so that symptoms of wilt rarely appear until mid-summer. In severe cases, however, the fungus may even reach the foliage and produce longitudinal brown streaks along the leaf petioles. The cessation of growth, followed by wilting and withering of the foliage, occurs when the passage of watery salts to the leaves is prevented owing to the blocking of the wood vessels by the fungal hyphæ. After the death of the haulm the hyphæ pass from the woody tissues into the surrounding cells where they continue to grow and finally assume the resting condition as black thick-walled hyphæ. If a fragment of an affected haulm at this stage is kept moist and warm the hyphæ grow out and produce whorls of branch hyphæ. These latter either bear small, slightly oval, conidia at the tip, or themselves produce whorled branch-hyphæ bearing terminal conidia. The function of these conidia in nature has not been studied, but presumably they may cause infection. In this country, however, there is no evidence that tuber infection occurs in any way except *via* the stolon by means of the vegetative hyphæ. *Verticillium albo-atrum* grows slowly at low temperatures and most rapidly between 68° F. and 77° F.; growth ceases entirely in the neighbourhood of 86° F. It follows that the disease is most serious in the warmer areas or hot summers of temperate countries such as Great Britain, whereas it is of little account in cold summers or in the heat of the sub-tropics.

CONTROL.—Tubers showing discolouration at the heel end when cut should not of course be used for seed purposes. It should be remembered, though, that the absence of this character is no criterion of freedom from Verticillium Wilt. Seed producers have a special responsibility for ensuring that infected plants, and their tubers, are rogued out before the crop is lifted. Pethybridge (1916) showed that tubers heated for twenty hours until the temperature reached 112° F. were still capable of producing a plant when planted whilst the fungus within the wood vessels was killed. Similar results had been obtained with Blight, but in neither disease is this likely to be of any practical value. There is no evidence that the disease can persist in the soil for more than one winter, even in countries where the disease is serious, In this country it has not been found to occur at all in the soil, so that any danger from this source should be removed by maintaining a normal four years' rotation.

(5) EARLY-BLIGHT OR TARGET SPOT (*Alternaria solani* ((E & M) Jones and Grout)

GENERAL APPEARANCE.—In some seasons it is not uncommon to find small concentric rings of dead tissue on potato foliage. This is the "target" stage of a disease which, in many countries, later spreads over the leaves until the foliage as a whole becomes dry and withered. The final appearance is similar to that of ordinary Blight, but since it usually becomes epidemic in U.S.A. and other countries before *Phytophthora* Blight it is designated "Early-Blight"; the more so as, in these countries, a form of tuber-rot may also develop (Goossens, 1933, 1937). In the British Isles the disease rarely, if ever, develops beyond the "target" stage and is of no economic importance. The symptoms, as they occur in this country, cannot be confused with those of any other foliage disease of the potato.

CAUSE of " TARGET " SPOT.—In the British Isles the spots are either sterile or great difficulty has been experienced in isolating any fungus from them. However, the fungus *Alternaria solani* has occasionally been isolated, and since this is responsible for the more serious disease of Early-Blight which first shows similar " target " spots on the foliage, there seems no reason to doubt that climatic factors alone prevent the disease assuming a serious form in this country. At the same time it is by no means certain that the " targets " are invariably produced by the Early-Blight fungus *Alternaria solani*, and the fact that perhaps the most common fungus associated with the spots is the supposedly saprophytic species *Alternaria tenuis* Auct, still further complicates the problem. Some brief description of *A. solani* seems to be called for, however, since it was reported (Salaman and O'Connor, 1934) to be " assuming an epidemic form in glasshouse and field at Cambridge in 1932-1934, and to be present in the latter year in potato-growing areas of Ross and Cromarty, and Aberdeen, the north-west coastlands of Scotland and the Outer Hebrides." Since then, slight attacks only have been reported from many counties of England.

The hyphæ are dark brown to olive in colour and ramify both the intercellular spaces and cells of the affected area. From these vegetative hyphæ arise branches which grow through the stomata of the lower surface and produce single terminal conidia. The conidia are many-celled and club-shaped ; they are attached by the broad ends to the hyphæ and have the free ends drawn out almost to a hair. In pure culture they have been found to occur in short chains and it is for this reason that the original name of *Macrosporium solani* has been changed to *Alternaria solani*. Each cell of a conidium is capable of germinating and producing a branched hypha, so that the chance of successful infection of a plant by way of the stomata is greatly increased. In contrast to *A. solani*, the saprophytic species *A. tenuis* produces much longer chains of conidia, each of which terminates in a blunt " beak " instead of tapering finely as in the former species.

The disease in its virulent form is associated with hot dry conditions and is particularly prevalent in sub-tropical countries.

It becomes severe in temperate areas only when exceptionally warm conditions prevail. In Belgium, for instance, Roth (1936) found that the disease reached its climax at temperatures of from 79° F. to 82° F. with alternating phases of dry and humid weather to facilitate conidial germination. In Germany Klaus (1940) considers that most strains of the fungus are of only weak pathogenicity. Sporulation occurs best at a temperature of 26° C. (78·8° F.) but may be found within the wide range of 1·5° C. (34·7° F.) and 34·5° C. (94·1° F.). Atmospheric moisture is of equal importance and sporulation is most frequent in a saturated atmosphere. It will occur under very weak illumination but sporing is definitely inhibited by total darkness or by a concentration of carbon dioxide greater than 0·5 per cent. On the contrary in this country, according to Dillon-Weston (1936), the sporulation of *Alternaria solani* is increased largely in light of high intensity; non-sporing cultures sporulating profusely within eighteen hours after exposure to intense white light.

CONTROL.—No special measures of controlling the fungus in this country seem to be necessary, and the spraying and dusting methods advised for Blight have been found very successful in controlling *Alternaria solani*. In South Africa, Wager (1945) recommends early morning spraying with Bordeaux mixture or dusting with copper-lime at the rate of 20 to 30 lb. per acre; the treatment in either case must be frequent enough to keep a covering of copper on the foliage. Nothing is known as to varietal susceptibility in this country, but Salaman and O'Connor (1934) recorded it as severe on Majestic, King Edward and Kerr's Pink, and rather less so on Edzell Blue; Golden Wonder being apparently immune. In U.S.A., it is reported by Le Clerg (1946) that only one of the varieties commercially grown shows marked resistance to infection with Early Blight, *i.e.* Menominee; a variety which is also highly resistant to Common Scab (page 375) and moderately so to Blight (page 334). Out of 445 seedlings tested 10 were resistant to Early Blight and of these, four also were resistant to Common Scab and a further two resisted Blight.

(6) DRY-ROT (*Fusarium cæruleum* (Lib.) Sacc.), and other species

GENERAL APPEARANCE.—This is a storage disease which may not become evident until two or more months after the tubers have been lifted in an apparently healthy condition. Dry-Rot is more prevalent in tubers stored in seed-boxes, bags, or loose on the floor of a store, than in clamped (pitted) potatoes so long as these latter are left undisturbed, but severe rotting may develop once the clamp has been opened. Normally little is seen of the disease until mid-winter, but from December onwards the number of tubers developing Dry-Rot may rapidly increase, particularly in first early varieties. The rot may occur on any part of the tuber but is usually associated with a bruise or wound. The first symptom is a slight shrinkage and darkening of the affected part followed, as the shrinkage continues, by the skin becoming wrinkled in the form of irregular concentric circles. The underlying tissue assumes a mealy, brown, appearance as it dries up and cavities develop which become lined with the fluffy white fungal mycelium. At the same time the fungus breaks through the skin to the surface where it forms fluffy white or pinkish pustules or cushions which, if scraped, are seen to be bluish at the base in most cases. Ultimately, what is left of the inside tissues turns almost black, the tuber becomes a mere "feather-weight" and is so hard as to be difficult to cut with a knife. (Fig. 57.)

SYMPTOMS LIKELY TO BE CONFUSED WITH DRY-ROT.—The dry form of rot caused by the Blight fungus (page 334) can be distinguished by the absence of fungal pustules as well as of the concentric wrinkling of the skin. These also serve to separate Dry-Rot from Skin Spot (page 309) which often shows a depressed area when large numbers of "pimples" coalesce; there will, however, as a rule be a sufficient number of "pimples" around the depression to leave no doubt as to the disease. Blackleg (page 393) and Pink Rot (page 351) rarely show any depression of the skin and should give no difficulty. The most probable source of confusion is with Gangrene (page 328) and there is little doubt that the two diseases are in fact frequently confused. Gangrene may show a wrinkled skin over the sunken area but this is not characteristically concentric, the diseased part is sharply delimited from the healthy underlying tissue and the greyish fungus growth is quite different from the pinkish-white mycelium of *Fusarium*.

DISTRIBUTION.—There is no doubt that Dry-Rot is an old disease of the potato tuber, though little work had been carried out with the disease until 1904, when Pethybridge (1916*a*) began his studies. It is known wherever the potato is grown and is one of the most serious diseases of the crop.

CAUSE OF DRY-ROT.—The most common cause of " Dry-Rot " in the main potato-growing areas of the world appears to be the fungus *Fusarium cæruleum* (Lib.) Sacc., though other species of *Fusarium* may also be important in certain regions. Thus Weiss *et al.* (1928) state that in North America the most frequently recorded species causing Dry-Rot are *F. cæruleum*, *F. sulphureum* Schl., and *F. trichothecioides* Woll. ; the first named being the most widely distributed. On the continent *Fusarium avenacearum* (Fr.) Sacc., was known to be implicated (*cf.* Schmidt, 1928) but it was not until 1945 that this fungus was isolated (though less frequently than *F. cæruleum*) from rotting tubers in this country (Moore, F. J., 1945) and, later, *F. culmorum* (W. Sm.) Sacc., was similarly isolated in Scotland (Dennis and Foister (1942) and, once only, in England (Moore, 1943). Both *F. avenacearum* and *F. culmorum* are widely distributed in the soil and are known to cause " Brown Foot-Rot " and " Ear-Blight " of Wheat. Although there is little doubt that *F. cæruleum* is by far the most common cause of Dry-Rot in the British Isles at present, conditions could easily arise to favour another species ; even fluctuations in the popularity of certain potato varieties may have to be taken into account, for Moore, F. J. (1945) most frequently isolated *F. avenacearum* from the variety King Edward VII and *F. cæruleum* from Majestic. Nothing is known as to the relative abundance of the two species in soils, but both are common and it is doubtful if the predominance of *F. cæruleum* as a cause of Dry-Rot can be explained in this way ; nor has this species any advantage over *F. avenacearum* in the ease with which penetration of the tuber is achieved. There are, however, considerable differences between the two species in the optimum temperature and humidity for growth and infection. Thus *F. avenacearum*, on artificial media, grows

FIG. 55.—Black Scurf (page 295).

FIG. 56.—Skin Spot (page 309).

FIG. 57.—Dry Rot (page 319).

FIG. 58.—Skin Necrosis (page 426).

best at from 24° C. to 27° C. (max. 36° C.) according to Moore, E. S. (1924), while the most favourable temperature for *F. cæruleum* is from 15° C. to 20° C., with a maximum temperature of 30° C. (De Haarn, 1937); and Moore, F. J. (1945) showed that at their respective optimum temperatures the former species grew at approximately twice the rate of the latter. The last-quoted author also demonstrated that while infection of wounded tubers by *F. avenacearum* required much the same temperature as for growth on artificial media, in the case of *F. cæruleum* infection was most frequent at 15° C., and no rotting occurred at all when the temperature was raised to 25° C., although growth at that temperature was still profuse on artificial media. All workers agree that Dry-Rot increases with increasing atmospheric humidity and it is in this way that Moore, F. J. (1945) explains the more extensive rotting in her experimental clamps as compared with laboratory-stored tubers at approximately the same temperature. Again, the two *Fusarium* species react differently to humidity for, according to Schmidt (1928), an atmospheric humidity of 80 per cent. saturation is necessary for penetration by *F. avenacearum* whereas rotting occurs at 50 per cent. humidity with *F. cæruleum*; this may partly account for Moore's (1945) statement that, while *F. avenacearum* was apparently common in some varieties in clamps, she had failed to isolate this species from tubers stored in seed-boxes or bags.

There can be no doubt that tubers are very frequently lifted in a contaminated condition, either directly or by the adherence of soil carrying the fungus. Small (1944) records that of 42 samples of soil scraped from seed-tubers *ex* Scotland and Northern Ireland, 37 carried the Dry-Rot fungus *F. cæruleum*, and Foister *et al.* (1945*a*) have shown that living mycelium, capable of causing infection, can be recovered from soil two years after the land had last been under potatoes. It must therefore be assumed that stored potatoes, whether in clamps, bags, seed-boxes, or loose on the floor of a loft, will probably be in close contact with the causal organism and that, once the tuber has been penetrated, the likelihood of active rotting will depend on such conditions of temperature and moisture as have been described above. As regards penetration, there is general agreement that bruises or wounds are almost indispensable. Nevertheless, Pethybridge and

Lafferty (1917) believed that penetration could occur through the breathing pores (lenticels) of the tuber, or by way of "Scab" pustules, or even through the undamaged "eye" or young sprout. Boyd (1947) also records that spread from an infected tuber to an undamaged one in contact does occasionally occur, and suggests that a localised toxic action on the part of a rotting tuber would permit the entrance of the fungus into an adjacent healthy one, Moore (1945), however, found no evidence of any increased susceptibility of healthy tubers arising from the accumulation of volatile excretions from infected tubers. Boyd (1947) demonstrated that in one stock of the variety Arran Pilot 77 per cent. of the Dry-Rot lesions originated from, or were associated with, pustules of Powdery Scab (*cf.* page 367). None of these workers, however, doubts the overwhelming importance of wounds as the means by which the fungus normally gains entrance to the inner tissues of the tuber, and Boyd has examined the likelihood of infection following (*a*) bruises which did not break the skin, (*b*) shallow wounds usually causing some skin damage and (*c*) deep incised wounds. He concluded that slight bruises which left the skin undamaged would normally not permit the entrance of the fungus for, under the three sets of conditions described, 0, 13 and 55 per cent. of the variety Doon Star; and 1, 21 and 59 per cent. of the variety Arran Pilot developed Dry-Rot. Boyd (1947) also showed that *F. cæruleum* is unable to penetrate through the protective "callus" produced by the surface cells of the wound, for even a severe wound was no longer liable to Dry-Rot attack between two and eight days after being formed; the time of course depending on the suitability of the conditions for tissue-healing.

Once the hyphæ of the fungus have passed the barrier of the tuber skin they spread both through the cells and the intercellular spaces of the "flesh," and the tissue dies. Ultimately, the hyphæ not only line the inner surface of cavities produced by the shrinkage of the tissues, but also burst through the sunken skin to the outside of the tuber; in both cases forming the fluffy pads or pustules characteristic of the disease. On these pustules of hyphæ are formed vast numbers of sickle-shaped spores, each of which is divided by crosswalls into (usually) four cells. Some hyphal cells also become rounded off and greatly increase the thickness of their walls, so forming a very resistant resting spore (chlamydospore) which in all probability enables the fungus to persist in soil, or in the dust of a loft, for a considerable length of time. The sickle-shaped spores are easily detached from the pustules, and their extreme lightness of weight ensures prolonged contamination of the atmosphere; Pethybridge and Bower (1908) demonstrating the presence of large numbers of these living spores on the floors, walls, and in the air of a loft containing tubers badly affected with Dry-Rot. These sickle-shaped spores are almost certainly the main cause of secondary infection of tubers during storage when the conditions of temperature and moisture suitable for germination occur.

EXTENT OF LOSS.—Early varieties are much more liable to attack than are later sorts. Of these former varieties May Queen, Ninetyfold, Reading Russett, Di Vernon, and Catriona are extremely susceptible. Sharpe's Express, Duke of York and Arran Pilot are often badly attacked, as are the second early or early maincrop varieties Arran Comrade and Doon Star. Bad attacks have also been recorded in the late variety Kerr's Pink, whilst on the other hand it is seldom that the early variety Epicure is affected. After considering the fluctuation in the amount of Dry-Rot from year to year Moore (1943) is of the opinion that the disease is worst after dry seasons, though this may in part be due to its greater prominence in the virtual absence of Blight. Losses of 50 per cent. frequently occur in boxed seed or in tubers spread on the floor, but in the clamp the loss is usually much smaller though equally severe losses have been recorded in reclamped potatoes. Sometimes the disease is only discovered when seed, apparently sound when planted, fails to grow, and failures of up to 60 per cent. of the crop have been reported from this cause (Moore, 1948). Usually such cases of rotting after planting are regarded as the result of "delayed action" on the part of a fungus already present on, or in, the tuber before planting, but Moore (1948) has drawn attention to the possibility of new infection from the soil after the seed tubers are planted. In one case he reports that 10 tons of Majestic remained sound after planting whereas 30 per cent. of the same quantity of Dunbar Standard, from the same source, rotted in the ground. Pethybridge and Lafferty (1917) first proved that the susceptibility of the tuber to attack becomes greater as maturation advances, and this fact may help to explain the higher susceptibility of many early-maturing varieties, as well as the steep rise in the incidence of rotting in the latter part of the storage period.

CONTROL.—Since the eradication of the fungus from the soil is not practicable, it seems clear that effective control must be based on (*a*) care in handling so as to avoid unnecessary bruising, (*b*) better storage conditions and (*c*) the practicability of tuber-treatment to prevent infection.

(a) *Handling.*—Small (1945, 1946) concluded from his experiments that the avoidance of bruising is an effective control of Dry-Rot, for undamaged tubers remained sound for a period of six months whether in clamps or seed-boxes. Under commercial conditions, however, some bruising is quite unavoidable ; Foister and Wilson (1943) showed that careful handling, with the object of minimising bruising, only succeeded in reducing the loss from 58 per cent. down to 31 per cent. The effect of bruising at lifting time appears to be less serious in inducing rotting than when wounds are incurred in later operations, which may possibly be related to the higher resistance of tubers to infection at an early stage of maturation. Certainly Boyd (1947) found good evidence for his belief that injuries inflicted by the riddle are of paramount importance, and that fair control of Dry-Rot is possible by merely modifying the present system of tuber-dressing ; thus hand-dressed tubers showed only a loss of 4 per cent., whereas machine riddled tubers developed 16 per cent. and twice riddled tubers 24 per cent. of rot. Moreover, according to Foister (1940), experiments on a commercial scale have proved the practicability, and advantages, of combining in one day all the operations of lifting, dressing the seed from the ware, and then disinfecting the seed portion in the way described below.

(b) It has been stated that less Dry-Rot develops as a rule in clamps than in seed-boxes, sacks, or in tubers stored loose on the floor. This needs the qualification that when tubers are reclamped immediately after riddling, the combination of the wounds then produced with the humid conditions of the clamp may result in a large increase in rotting (Boyd, 1947) ; who also states that it is only under such circumstances that many Scottish growers become aware of the disease at all.

Bagging the seed after riddling has much the same effect as reclamping, particularly when such storage is unduly prolonged before planting. Whether riddling is followed by clamping or bagging it is important to avoid adding to the humidity of the stored tubers, and the operation should only be carried out with dry tubers ; Boyd reports that the amount of rot which developed in sacks on wetted tubers increased from 16 to 23 per cent. On the other hand, there is the possibility that infection of tubers exposed loose or in boxes may be unnecessarily high if, as Small (1945) believes, the fungus can persist in a viable state from one season to the next in the dust of the store. All seed-boxes and sacks, as well as floor, walls and ceiling of the store should therefore be disinfected by spraying either with a 2 per cent. solution of copper sulphate (bluestone) or 5 per cent. formalin ; in which latter case the operator should wear a gas-mask to protect the eyes and throat from the penetrating fumes. Seed stored in boxes or on the floor should be so arranged as to facilitate inspection and the removal of infected tubers, with the minimum of disturbance and risk of bruising. For the same reason the store should be rat-proof. Again, while it is advisable to keep the store cool, care should be taken to prevent chilling ; for this predisposes the tubers to attack by *F. cœruleum.* Thus McIntosh (1944) found that a sample of tubers which, when protected from frost, showed 13·5 per cent. of Dry-Rot, developed 23·5 per cent. and 35·5 per cent. when exposed to frosty weather on several successive days for three and a half hours and seven hours respectively.

(c) *Tuber Disinfection.*—(i) *Liquid Dips.*—Organo-mercury compounds have been increasingly used in recent years as a means of controlling plant diseases, and Foister (1940) has shown that a good measure of control of Dry-Rot is obtained by immersing tubers for one minute, at lifting time, in any one of a number of proprietary substances containing such compounds. The object should be to dissolve the substance in sufficient water to give a 0·1 per cent. solution of the active ingredient (*cf.* Appendix I, page 649), and this is usually achieved by following the directions of the manufacturer. A somewhat less effective control is afforded by dipping for about a quarter to one-half minute in a 1 per cent. solution of formalin (2 pints in 10 gallons of water). It must not be forgotten that organo-mercury compounds are highly poisonous to man and agricultural stock, and that evaporation of the water merely ensures that a dry, poisonous, film is retained on the tuber; from which it follows that only tubers destined for planting may be treated, and no safeguard is provided by this method against Dry-Rot in ware tubers. Foister considers, as a result of commercial experiments, that there is nothing impracticable in combining the operations of lifting, dressing out the seed, and then treating the latter with organo-mercurials. There is the further advantage that immediate treatment after lifting is desirable for the control of other tuber-borne diseases, *e.g.* Blight (Greeves, 1937) and Skin-Spot (Greeves and Muskett, 1939).

The problems were again investigated by Foister and Wilson (1943) and the conclusion was reached that twice dipping at lifting time, whether of normally lifted or " greened " tubers, gave no additional advantage over single dipping, and in no case was the subsequent development of Dry-Rot reduced below 4 to 5 per cent.; the failure to obtain complete control by these means is apparently partly due to the dipping fluid failing to penetrate thoroughly into the deepest wounds (Boyd, 1947). Small (1945) pointed out that the supply of labour for tuber-disinfection at lifting time is one difficulty, and showed that adequate protection against Dry-Rot was, in fact, provided by treatment in winter when clamps are opened and riddled for seed. In this statement he is confirmed by the work of Boyd (1947) which, incidentally, emphasises the relatively small effect produced by " digger " injuries. Boyd's results also make it clear that any further delay after riddling, *e.g.* until the arrival of the seed on the " purchasing " farm, is rarely of any use in preventing the development of Dry-Rot. This worker fully confirmed Foister's conclusion that dipping seed which was to be stored in boxes, at lifting time, gave adequate protection since, of course, no further riddling would be required. When, however, such early treatment was given to an experimental lot of seed, which was then clamped until December and again riddled without further treatment, he obtained only poor protection against the subsequent development of rotting.

(ii) *Dusts.*—Among the factors which have prevented the large-scale adoption of protective " dips " are (apart from the high cost) the difficulty of manipulation, and the highly poisonous nature of the dips which limits their use to " seed " after riddling. A cheap, non-poisonous dust seemed to be the answer to most objections and a good deal of progress can be reported in the efforts to find an efficient dust of this description. Foister *et al.* (1945*b*) have shown, as a result of large-scale experiments in Scotland over a period of three years, that thymol, used at the rate of 12 oz., made up to 10 lb. with kaolin for each ton of tubers, was effective. The control achieved was "excellent" when the treatment was applied twice (once at lifting and again on riddling) and was on the average slightly better than that given by a single dip with an organo-mercurial at riddling. Treated Catriona, Arran Pilot and Doon Star seed, which was despatched from Scotland to England between December and March, showed in April only from 1 to 5 per cent. rot as against from 17 to 46 per cent. of Dry-Rot in the untreated controls sent at the same times. Compared with liquid dips the dry treatment was inexpensive, but some tubers were severely damaged by the thymol; Arran Pilot being more susceptible than Doon Star. Boyd (1947) continued the work and found that even a lower thymol concentration of 6 oz. per 10 lb. per ton reduced the amount of Dry-Rot from 16 per cent. to 0·3 per cent. Many inert carrier substances were tried but none was so satisfactory as kaolin. Boyd found that immature tubers of all the varieties tested (Arran Pilot, Doon Star, Sharpe's Express, Catriona and Ninetyfold) were much more susceptible to thymol injury than were the fully mature tubers, and no late-lifted tubers showed severe damage; even when bruised in the riddle before treatment with thymol, the injury due to the chemical was recorded as "slight," but wetting the tubers increased the phytocidal action of the thymol. Of the varieties tested, Ninetyfold and Arran Pilot proved most susceptible to thymol damage and Doon Star least so, and some injury was inflicted at concentrations below that required for adequate protection against Dry-Rot; even with only 1 oz. per 10 lb. per ton the dust could not be regarded as wholly satisfactory in this respect. Manufacturers have been no less busy in their efforts to find a non-poisonous but effective dust and one such substance has proved most promising (Anon, 1948). This dust, based on 2.3.5.6-tetrachlornitrobenzene, appears to be satisfactory in many respects, but full information is still required as to risk of tuber damage by the use of the dust before it can be regarded as having passed finally from the experimental stage; the same must at present be said with regard to the claim that the dust is non-poisonous to man or stock, although it may be conceded that tetrachlornitrobenzene is of such a low order of toxicity that it may probably prove to be non-poisonous when used as directed by the makers.

(7) GANGRENE (*Phoma foveata* Foister)

GENERAL APPEARANCE.—The disease begins as a small depression differing from Dry-Rot in the tissues remaining reasonably firm. Gradually the depression grows until it forms a "thumb-mark" of from 1 to 2 in. in diameter (Fig. 70). Little harm results if the disease makes no further progress although a little reddish liquid, probably infective, either exudes naturally or may be expressed from tissues not yet dried up. When the lesion dries it may easily be removed by the finger-nail, leaving a clean hollow. Cutting a tuber at an early stage of attack shows the internal tissues to be light-brown in colour, slightly watery and mealy as in early stages of Dry-Rot, but later the colour deepens to salmon-pink with a touch of grey and the tissues begin to shrivel, darkening as they do so to grey or even black. As the rot develops both in surface area and internally, most of the tissue may be involved so that the tuber collapses to form a shrunken, wrinkled mass as in Dry-Rot. Internally cavities arise which are lined with a loose felt of mycelium ranging from pink to brown in colour. No white or pink cushions develop as in Dry-Rot but, instead, minute black bodies the size of a pin's head may burst through the skin in small scattered groups or in long curved lines more or less concentrically arranged. The internal rot is always well delimited from healthy tissue by a darker, narrow, hard zone.

SYMPTOMS WITH WHICH GANGRENE MAY BE CONFUSED.—The tuber disease most resembling Gangrene is Dry-Rot (page 319) but, apart from the differences already noted above, the wrinkled skin of the Gangrene-affected tuber is more reminiscent of a network than of the concentric wrinkling characteristic of Dry-Rot. Occasionally, the depressions in the skin may be extensive, but dry and very shallow so that the condition may be confused with symptoms of Blight (page 334); internally, however, the tissue is not rusty-brown, as in Blight, but is salmon-pink, darkening to orange in colour.

DISTRIBUTION.—"The disease has been found in various stocks of a number of well-known varieties in most of the potato-growing districts in Scotland" (Alcock and Foister, 1936), and Foister (1940*a*) states that it occurs also in Eire, Northern Ireland, and in England and Wales. Moore (1943, 1948) reports Gangrene from many counties in England and Wales, but how far these cases are due to the importation of contaminated seed from Scotland and Ireland is uncertain. Alcock and Foister state that the disease has been found naturally in the following varieties.

First Earlies—Arran Crest, Arran Pilot, Arran Scout, Ballydoon, Di Vernon, Doon Early, Duke of York, Eclipse, Epicure, May Queen, Sharpe's Express, Witchhill.

Second Earlies—Arran Signet, Catriona.

Early Maincrop—Arran Banner, Arran Consul, Doon Star, Gladstone, Great Scot, King Edward, Majestic.

Late Maincrop—Arran Cairn, Kerr's Pink.

CAUSE OF GANGRENE.—The disease was first suspected as being distinct from Dry-Rot in February 1936 by Mr R. J. Scott of the Scottish Department of Agriculture. In the same spring it was studied in detail by Alcock and Foister (1936) and the present account is largely taken from their work. Later, the causal fungus was described by Foister (1940*b*) as a new species of the genus *Phoma* under the name *Phoma foveata*. It is a member of the Fungi Imperfecti characterised by the production of conidia (pycnospores) within minute, black, carbonaceous fruit-bodies known as pycnidia. These pycnidia burst through the tuber-skin and appear to the naked eye as black "pinheads" occurring either singly or fused in small groups arranged more or less concentrically along curved lines. Under suitable conditions the pycnospores exude from the pycnidia either as a yellowish-cream mass (Foister, 1940*b*) or pink, drying to a "carrot" colour (Dennis, 1946). The pycnospores appear colourless under the microscope, however, and are mostly one-celled though occasionally two, and even three-celled spores are to be found. As in the case of Dry-Rot, *Phoma foveata* has been proved to be soil-borne (Foister *et al.*, 1945*a*); contaminated tubers showing the disease only after a period of storage. Although there is no reason to doubt that the disease *can* be spread in storage by means of the pycnospores, this is less likely to happen than in the case of Dry-Rot since the pycnospores are normally embedded in a mucilaginous gum, and their transport from one tuber to another would therefore usually depend on the spore-loaded gum adhering to some marauding insect or other animal; Foister (1940*a*) also expresses the view that Gangrene does not spread so readily in boxes as does Dry-Rot. Infection of tubers of many varieties has been obtained in the absence of any kind of wound but many more became infected when cultures of the fungus were introduced into a wound on the tuber. Bruised tubers of Abundance and Doon Star contracted the disease after being placed in contact with a portion of a tuber affected with Gangrene, so that there is no doubt that the disease can spread in this way during storage. Although Gangrene may occur in company with Dry-Rot on the same tuber, the two diseases are quite distinct and each may occur in the absence of the other. Other species of *Phoma* have been recorded on potato but their relationship is still largely undetermined; Moore (1943) accepting only *P. foveata* Foister, *P. solanicola* Prill. & Del., and *P. tuberosa* Mel. *et al.*, as reasonably well authenticated. Of these, *P. solanicola* occurs on the haulm only and the other two species solely on the tuber. *P. tuberosa* has not been identified with certainty in the few records of a Phoma-Rot of tubers in England and Wales (Pethybridge, 1926) though what is believed to be this species has been isolated from Scotland by Dennis (1946). It was first found as a wound parasite of tubers following attacks of Powdery Scab (page 367) in U.S.A. (Melhus *et al.*, 1916) who describe it as producing more or less circular depressions, often hard and bony. When these circular lesions are removed, as can easily be done, they leave behind a clean and smooth cavity resembling a button; hence the name "Button-Rot" applied by farmers to this disease. Both the description and illustrations of the disease by these authors would certainly be identified in this country with the rot caused by *P. foveata* but, whereas the pycnidia of *P. foveata* are borne on a pad of mycelium known as a stroma (Moore, 1943), Melhus *et al.* state that a definite stroma is absent in the case of *P. tuberosa*.

EXTENT OF LOSS.—No estimate can as yet be given of the average loss due to this disease, though it is probably heavy, because of its confusion with Dry-Rot. Scott reported an 80 per cent. loss in certain stocks during the winter of 1935-1936, and even higher losses have been recorded in some cases of boxed tubers. Like Dry-Rot the disease is apparently more prevalent in the seed-box than in the clamp or pit, though even under these latter conditions cases have occurred of a 50 per cent. loss. Although only recently recognised as distinct from Dry-Rot, it or a very similar disease is known to have affected the variety Doon Star since 1927. As in the case of Dry-Rot, Gangrene is usually more prevalent in early maturing varieties than in "lates," although moderate infections have been found in such late varieties as Kerr's Pink.

CONTROL.—All available information suggests that the measures found effective in controlling Dry-Rot of potatoes caused by *Fusarium cæruleum* (page 324) provide the best means also of avoiding loss from Gangrene. It may be, however, that chemical treatment of tubers will prove somewhat less effective, but experimental evidence at present is lacking.

(8) BLACK DOT (*Colletotrichum atramentarium* (Berk. & Br.) Taubenh.)

GENERAL APPEARANCE.—The disease which is associated with this fungus shows many of the symptoms common to all "wilt" maladies. There is a slight yellowing of the foliage followed by a flaccid upward curling of the margins, both symptoms beginning in the uppermost leaves and spreading downwards until most of the foliage becomes affected. Under dry-weather conditions the whole plant may droop and wilt, finally assuming a dry withered appearance as though fully mature some weeks before the normal maturation of the variety. As in other cases of wilts, there is a tendency for aerial tubers to form in the axils of the leaves. A characteristic symptom is the rotting of the outer tissues of the roots, stolons and even the base of the haulm, so that the affected plant is almost as readily pulled up as when attacked by Blackleg (page 393). When the rotting outer tissues of the haulm are peeled off there is to be seen a characteristic pale mauve or amethyst colouration of the inside of the tissues bordering the pith cavity (Pethybridge, 1919). Affected stolons, as a rule, rot some little distance from the point of attachment to the tuber, so that the occurrence of tubers with half an inch or so of stolon attached should arouse suspicion.

The wilting symptoms do not usually become evident until the normal time for flowering approaches, *i.e.* until the plant is mature. At this time, or still later when the haulm is already dying, sclerotia which are no bigger than pinheads can be found under the rotting tissues as well as lining the pith cavity and even within the wood vessels. When examined with a lens the sclerotia are seen to be covered with stiff upright black bristles (setæ). The tubers from an affected plant may show grey discoloured areas on the skin after some weeks of storage, on which sclerotia which are even smaller than those in the haulm can be found on examination with a lens.

SYMPTOMS LIKELY TO BE CONFUSED WITH BLACK DOT.—Leaf Roll (page 437) foliage symptoms can be distinguished by the rigidity of the uprolled leaves and by the fact that usually only the lower half of the foliage is affected. The presence of minute sclerotia, with their setæ, as well as the mauve colouration of the pith cavity walls, enable Black Dot to be separated from Stalk-Break (page 305), Grey Mould (page 307), and Verticillium Wilt (page 314). The absence of blackening at the base of the haulm distinguishes it from Blackleg (page 393). In the same way the absence of any white-crusted fungus on the haulm helps to prevent confusion with Black Scurf (page 295), confirmation being found in the quite different lesions on underground parts of the plant. Affected tubers may, however, easily be diagnosed, in error, as suffering from Silver Scurf (page 312), or perhaps as an early stage of Gangrene (page 328). Neither of these diseases, though, exhibit the characteristic black setæ of Black Dot.

CAUSE OF BLACK DOT.—The symptoms were first described in France by Ducomet in 1908 under the name of " Dartrose," the fungus, then named *Vermicularia varians*, being abundant on the affected plants. Ducomet considered he had proved the pathogenicity of this fungus and its power to invade the haulm from the tuber-borne sclerotia. Since then many efforts have been made to confirm Ducomet's results, but usually without success. The most positive statements in support of Ducomet were made by Dickson (1926) who, however, believed that the fungus (which he showed to be more correctly named *Colletotrichum atramentarium*) to be at most a very weak parasite, capable only of attacking weak debilitated plants, or possibly vigorous ones under exceptional circumstances. This view is also that of Crépin (1922), while Shapovalov (1923) found it only as a secondary organism on tubers affected with Powdery Scab (page 367). Foex (1933), in investigating an outbreak in France, was unable to get positive results from artificial inoculation of this fungus to healthy plants and came to the same conclusion as Crépin. Chamberlain (1935) also found in New Zealand that, although common on wilted plants, the *Colletotrichum* was itself unable to produce a wilt.

In this country interest has largely centred on its relation to "Potato Sickness" (page 205). Cheal (1931 and earlier papers) came to the conclusion in Lincolnshire that the part played by this fungus was insignificant, a view supported by Millard, Burr, and Johnson (1932) in Yorkshire. Ogilvie and Mulligan (1930), however, consider that the results they obtained at Bristol indicate the need for further investigation of the role played by *Colletotrichum*. The verdict, then, would appear to be one of "not proven" with regard to the fungus being responsible for the symptoms attributed to it. Yet the possibility of its being an active parasite under certain conditions should be conceded for the present, the more so since the fungus has been recorded on seed tubers received overseas from Scotland (Bensaude, in the Azores, 1927). The life-history, so far as it is known, has already been given under "General Appearance," except for a description of the sporing stage. The spores (pycnospores) are slightly curved, single-celled, but containing one to three oildrops which give the impression of the cell being septate. They are colourless, and develop within pycnidia having much the same appearance as the black sclerotia.

CONTROL.—Proper rotation of crops should prevent the soil from becoming unduly contaminated with the fungus. Special care seems to be called for in gardens, however, since a very serious disease of tomatoes under glass is caused in this country by *Colletotrichum atramentarium*, and contaminated soil may therefore be returned to a garden after the periodical renewal of soil in the glasshouse. It is probable that any of the substances recommended in Appendix I (page 649) for tuber treatment will kill the small sclerotia so borne, but Dickson (1926) in Canada advises the use of hot formalin for this purpose.

CHAPTER XXIII

DISEASES CAUSED BY PHYCOMYCETOUS FUNGI

A. OOMYCETES

(1) POTATO BLIGHT (*Phytophthora infestans* (Mont.) de Bary)

GENERAL APPEARANCE.—The disease usually occurs from May to September or later in the form of dark, discoloured or "water-soaked" areas on the foliage. Frequently, it first attacks the lower leaves and may therefore be overlooked for a time, but later the upper foliage becomes affected. In dry weather the diseased patches may remain dry and brown and little or no spread to healthy plants occurs, but in warm, moist weather the whole plant may be reduced to a wilted, blackened mass in a few days, and its spread throughout the crop is equally rapid. The disease can be identified, especially in the earlier stages, by examining the lower surface of the affected leaf, when a sparse, whitish mould will be observed at the junction of the diseased and healthy tissues. Infected tubers also show discoloured, "water-soaked" areas on the skin, below which the flesh becomes spongy and a rusty-brown colour to a variable depth. No white mould develops on the tubers. Under wet conditions the killed portions of the tuber may be invaded by putrefactive bacteria which set up a secondary slushy wet rot; indeed, this condition is so common that it is often the only form of Blight recognised in the tuber by the grower. The disease in the tuber should be looked for both at lifting and subsequently during the storage of the crop (Figs. 59, 60, 61).

SYMPTOMS WITH WHICH BLIGHT MAY BE CONFUSED.—The fungus *Botrytis cinerea* produces somewhat similar symptoms on the leaf but can be separated from Blight by the fact that the diseased patches usually are confined to an area near the tips of the leaf, and the dead tissue, both on the upper as well as the lower surface, becomes covered with the smoky-grey mould of the Botrytis (page 307). In the tuber, Blight may be confused with Pink Rot (page 351), Watery Wound Rot (page 354), Stem Eelworm (page 231), Tuber-Rot Eelworm (page 236), Spraing (page 427) and Internal Rust Spot (page 425), and possibly with bad cases of Skin Spot (page 309).

DISTRIBUTION.—Although Blight was not recorded in Europe before 1840, there is reason to believe that it already existed in South America, and it is possible that its failure to reach Europe with the early introduced tubers was due to diseased tubers rotting during the long voyages under "sail." However that may be, the disease rapidly assumed epidemic proportions throughout Europe, and in 1845 and 1846 the very heavy losses caused by Blight reduced Ireland to famine conditions and caused much hardship in many other areas. Since then Blight has taken toll of the potato crop to a greater or less extent every year, and with the possible exception of viruses, causes more loss in the aggregate than any other potato disease. The general alarm produced by the ravages of Blight had much to do with the organisation of Government services for the control of plant diseases and pests in all the progressive countries of the world. It occurs wherever potatoes are grown, but under dry conditions it rarely assumes epidemic proportions. In India, for instance, it occurs mostly in Assam and the foothills of the Himalayas, where potatoes are grown at an altitude of 4000 to 10,000 ft., under which conditions rain during the day and heavy dew at night are generally expected; whereas in the plains the crop is taken in winter (from October to March) and, according to Dastur, there is little rain or dew formation, with the result that the disease is rare. Similarly, in Canada and U.S.A., the disease is much more serious in the cooler wet eastern areas than in the dry Middle West. In the British Isles, Blight is less serious in the drier eastern counties than in the west. It was at one time believed that Blight originated each year in the south-west of England and swept in a north-easterly direction over Great Britain. That is not the case, although the warm, wet, springs in Devon and Cornwall are suitable for the early development of the disease, and the first records each year usually come from these two counties.

CAUSE OF BLIGHT.—The white mould we have noted as occurring at the margin of diseased patches on the leaves consists of the non-sexual fruiting hyphæ of the fungus

Phytophthora infestans. Each is a branched, tree-like structure with characteristic nodular swellings on the branches, each branch bearing at the tip a pear-shaped, easily detached body known as a conidium. The conidia, which are blown on to a leaf, may germinate by the protrusion of a hyphal-like germ tube which is capable of entering the leaf either through one of the breathing pores (stomata) or directly through any cell wall. A film of dew on the leaf surface is necessary for this to take place and a fairly warm temperature approaching 75° F. When the temperature falls to 55° F. or less, there is a greater chance of heavy dew and the conidia become converted to zoosporangia. This does not involve any change in appearance, but the protoplasm divides up internally to form a small number of biciliate zoospores. Each zoospore can move in the film of water for a period varying with the temperature, and then after losing its cilia is capable of causing infection in the same way as the conidium. It will be noticed, however, that the risk of infection due to a conidium has been increased by the formation of zoospores, and hence the rapid development of the disease under dewy cool night conditions followed by a warm moist day. Whether infection occurs by conidia or zoospores the development of the disease is the same, the hyphæ spreading mostly between the cells, with here and there a small haustorium capable of penetrating the cells and feeding upon the plant protoplasm, so producing the dead brown areas visible to the naked eye. Eventually, some hyphæ again grow through the stomata of the lower surface of the leaf and produce a further crop of conidia. Although the hyphæ of the fungus can penetrate from the leaf into the haulm there is reason to believe that they do not find their way down to the tubers. Infection of tubers is due to conidia falling on the soil and being washed down on to the exposed or buried tubers, in which infection is caused in the same way as in the leaf. The degree of penetration into the soil is influenced by its texture but, contrary to what one might expect, Jones *et al.* (1912) have given good evidence that more tubers become infected, and at a greater depth, in clay than in sandy soils. Conidia are regarded as short-lived bodies and Murphy (1922) has shown that soil so contaminated loses its power to infect tubers after the lapse of from three to six weeks. On the

FIG. 59.—Blight on Foliage (page 334).

FIG. 60.—Blight; external symptoms on tuber.

FIG. 61.—Blight; internal symptoms on tuber.

FIG. 62.—Pink Rot; internal symptoms on tuber (page 351).

other hand Miss de Bruyn (1922) demonstrated the germinability of conidia after two months in moist soil and after two years in peat; she did not, however, show that such conidia retained the power to cause infection. The hyphæ within the tubers, however, can persist throughout the storage period, and slightly affected tubers may be overlooked and used inadvertently as seed. When this occurs, the most frequent result is a miss in the drill owing to the death of the sprouts. Those sprouts, however, which survive will either produce a normal plant or, as shown by Salmon and Ware (1926) and by Alcock and McIntosh (1927), will early develop the white fruiting hyphæ of the fungus on the leaves; the production of conidia above ground from such plants is believed to be the most frequent cause of the first appearance of the disease in the growing crop. Nevertheless, several other possibilities must be examined. (1) Diseased tubers left in the soil, or remaining after a pit has been cleared will only be less dangerous than planting infecting seed (as a source of initial infection) in being probably some little distance from the current year's crop. (2) Diseased tubers may rot in the ground and the fungal mycelium may survive as a saprophyte until potatoes are again taken in the rotation. Miss de Bruyn (1926) has given evidence of the saprophytic existence of *Phytophthora* in the soil as mycelium. Brooks (1919) also obtained field results in Cambridgeshire which suggested this possibility of saprophytic survival, but the weight of evidence at present is against this occurring except in very exceptional circumstances. (3) There is the final possibility of sexual fruiting bodies (oospores) in the soil being responsible for the persistence of the fungus between two potato crops in the rotation. These bodies have been seen in pure cultures under laboratory conditions and, according to de Bruyn (1926), also in the soil. They can withstand very low temperatures and there seems to be no theoretical

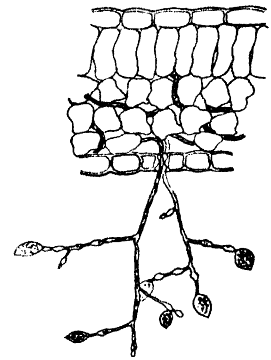

FIG. 59*a*.–*Phytophthora infestans*. Section of leaf showing intercellular hyphæ and two conidiophores which have grown through a stoma and bear a number of conidia.

reason why the fungus may not survive in this way. Oospores, however, have never been seen to germinate and, for the present, they are not regarded as a likely method of initiating Blight in the crop. The development of the oospores is similar to that in *Phytophthora erythroseptica* and is described on page 353. (4) There are few records of the natural infection of wild Solanaceous plants by *Phytophthora infestans* but it is stated by Moore (1943) to have occurred on *Solanum crispum* in Devon in 1936 and 1938, and in Somerset in 1939; it was found on *Lycium halimifolium* in Cornwall in 1942. Spontaneous infection of *Solanum dulcamara* (Bitter-Sweet) was observed during 1947 in Maryland, U.S.A. (Cox, 1948), and was successfully inoculated into other bitter-sweet plants and into tomato, petunia and chilli (*Capsicum*), but not into *Solanum carolinense* or tobacco. The possibility that a perennial host such as bitter-sweet may serve as a means of over-wintering of Blight is a very remote one and is discounted by Peterson (1947) who, in reporting the successful inoculation of *S. dulcamara*, observed some resistance to infection and noted that inoculated leaves yellowed quickly and fell off.

EXTENT OF LOSS.—This is, of course, very variable according to district and season, but even in dry years it is very rarely a negligible amount. In wet seasons Blight may have disastrous results, much of the crop being unmarketable from the combined effects of this disease and of saprophytic rotting organisms, which spread a soft rot from tubers in the pit, affected with Blight, to others which are quite healthy. In U.S.A. the average loss during the ten years 1926-36 from Blight is said to have amounted to nine million bushels. According to Melhus (1945) this disease caused a loss in the upper Mississippi valley of twenty-five million bushels in 1942, while Chester (1946) states that 25 per cent. of the crop in the State of Maine, U.S.A., rotted in storage during the winter of 1943-1944, chiefly from Blight followed by other storage rots. Losses frequently bear little relation to the amount of foliage destruction. An early attack, prevented from spreading by prolonged dry weather, usually has little effect on the keeping power in the clamp, whereas an apparently slight attack on the foliage which develops late or is prolonged into the autumn may have a disastrous effect. This well-known fact was recently (Bonde and Schultz, 1949) emphasised in U.S.A., where under late (but slight) attacks upwards of 54 per cent. of tubers have rotted in the clamp. The disease was first recorded in Victoria, Australia, in 1909 (Anon., 1946) and this was followed in the season 1910-1911 by an epidemic which destroyed 75 per cent. of the crop. Incidentally, it may be mentioned that serious losses in outdoor tomato crops may be caused by this disease.

CONTROL OF BLIGHT

(1) RESISTANCE OF COMMERCIAL VARIETIES.—The rapidity with which the disease may assume epidemic form under favourable conditions makes Blight particularly a disease in which the failure of one grower to take reasonable precautions may have serious repercussions on the health of the potato crop of his neighbours. On the other hand, there is little or no risk of the disease hibernating in the soil in any way comparable with that described for Wart disease (page 357), and soil treatment is therefore unnecessary. Relative resistance to attack is shown by some commercial varieties, especially late-maturing ones, but is not a constant character either from season to season or in all kinds of soil conditions, and varieties which have exhibited a degree of resistance to Blight have usually lost any claim to this after some years of cultivation, *e.g.* Champion and Magnum Bonum. Miss Löhnis (1923) is of the opinion that tuber resistance to Blight is primarily determined by the difficulty of penetration, and that in this respect the structure of the lenticels is important. She found that, when grown in clay, the lenticels were filled with unsuberised cells in contrast to the protective suberised layers of cells in the lenticels of tubers of the same variety grown in sand. This difference, in her view, explained why 103 tubers out of 155 contracted infection *via* the lenticels in a clay soil as against only 13 out of 158 inoculated in a sandy soil. Nevertheless, it is possible on the basis of field experience to group varieties according to the apparent susceptibility of the tubers to contract infection in most circumstances. Thus, among the varieties whose tubers show some resistance, are Arran Consul, Golden Wonder, Royal Kidney and, for a " first early," Sharpe's Express. Varieties with moderately susceptible tubers include Abundance, Ally, Arran Signet, Ballydoon, British Queen, Doon Star, Dunbar Rover, Great Scot, Majestic, Orion, The

Alness, Ulster Chieftain and Ulster Monarch. The most susceptible sorts include Arran Comrade, Catriona, International Kidney, King Edward VII, May Queen, Ninetyfold, Puritan, Up-to-Date and Witchhill. A more complete list may be found in the "Miscellaneous Publications No. 3," published by the Department of Agriculture for Scotland. One of the pioneer German workers on Blight (K. O. Müller) and his colleague L. Behr have recently (1949) expressed the view that, while the cells of both susceptible and resistant tubers are destroyed by the parasite, in the former case the cells may continue to live for from six to fourteen days at 66° F. to 70° F.; but become necrotic and die in resistant tubers within one or two days—types intermediate between these two extremes also being known. At the same time the necrotic cells become useless as food for the fungus, and the mycelium is not only unable to sporulate but even to progress beyond the necrotic zone. According to these workers it is the fungal mycelium which secretes the substance ("phytoalexin") which, by inducing necrosis, is assumed to retard the penetration of the hyphæ, and therefore susceptibility is dependent on the extent to which the hyphal growth-rate exceeds that of the formation of phytoalexin. In Holland, Helen de Bruyn (1943) has developed a technique for estimating the relative susceptibility of tubers to Blight. Essentially this consists of (1) maintaining a standard culture of the fungus on certain varieties, (2) inoculating a suspension of zoospores into the tuber to be tested (in the wound produced by a cork-borer and then replacing the plug of tuber) and, (3) after five days, halving the plugs and keeping them in a dark, humid atmosphere at a temperature of 10° C. (50° F.) to allow of observations every three days for a fortnight. This temperature is unfavourable for the development of the fungus which, instead of producing copious mycelium, induces a brown necrosis of the tuber flesh in many varieties. It is in such varieties that the differences in tuber susceptibility are most marked, rather than in others in which extreme susceptibility even under adverse conditions is shown by extensive mycelial development.

(2) BREEDING FOR RESISTANCE.—The problems encountered in the attempt to breed new varieties for resistance to Blight have been referred to in Chapters VIII and XX; among the most difficult of which is the existence of strains of the fungus

possessing very different degrees of virulence. The problem confronting the breeder, therefore, is to produce varieties immune from as many as possible of these fungus strains. If *resistance* rather than *immunity* is aimed at, however, the solution may prove to be only a temporary one. Reddick and Crosier (1933) showed that a strain of *Phytophthora infestans* taken from tomato was abnormally virulent both on tomato and on normally resistant varieties of potato but, after a few generations on slices of raw potato tubers, the culture could no longer be distinguished from other cultures originating from susceptible potato varieties ; the virulence of the tomato strain had been reduced by providing it with a slightly different kind of food. Later, Reddick and Mills (1938) demonstrated in much the same way that a " pedigree " strain from a single lesion of the disease on the very susceptible American variety Green Mountain, *intensified* its virulence as it was successively " acclimatised " on varieties showing an increasingly higher degree of resistance to Blight ; whereas no change in virulence occurred when the passage was from Green Mountain to Green Mountain. It must therefore be admitted that there can be no certainty that a variety, proved to be highly resistant, will not ultimately succumb to the attack of an abnormally virulent strain of the fungus produced in this way. Reddick and Mills, in fact, explain the collapse in the originally resistant variety Champion in Ireland after its introduction, in 1876, into areas where the susceptible varieties Regent and Victoria suffered severely from Blight, as being due to the " build up " in virulence of the normal strain of the fungus. On the other hand, Davidson (1928) restored the power of resistance to this variety by building up a stock relatively free from virus infection, and so encouraged the hope that control of virus diseases in other varieties might also have the effect of reducing the loss due to Blight. A common effect of virus infection of the " mosaic " type is to hasten maturation, and so any such relationship, as Davidson suggested, between virus and Blight infection would tend to support the well-known view that potatoes are most severely attacked by Blight immediately they have passed full growth. This was the view expressed by Müller (1928) after a study of Blight in some 700 commercial varieties in Germany. He attributed the varying reaction to Blight of " early " and " late " varieties to the different time at which they reached maturity, and believed that an important aim of the plant breeder should be to retard maturation by from eight to fourteen days. Nevertheless, Beaumont (1934) and his collaborators, in trials in many parts of England and Wales, failed to find any connection between the stage of growth of the plant and the onset of Blight.

But despite these difficulties, much progress has been made in the breeding of varieties possessing almost, if not complete, immunity from Blight without unduly sacrificing other qualities necessary to commercial success. Thus, Thung (1947) crossed *Solanum tuberosum* with various wild species and found the F_1 offspring in the cases of *S. demissum* and *S. antipoviczii* to be completely resistant ; *S. andigenum* offspring showed 80 per cent. resistance, and *S. caldasii* 90 per cent. resistance. When crossed with commercial varieties of potato *S. andigenum*, *S. antipoviczii*, *S. caldasii* and *S. demissum* showed 29, 33, 39 and 33 per cent. resistance respectively. In most of the breeding work in America, and at Cambridge and Edinburgh, the wild species *S. demissum* has been used as a source of those chromosome units (genes) on the presence of which resistance depends. Thus, in U.S.A., Reddick and Peterson (1947) record the production of several commercially successful varieties, and Mills (1947) reports that resistant varieties in Pennsylvania gave more than double the yield of susceptible sorts in the absence of protective spraying. In the British Isles the work of Black at the Scottish Plant Breeding Station is noteworthy. In a series of papers (1943, 1945*a* and *b*, 1947 ; Black and Haigh, 1947) he records the existence of several strains of the fungus. Of these, strain " A " is the most virulent and the one commonly found in commercial fields, while strains " B," " C " and " D " have appeared on the experimental plots as modifications of strain " A " ; possibly similar modification also occurs in commercial crops. Seedlings from the immune wild species *S. demissum* could be separated into five types, viz. (1) plants immune from " A," " B " and " C " strains ; (2) plants immune from " A " and " B " but susceptible to " C " ; (3) plants immune from " A " and " C " but susceptible to " B " ; (4) plants immune from " A " but susceptible to " B " and " C " ; (5) plants susceptible to A," " B " and " C." Strain " D " appeared on a seedling immune from strain " A," and was subsequently shown to be incapable also of attacking seedlings in groups (2) and (3) above; it is probably a weakened form of strain "C." Black considers Blight resistance to be controlled by major genes such that one confers immunity from strain "A," another controls immunity from strains "A" and "B," a third immunity from strains "A" and "C," and a fourth immunity from strains "A," "B" and "C." In addition, minor genes appear to determine the degree of susceptibility in susceptible varieties and act as modifiers in resistant sorts.

(3) CONTROL BY CULTURAL PRACTICES.—For the present, however, the grower must rely on other methods for controlling Blight, and fortunately these are available. The precautions to be taken may be grouped for convenience according to the time of year at which they become necessary.

(a) *Precautions at Planting.*—Seed tubers should be carefully examined and any showing either weak sprouts or the slightest sign of Blight should be rejected and destroyed. Unnecessarily close spacing of the seed tubers should be avoided, for the result is to overcrowd the foliage and to maintain a damp atmosphere within the crop which facilitates the development of Blight. Too shallow planting often leads to tuber infection.

(b) *Precautions during the Growing Season.*—Potato groundkeepers in other crops and around old pits should be destroyed to prevent them from serving as sources of infection to the new crop. The potato rows should be well earthed up and the sides made compact, not only to encourage tuber growth, but to direct any conidia falling from the foliage into the furrows and away from the growing tubers. Above all, the foliage must be protected from infection by completely coating both surfaces of the leaves with a poisonous copper compound in the form of either a powder or a liquid spray.

(i) *Powders* in common use are proprietary substances and the grower should require a guarantee that the one used complies with the standards described in Appendix I (page 645). Dusting with powders against Blight is best regarded as being still in an experimental stage and will, no doubt, improve with experience. At present, however, there is ample evidence from careful trials to prove that powders are not as efficient in covering the foliage or in controlling Blight as the best liquid sprays. Nevertheless, dusting is becoming increasingly popular, especially where the water supply presents difficulties, and in many districts the operation is carried out by professional firms under some form of contract which includes the supply of both powder and the special dusting machine. The first application should be made before the final earthing up of the crop and should be repeated five or six times at intervals during the summer.

(ii) It is common knowledge that the mixture of copper sulphate and ground quicklime with water formed the first known *spray liquid* to be used to control fungus diseases of plants. It was not easy to prepare, however, and until comparatively recently Bordeaux mixture (as it was called from its first use near Bordeaux in France) met with severe competition from a somewhat similar liquid known as Burgundy mixture in which the quicklime was replaced by "washing soda." The modern method, however, is to prepare Bordeaux mixture with "hydrated lime" in place of quicklime and little is now heard of Burgundy mixture though the preparation of both is described in Appendix I (page 645). The most recent development is the introduction of a number of proprietary liquids which are convenient to prepare and most of which are efficient. Many of these proprietary substances have been tested under field conditions against Blight, but none appears to have any advantage over the cheaper Bordeaux mixture (Large and Beer, 1946). Whatever the choice of spray, the first application should always be given *before* Blight occurs on the foliage in order to destroy the first conidia produced on the crop, or reaching it from external sources. The date at which Blight first appears differs both with locality and season, and the best guide is the past experience in the grower's own district. Normally the disease may be looked for, in the south, at any time after the beginning of June, and from the end of June onwards over the greater part of Great Britain. With wet weather in May or June these dates may easily be advanced several weeks. Many efforts have been made to correlate Blight epidemics with particular weather conditions, and Van Everdingen (1926) affirmed that an epidemic spread of the disease, in Holland, would occur only when certain meteorological conditions coincided. These are (1) dew formation during a period of at least four night hours; (2) a minimum night temperature of 50° F.;

(3) a mean cloudiness on the following day of at least 0·8, *i.e.* 80 per cent. of the sky overcast with clouds; and (4) a rainfall on that day of not less than 0·1 mm. Within fifteen days of these conditions being recorded an epidemic outbreak might be expected to occur. However that may be in Holland, it was shown by Wiltshire (1931) that it was by no means invariably true of Great Britain. Many of the conditions indicated by Van Everdingen are interdependent and Beaumont (1933-1936) considers that for all practical purposes they can be reduced to two, *i.e.* a minimum temperature of 50° F. and a relative humidity not falling below 75 per cent. for at least two days; a conclusion which has since been confirmed in France (Foex, 1941). Grainger (1950*a*) has pointed out that in S.W. Scotland the normal temperature and humidity are too low up to the end of June for the formation of spores by the over-wintering mycelium of *Phytophthora*. Until that date, therefore, the short exposure (forty-eight hours) to the higher temperature and humidity required by Beaumont's Rule has no relevance to the spread of Blight, and records over the period 1944 to 1948 showed that forecasts of Blight attacks under such conditions would be invalid; though after the end of June reasonable conformity to the Rule obtained in Ayrshire. This "zero-time" of validity for Beaumont's Rule varies with the district and might be a fortnight earlier in Dumfries, and even a month earlier in West Perth, than in Ayrshire. In U.S.A., Melhus (1945) reported that Blight never assumed a virulent form in the Upper Mississippi valley if the mean temperature during June and July never exceeded 70° F. and on this fact based a "Forecasting Service" for growers, which in 1943 was said to have prevented much loss as a result of timely warning of the existence of temperature conditions favouring Blight (Chester, 1946). There are, however, difficulties, and indeed dangers, in broadcasting advice over a large area, based on weather conditions existing at a few Meteorological Stations. For the present, therefore, growers cannot do better than to rely on Beaumont's conditions tempered with local experience in deciding on the first date at which to spray. The number of subsequent applications will depend on the continuance of these conditions or the severity of Blight attacks in the neighbourhood. In exceptionally dry summers the one application might suffice,

but normally the grower must expect to spray twice or three times at intervals of about three weeks.

It is frequently forgotten that the loss due to Blight is not solely measured by the number of infected tubers for, to this, must be added the direct loss in tuber formation as a result of the destruction of the foliage. Failure to take this fact into account may prove very misleading. Thus the effect of a slow-spreading attack in East Anglia during 1941, which was prolonged into the autumn, was to produce heavy losses in storage—in some cases reaching 50 per cent. Contrasting with this, the following year saw such rapid spread of the disease that complete destruction of the foliage occurred in many districts by early August ; so that comparatively few tubers contracted infection during lifting, and storage losses only averaged about 3 per cent. (Dillon-Weston and Taylor, 1944). As will be seen later (page 348) some of the 1941 losses in storage could have been prevented, but the early death of the foliage in the following year deprived the crop of from one to two months' growth and the reduction in tuber production must have been heavy. Using an average curve of yield in a " Blight-free " crop of Kerr's Pink as a basis for calculation, Grainger (1950*b*) estimates that the loss in tuber *production* directly attributable to Blight on the foliage is about 25 per cent., and that this occurs in years of early development of the disease. On the other hand, he believes that the amount of Blight found in the tubers is greatest when Blight develops only slowly on the foliage (*cf.* Table XVII above). Beaumont and Large (1944) found that two sprayings at the beginning and end of July gave gains in yield of from 2·5 to 5·2 tons per acre over

TABLE XVII

Loss Due to Blight (adapted from Grainger, 1950*b*)

Year	Per cent Blight on Tubers [1]	Per cent Reduction in Yield [2]	Per cent Total Loss
1945	9·6	25	34·6
1949	11·9	16	27·9
1948	15·6	9	24·6
1947	19·9	6	25·9
1946	29·0	0	29·0

[1] Estimated by experiment
[2] Calculated from yield curve of healthy crop

unsprayed crops ; a result which was in part due to the prolongation of the growing period of the crop. In areas where the disease is liable to assume epidemic proportions before the end of July (*i.e.* in the west and south-west of Britain) there can be no doubt of the need for protective spraying or dusting of the foliage ; there is ample evidence over the last forty years that, under such conditions, sprayed crops yield from 1½ to 2 tons of saleable tubers per acre more than unsprayed crops. The golden rules for spraying may be summed up as (1) spray early, (2) spray too often rather than too seldom, and (3) use a fine nozzle to ensure a mist spray and direct it upwards from the ground-level on to the lower surfaces of the leaves. Yet it should not be assumed that spraying is invariably successful. Apart from the failures due to inefficient application of the spray, the operation may be wrongly timed so that the disease already has become serious before the first spray application, or the onset may be delayed and the spray washed by rain from the foliage before the attack commences. Further, there is good evidence that late frosts may injure sprayed foliage and cold sea-fogs produce a " scorch." Occasionally, injury may be caused by copper poisoning of the leaf tissues if spraying follows a severe aphid attack or, much more frequently, when spraying is carried out in the vicinity of factories which may be discharging acid fumes into the atmosphere. When the attack of Blight comes late in the season the precautions given under (c) below should be adopted.

(c) *Precautions near Lifting Time.*—The measures already taken will have prevented the infection of most of the growing tubers, but much of the value of spraying may be vitiated by a late August or even September attack, which releases quantities of conidia on the soil surface from which they may be washed down upon the tubers. This results in many tubers becoming infected just prior to lifting, and many more are infected by digging the crop whilst the foliage still carries an abundance of living conidia, particularly as the operation of lifting inevitably bruises many of the tubers and so ensures easy access by the germinating conidia. These late tuber infections cannot be detected when the crop is pitted and, as Murphy and McKay (1924) have shown, most, if not all, of the loss in storage can be attributed to such tubers which have been inadvertently pitted.

It is doubtful whether the protective spraying of foliage during these late attacks of Blight is worth while, for the direct damage caused by the passage of the spraying machine through a crop at this advanced stage of growth may be considerable, and there is, in any case, no great addition to the yield of tubers to be expected. The problem is rather how to prevent the continued infection of tubers already formed, which will certainly occur so long as living spores are discharged by the infected "tops" on to the soil. Some relief can be found by cutting and removing the haulms or shaws from the field at least three weeks before the tubers are lifted; or by delaying lifting for the same length of time after the haulms have died down. In either case some infection of tubers will probably occur during this three-week waiting period but, since at the end of that time most, if not all, of the spores will have died, there is little risk of tuber infection following contamination with spores at lifting time and so heavy losses in storage may be avoided.

The practice is therefore growing of spraying with a liquid to kill haulms and foliage and, with them, the Blight fungus and many weeds. Great activity is being shown in many parts of the world in testing substances in an effort to discover the ideal killing agent. This should be an easily prepared liquid or dust which, at low cost, causes a rapid destruction of the haulm as well as of the foliage even in wet weather; it should not affect the skin of the operator, have no corrosive action on metal or clothing and leave no ill-effects on the tubers or soil. The more important of these substances are described below and in Appendix I, page 645, and the conclusions to be drawn from their action in the field may be summarised as follows. Copper sulphate is of little value, even at 5 per cent. concentration, but 3 per cent. copper sulphate to which has been added 1 per cent. common salt is effective against foliage but less so against the haulm; it is cheap, easy to obtain and use but, like all copper compounds, it is mildly corrosive of brass and is deposited on the inside of iron containers. Other compounds of copper have been tested but are scarcely more effective than the sulphate and are considerably dearer to apply. Sodium chlorate applied as a 1·5 per cent. solution appears to be more efficient than the copper sulphate and salt mixture, but less so than either sulphuric acid or tar acid. It is by far the cheapest to apply, is non-corrosive but, because of its inflamability, clothing on which the liquid has dried may easily ignite. Tar-Oil washes such as are used for the spraying of fruit trees have been tested but cannot be recommended because of their cost, slow action, and relatively poor killing action on the haulms. All these substances have been tested recently by Wilson *et al.* (1947) and none is considered to rival either sulphuric acid or some of the tar acids marketed under the trade initials T.A.C. These tar acids are still in the experimental stage as regards their practical value as killing agents, but they are by far the most promising non-corrosive substitutes for sulphuric acid yet tried, being practically as rapid and effective in killing haulm and foliage in dry weather as sulphuric acid, and even more so in heavy rain. Unfortunately the tar acids are much the most expensive of all the substances tested and, because some (the low-boiling fractions) are serious skin irritants, they have had to be discarded.

One of the first liquid sprays to be tried out was sulphuric acid (brown oil of vitriol) at concentrations varying between 8 and 25 per cent., and the rapidity and efficiency of its action have combined to make it the most popular substance in use—at any rate when large acreages are sprayed under contract. Where the operation is carried out by the grower it is rare that sulphuric acid can be used because of the relatively high cost of application and its extremely corrosive action on metal, clothing and the human skin. Until, therefore, new non-corrosive treatments become available, or there is a substantial fall in the price of tar acid compounds, the home operator should not despise the use of sodium chlorate or even of the copper/salt mixture. The choice of substance may to some extent be determined by the susceptibility of the haulms; when young they are readily killed, become more resistant as the season advances but are easily destroyed near the end of growth. No residual effect on the soil or on the tubers has been observed, except that " setting " of tubers is accelerated by the destruction of the " tops " but, in order to get the full advantage of this, the lifting should be delayed for at least a fortnight or longer after spraying (Wilson *et al.*, 1947).

It is not only the producer of " ware " potatoes (which require winter storage) who would benefit from the use of haulm-destroying substances for, in the case of the exporter—particularly those growers of early varieties which may have to be lifted during an epidemic spread of Blight—the destruction of the potato " tops " may save much rotting of the crop during transit; this has been well demonstrated in Jersey by Small (1935). The practice is also rapidly extending among growers of seed potatoes, and Main and Grainger (1947) point out that destruction of the tops is a useful means of controlling tuber-size in seed potato crops; for this purpose these writers found that the best results were obtained with a copper-containing spray to which had been added 1·2 per cent. sodium chlorate. With this combination a crop of the variety Arran Pilot gave 8 tons of seed per acre, 2 tons of ware and 10 cwt. of " thirds " or " chats." The sprayed crop showed only 0·1 per cent. Blight infection of the tubers as compared with 30 per cent. in unsprayed control crops.

Care should be taken when lifting the crop that all tubers visibly affected with Blight are discarded and destroyed for, otherwise, they may be the cause of heavy losses in the clamp. This is not because Blight itself spreads under these conditions to healthy tubers (Murphy and McKay, 1924) but the dead, rotted, tissues of Blight-affected tubers provide an excellent food on which secondary, wet-rot organisms can thrive and spread, under suitable conditions, to healthy potatoes. Recently the claim has been made (Eddius, 1945) that even Blight may spread to healthy tubers when potatoes are stored in bags under wet conditions for long periods of time. Certainly the storage conditions greatly influence the extent of the loss caused by the inclusion of infected tubers (Wilson and Boyd, 1945). These writers point out that in dry, well-constructed clamps, Blight-infected tubers usually become dry and shrivelled but, under wet conditions, these tubers form pockets of wet, rotted, tissue developing high temperatures (sometimes over 112° F.) favourable for the growth of rot-producing bacteria, and other organisms. The high temperatures lower the vitality of adjacent tubers, which are then destroyed by the bacteria with yet further extension of the rotting, until the entire clamp may collapse. It has been emphasised by Samuel (1946) that if clean tubers, free from diseases, are clamped in dry conditions, allowed to " sweat " properly before the clamp is earthed up, and are properly protected against frost and rain, it is seldom that serious storage troubles occur. One real difficulty is that tubers merely contaminated with Blight spores at lifting time cannot possibly be detected, and there is considerable risk that infection will occur in the clamp and a rot started which, as we have seen, may spread throughout the clamp. So far as "seed" is concerned the infection can be prevented by dipping the tubers at lifting time either in a 0·1 per cent. solution of mercuric chloride for ninety minutes, or for thirty seconds to one minute in a 0·1 per cent. solution of an organo-mercurial compound (Greeves, 1937). This writer states that a delay of even a day or two after lifting very considerably reduces the efficacy of the treatments. Since the two substances are poisonous to man and stock, the treatment cannot, of course, be used for ware, or for "chats" destined for use as stock-feed (*cf.* Appendix I, page 649).

(2) PINK ROT (*Phytophthora erythroseptica* Pethy.)

GENERAL APPEARANCE.—Potato foliage may occasionally show signs of yellowing from July onwards and may finally droop in a typical wilt. Beyond the fact that wilting only occurs late in the season, there is nothing to distinguish it from other forms of wilt. In all cases it is due to interference with the passage of watery salts from the roots, and results not only in wilted foliage but often in the production of small aerial tubers on the haulm at ground-level. When lifted, the tubers are seen to be almost invariably infected from the heel end, the tuber skin being discoloured. Such a diseased tuber is firm and elastic, but if pressed hard will exude a watery fluid; it has a faintly pungent odour if the tuber is cut open and so exposed to the air, the diseased flesh gradually turns salmon-pink in colour and ultimately becomes a deep purplish black, being thus clearly marked from the healthy portion of the tuber. (Fig. 62.) White (1946*a*) has distinguished three zones in the infected tuber: (1) living and uninvaded tissue; (2) living tissue in which the semi-permeability of the cell protoplasm is being destroyed by the invading intercellular hyphæ and (3) the dead tissue in which the fungus exists as a saprophyte. The characteristic salmon-pink colouration produced in this tissue on exposure to the air is said to be due to the oxydising effect of the enzyme tyrosinase.

SYMPTOMS WITH WHICH PINK ROT MAY BE CONFUSED.—The demarcation line between diseased and healthy portions of the tuber serves to distinguish this disease from the diffused pink colouration characteristic of healthy tubers of some varieties when the flesh is exposed to air. Blackleg (page 393) may be distinguished by its rotting effects on the haulm and the formation of cavities in the diseased part of the tuber, whilst Watery Wound Rot (page 354) is usually easily separated from Pink Rot by the soft wet rot which develops and the absence of foliage symptoms. In Verticillium Wilt the tuber flesh frequently shows a brown ring just below the surface (page 314).

DISTRIBUTION.—Pink Rot was first recognised in 1909 and described by Pethybridge (1912) in affected tubers from the west of Ireland. Of recent years it has been found in a number of counties of Great Britain, *e.g.* Berwickshire, Lanark, Sutherland and Midlothian in Scotland, Flintshire in Wales, and Shropshire, Lancashire, Berkshire, Kent, Hertfordshire and Durham in England. The disease is also reported from many counties in Ireland. Almost always it occurs where potatoes are grown repeatedly on the same ground, and it is invariably worst under wet weather or waterlogged conditions. In Tasmania it is said to be most common in warm autumn weather, especially in soil which was moist before the tubers were dug (White, 1946).

CAUSE OF PINK ROT.—The causal fungus, *Phytophthora erythroseptica*, is closely related to the one causing Blight, from which indeed it is only separated by small differences in structure and by its abundant production of oospores within the tissues of haulm and tuber, as well as the infrequency with which conidia are produced. The effect produced on the tuber by this fungus is also quite different from that due to *Phytophthora infestans*. Oospores are liberated from rotting haulm or tubers and remain living in the soil for at least four years. The method of germination of the oospores is still uncertain, but either by oospore germination or the persistence of the hyphæ from rotting tissue, a mycelium is produced which invades the tuber. This occurs usually *via* the stolon, but may also result from direct infection of the eyes or through bruises. The infection-hyphæ branch frequently and spread between the cells, destroying their contents and so causing a

FIG. 63.—Watery Wound Rot (page 354).

FIG. 64. Wart Disease (page 357).

FIG. 65.—Powdery Scab on tuber (page 367).

FIG. 66.—Powdery Scab on roots (page 367).

rot to set in. According to Jones (1945), although growth occurs at a minimum temperature of from 4° C. to 8° C., the optimum is 24° C. (75·2° F.) and all growth ceases at 34° C. Conidia are not formed unless the infected tissue is suffused with water, and Pethybridge has shown that the disease does not spread from one tuber to another in the pit. The oospores are formed in an unusual manner, in that the female organ, or oogonium, containing the unfertilised oosphere or "egg," develops on a hypha below the male organ, or antheridium, penetrates the male organ and after fertilisation emerges as a swollen globular body within which the fertilised oosphere develops as a thick-walled oospore. When first decribed by Pethybridge (1913), this method of fertilisation was believed to be unique, but is now known to be shared by several species of *Phytophthora*, including the Blight organism. More recent Irish work (Cairns and Muskett, 1933) has shown that forms of typical "pink rot" can be produced by several species of *Phytophthora*, e.g. *P. cryptogea*, *P. megasperma* and a form of *P. cactorum*.

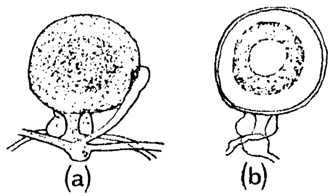

FIG. 62*a*.—*Phytophthora erythroseptica*. Oospore Formation.
(*a*) The globular oogonium has penetrated the antheridium which is seen surrounding the funnel-like stalk of the oogonium. (*b*) A mature oospore. (*After* Pethybridge.)

EXTENT OF LOSS.—This is difficult to estimate since there can be no doubt that its effects are sometimes (perhaps often) confused with Blight. In the west of Ireland, Pethybridge states that the loss may exceed that due to Blight in some conditions.

CONTROL.—It is likely that infected plants occur more commonly in crops than is suspected. With any ordinary rotation, however, there is little danger from infected tubers which rot in the ground, although de Bruyn (1922) has shown that both oospores and the saprophytic mycelium may over-winter in the soil. Any such infected tubers which are inadvertently stored for replanting will certainly rot before they can be used. It is clear, though, that the pit itself may become contaminated in this way, with the result that volunteer plants arising from pits may become infected and so serve to return a new supply of oospores to the ground. Eventually the site may become highly dangerous if used regularly for pitting or if it is incorporated into the arable acreage. Recognition of the special danger from infected pits and the maintenance of proper rotations will prevent this disease from establishing itself. Clamping or pitting dry tubers only and the proper aeration of the pit are of great importance in preventing loss from Pink Rot.

(3) WATERY WOUND ROT (*Pythium ultimum* Trow.)

GENERAL APPEARANCE.—The disease affects the tuber only, and so far as is known is even incapable of attacking tubers so long as these are attached to the plant. Invariably, the disease can be traced to a bruise through which the fungus has gained entrance to the inner tissues. The affected part of the skin is discoloured and moist, with a dark boundary line usually separating it from the healthy part of the skin. Internally the diseased tissue may at first show no obvious discolouration, but when air has been admitted it changes gradually from a greyish colour to brown and finally becomes almost black, sometimes with a slight pinkish tinge. Usually the diseased portion of the flesh is clearly marked off from the healthy portion by a dark boundary line. The affected tuber rapidly becomes squashy and rotten so that a slight pressure causes large quantities of liquid to exude, and nothing is left beyond a thin papery skin. Sometimes, however, the rot is retarded in the neighbourhood of the vascular ring and cavities may thus be produced. At first the diseased tissues have only a faint " fishy " odour, and the slightly pungent, chlorine-like smell of Pink Rot does not occur. (Fig. 63.)

SYMPTOMS WITH WHICH WATERY WOUND ROT MAY BE CONFUSED.—In the final stage of tuber rotting it will usually be impossible to determine the cause except by microscopical examination and by culturing the organisms found. Apart from this, however, Watery Wound Rot may be confused with Blight, Blackleg and Pink Rot (pages 334, 393, 351 respectively). All these three diseases, however, may occur in tubers whilst still attached to the plant. The completeness of the rot and the dark boundary line between diseased and healthy tissue help to distinguish the disease from Blight. It does not enter the tuber from the heel end as in the case of Pink Rot and Blackleg, but invariably starts from a bruise. The colour changes in the flesh are different from those found in Pink Rot and the tissues are never of a rubbery consistency.

DISTRIBUTION.—Apart from a reference by Sadebeck to a disease found near Coblenz in 1875, nothing appears to be known of any disease on potato caused by a species of *Pythium* until 1916, when Hawkins described the disease known as "Leak" in potatoes in California. In this country it was first recognised as a distinct disease by Pethybridge and Smith (1930) in numerous cases of rotting which occurred in tubers during the hot summer of 1929. It was most prevalent in the eastern counties of England, particularly in Lincolnshire and Cambridgeshire, but also occurred in Shropshire. Since then it has been identified in many counties of England, Wales and Scotland, though spasmodically and apparently always associated with hot summers. In 1929 the varieties most attacked were King Edward, Majestic and Eclipse, with Boston Kidney and Epicure involved to a less extent.

CAUSE OF WATERY WOUND ROT.—The identity of the organism causing the disease has been the subject of controversy. Hawkins (1916) in describing the similar, if not identical, disease known in California as "Leak," ascribed it to the fungus *Pythium de Baryanum* Hesse, and the same conclusion was reached by Pethybridge and Smith (1930) in the first description of Watery Wound Rot in this country. It is now known, however, that the causal fungus, unlike *Pythium de Baryanum* as described by Hesse, never produces zoospores —the asexual method of reproduction invariably being by means of true conidia germinating by the extrusion of germ-tubes. Important differences also in the sexual organs (for details of which the reader should consult Middleton, 1943) were pointed out by Drechsler (1927) who considered that the organism most closely fitted the description of *Pythium ultimum* Trow; hitherto regarded solely as a saprophyte. Drechsler's view has been generally accepted, but this does not, of course, imply that *P. de Baryanum* is not an important pathogen; indeed even potato "Leak," in Idaho, was ascribed to *P. de Baryanum* as recently as 1945 by Blodgett and Ray, and was stated to have been long known as a disease of "earlies" but had never before been encountered in storage. Both species of *Pythium* are pathogenic on an extremely wide range of host-plants, including many market-garden crops, and this fact may seriously complicate the problem of controlling the diseases in badly contaminated soil. Pethybridge and Smith, from whose descriptions most of the information below is taken, were unable to obtain infection through the unbroken skin of the tuber, but the fungus readily established itself in the internal tissue when wounds or bruises were made. Once inside, the hyphæ traversed both the cells and the intercellular spaces, in which it differs from the fungi causing Pink Rot and Blight, which are restricted to the spaces between cells. The sexual reproductive spore is an oospore, formed by the union of the contents of a male cell or antheridium with the contents

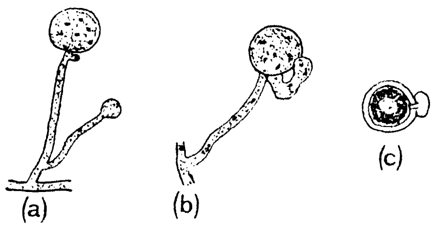

FIG. 63*a*.—*Pythium ultimum*. Three Stages in Oospore Formation.

(*a*) Multi-nucleated oogonium from the top of the stalk of which is just arising an antheridium lower down is an abortive oogonium. (*After* Trow.)
(*b*) Fertilisation of the oogonium by the antheridium.
(*c*) Mature oospore with attached remnant of the antheridium.

of a female cell or oogonium. These two sexual organs arise usually on the same hyphal branch, the male antheridium being club-shaped and applying itself to the spherical female oogonium. The protoplasmic contents of the oogonium form a dense, central and uni-nucleated mass or oosphere (the egg), and it is the union of the antheridium nucleus with that of the oosphere which constitutes fertilisation. The now fertilised oosphere surrounds itself with a cell wall, independent of the outer oogonial wall, and so forms the sexual resting spore or oospore. The mature oospores are liberated into the soil on the rotting of the tuber and are probably able to remain viable under such conditions for more than one year. With suitable conditions of moisture and temperature, they germinate by extruding a germ-tube. Should the germ-tube come in contact with the bruised surface of a potato tuber it enters the tissues and, growing both through and between the cells of the tuber flesh, sets up a rot as already described.

EXTENT OF LOSS.—Under the most favourable conditions for the development of the disease, *i.e.* the coincidence of an abundance of bruised tubers and high temperatures, the losses may be very severe. In 1915, for instance, it was estimated by Hawkins that the 40,000 acres of potatoes grown in the delta region of the San Joaquin river in California showed a loss of from 50,000 to 150,000 dollars as a result of rots caused by this fungus. Fortunately in this country it is only in exceptionally hot summers that losses have been severe. At the same time it would be foolish to assume that cases of loss in tubers during storage may not be more often due to *Pythium ultimum* than is at present realised.

CONTROL.—Pethybridge and Smith record the fact that serious loss occurred in 1929, mostly on farms where little care was taken to gather up and destroy all diseased tubers found at lifting time, whereas their neighbours, who did this as a matter of routine, did not suffer at all. The importance of taking such steps is evident when we remember that any diseased tuber, on rotting, will liberate very large numbers of oospores into the soil, in which they may rest for several years until potatoes again occupy the same land. Control is therefore a matter of proper rotation of crops and of immediate destruction of all diseased tubers. To what extent bruised seed potatoes are liable to contract Watery Wound Rot from soil-borne oospores, after planting, has not been investigated in this country, but Newton and Lines (1947) report the disease as causing heavy losses in British Columbia, especially in heavy soils and wet weather. They showed that the common practice of dusting cut seed tubers with hydrated lime or sulphur is useless, and that copper oxide aggravates the rotting; on the other hand, satisfactory control was obtained by the use of organo-mercury compounds.

B. ARCHIMYCETES

(1) WART DISEASE (*Synchytrium endobioticum* (Schilb.) Percival)

GENERAL APPEARANCE.—Wart disease attacks the potato plant during the growing season, though it is seldom discovered until the crop is lifted. This is because only the tubers are usually affected, unless the soil is very heavily contaminated, when the disease may occur as small warts on haulm and leaves near the ground-level. The small white outgrowths occasionally found on potato roots are caused by the Powdery Scab organism (page 367), there being no record of Wart disease on any root tissues. It can be found from the end of June onwards as small irregular whitish outgrowths in the region of the eyes, and sufficiently resembling a small cauliflower to justify the name "cauliflower disease," which was commonly used in old descriptions. Later, they grow to a considerable size which, in very susceptible varieties like Arran Chief or Up-to-Date, may exceed that of the unaffected part of the tuber. At the same time the colour of the wart darkens until it becomes quite black, and eventually the whole wart decomposes into a putrid mass which, by its rotting, adds considerably to the contamination of the soil with this disease (Fig. 64).

SYMPTOMS WITH WHICH WART DISEASE MAY BE CONFUSED.—The symptoms of Wart disease are so characteristic that there should be no difficulty in its identification, though exceptionally severe attacks of Powdery Scab may very occasionally lead to confusion (page 367). It also sometimes happens that seed-tubers in which the eyes have been destroyed by diseases, or other cause, may develop a hard woody outgrowth at the heel end, which might be mistaken for Wart disease. Occasionally some eyes may show a form of bud proliferation which simulates wart disease and has tentatively been attributed to over-heating of tubers during storage (Fig. 23), (Moore, 1948).

DISTRIBUTION.—Although probably a very old disease, there are no definite records of the occurrence of Wart disease in the British Isles before 1893,[1] in which year, according to Hilli, it reached Finland in consignments from this country. Wart disease was first scientifically studied by K. Schilberszky in tubers from Upper Hungary (now Czechoslovakia) in 1896. In 1902 Potter recognised this newly described disease on tubers received from Cheshire, and within the next few years its occurrence was confirmed in both Scotland and Ireland.

Wart disease became compulsorily notifiable to the Ministry of Agriculture in 1908 under the provisions of the Destructive Insect and Pest Act of 1907. This was followed in 1909 by

[1] In the Royal Scottish Museum, Edinburgh, there is a record of the presentation in 1860 of a model of a tuber showing a cauliflower-like growth from an eye.

G. C. Gough's (1920) discovery that certain varieties remained unaffected in badly contaminated land, *i.e.* they were immune from attack by the Wart disease organism. Trials carried out successively at Harper Adams Agricultural College and at Ormskirk confirmed this outstanding discovery and led to the institution of the Official Potato Testing Station at Ormskirk, until recently under the control of the National Institute of Agricultural Botany. The breeding of varieties immune from Wart disease was very greatly stimulated and the testing of these new varieties was undertaken at Ormskirk and in Scotland. The importance of this work, and that of the Potato Synonym Committee of the N.I.A.B. and the similar Scottish Committee, can scarcely be overestimated, since it has provided the means of assessing the value of a new variety to the grower and of protecting him against the pernicious system of reintroducing old varieties under new and expensive names.

Meanwhile the occurrence of Wart disease was being confirmed in many parts of the country, and in 1923 a " Wart Disease Order " scheduled as an infected area the whole of Wales and Monmouth, Lancashire south of the river Ribble, the counties of Cheshire and Stafford, and parts of Shropshire and Worcester, together with isolated parishes in adjacent counties. Scattered localities in a number of other counties were similarly scheduled. In Scotland the disease is practically restricted to the midland and southern counties, whilst in Ireland it is known to occur in counties Down, Louth and Donegal ; it has also been recorded from the Isle of Man.

There is reason to believe that Wart disease remained localised so long as the popular varieties grown were Victoria, Regent, Champion, Magnum Bonum, Maincrop, Abundance and Bruce, for of these only Magnum Bonum is susceptible to attack. With the raising of such varieties as Up-to-Date, British Queen, King Edward, President and Arran Chief, all of which are susceptible, the disease forced itself upon the attention of growers, and records of new outbreaks began to multiply. The spread was still further accentuated during the war of 1914-1918 when certain restrictions on the movement of potatoes had temporarily to be abandoned. Concentration on the breeding of new varieties immune from the disease, however, has now given us a considerable number of popular " immunes," and perhaps two-thirds of the potatoes now grown in this country consist of such varieties. This fact, and the scheduling of infected areas from which the movement of potatoes was prohibited, have very much reduced the economic importance of Wart disease. Even in scheduled areas the disease is frequently worst in the immediate neighbourhood of industrial populations where town refuse is often used as a manure. Elsewhere, the disease occurs mostly in small gardens and allotments ; and in Anglesey, the whole of which county was scheduled, Wart disease is known only in some four or five widely separated gardens. Further, although isolated records of infection have now been made in most English counties, the number of such records has actually diminished in parts of scheduled areas within which, of course, there has been free movement of potatoes. This changed situation has been recognised by an amended Wart Disease Order of 1941 which abolishes both the scheduling of infected areas and the need for " Clean Land " certificates for seed potatoes grown in such areas. Under the new Order, however, all outbreaks must still be notified, and it remains an offence to plant non-immune varieties on land on which Wart disease has been known to occur at any time. Free movement of ware or seed is now permitted throughout Great Britain, except in a " Protected Area " around the Wash in East Anglia, in which the only potatoes which may be planted, or moved into the area for planting therein, are those receiving an official certificate to the effect that they are of a high standard of health and that Wart disease has not been known to have occurred on the land on which they were grown. Even more stringent Regulations have been issued in some other countries, *e.g.* Czechoslovakia, where an Order (Anon., 1942) prohibits the growing of solanaceous plants, other than immune varieties of potatoes, in infected areas and requires the disinfection, by means of 10 per cent. formalin, of all wagons used to transport potatoes from infected areas, on the completion of each journey.

It is difficult to account for the occurrence of Wart disease in Britain since the causal organism is not known to be capable of a separate, saprophytic existence in the soil, and it has not yet been found attacking any plant other than potato in nature. However, its occurrence on weed plants belonging to the same family as the potato is not improbable, since several such plants have been artificially infected (Cotton, 1916, and Glynne, 1925), *e.g.* black nightshade and woody nightshade, and the fact that no external " warts " develop on these plants when infected would very much reduce the chance of the disease being recognised. As regards foreign countries, Wart disease is known to occur throughout Europe, except possibly in Spain, Rumania and Italy. It has been found in Newfoundland, Canada and the mining districts of Pennsylvania and, recently, in South America where it is doubtless indigenous, though Fagundes (1944) claims that the disease has only been reported from Peru. The occurrence of the disease in many of these countries is certainly due to the importation of infected tubers, and this fact has had much to do with the restrictions, often amounting to total prohibition, now imposed by most countries on the importation of potatoes.

CAUSE OF WART DISEASE.—Certain relatively primitive forms of Phycomycetous fungi are grouped together in the Order Archimycetes. Among them are the organisms respectively responsible for two serious diseases of the potato tuber, *i.e.* Wart Disease and Powdery Scab, the inter-relationships of which are discussed on page 369. The causal organism of Wart Disease, known as *Synchytrium endobioticum*, occurs in the soil in the form of brownish black, thick-walled resting cells or sporangia, which are extremely resistant to weathering in the soil and to chemicals applied with the object of destroying them. There are few records of land, once contaminated, ever becoming clean. Holmberg (1944), however, claims that, in Sweden, contaminated land under arable crops other than potatoes for sixteen years had lost the power to infect, whereas under similar circumstances grassland was still highly " infective " when the susceptible variety Up-to-Date was planted. Teigland (1945) also states that resting spores retain their vitality in Norway for fifteen or sixteen years. According to Weiss (1925) the most favourable conditions for the germination of the sporangia are found when the soil is wet and its temperature lies between 50° F. and 80° F., although at the higher temperature germination and infection will occur even if insufficient water is present to permit of good plant growth. The necessary soil temperature is reached in a normal year by the end of May and continues until October, but the requisite soil moisture is found much more frequently in the west than the eastern counties. Even at Ormskirk, however, with its thoroughly contaminated soil, infection of susceptible varieties sometimes did not occur during trials in dry summers. A germinating sporangium liberates a number of minute, naked masses of protoplasm, each equipped with a single protoplasmic hair (cilium) with which the zoospore, as it is called, is enabled to swim actively in the film of water which occurs in all but the driest of soils.

The fate of the majority of the zoospores is unknown, but those which reach a potato tuber lose their cilia and are able to penetrate into the unprotected epidermal cells of the " eye " and, by feeding upon the protoplasm of the potato cells, each zoospore enlarges until it fills most of the cell. The parasitic protoplasm now temporarily surrounds itself with a firm, two-layered, wall. Later, the delicate inner layer of this wall is forced through a pore of the outer wall so that it forms a thin-walled vesicle into which the organism passes. The nucleus now divides several times, and further internal walls appear so that a " sorus " is produced consisting of from three to five compartments or sporangia. Within each sporangium repeated divisions of the nuclei give rise to large numbers of uniciliated zoospores similar to the original invading zoospore. Meanwhile the irritation set up by the infection induces the surrounding healthy cells to grow rapidly and, by continuous division, to produce a minute " wart " ; the wart itself enlarging rapidly in size owing to successive infection by zoospores. The mature zoospores are liberated by the bursting of the infected potato cell-wall and the sporangial walls, so that the zoospores can now enter a new potato-cell and start the cycle of development over again by the production of more summer sporangia with their included zoospores. Sometimes, however, two zoospores fuse together and the new compound zoospore, or zygote as it is called, causes infection of a potato cell in the usual way. The invading zygote does not, however, form summer sporangia but passes into a state of rest by surrounding itself with a very thick resistant wall. These are the winter resting sporangia which are ultimately released by the rotting of the warted tissue, and so contaminate the soil (*cf.* Curtis, 1921).

It is probable that no variety of potato can prevent the entrance of the Wart disease organism, the difference between the immune and non-immune variety being in the nature of the reaction of the plant cells after infection. With non-immunes this takes the form of rapid proliferation of cells which results in the formation of a " wart," while in immunes the protoplasm of the invaded cell either kills the zoospore or, in most cases, the underlying cells form a loose tissue which sloughs off together with the infected cell. In the latter event the organism may have progressed as far as to produce summer sporangia, and even occasionally winter sporangia (Glynne, 1925, 1926), which are thus returned to the soil with the discarded tissue. Immunity, in so far as it describes the successful prevention by the plant of wart formation, is absolute and is inherited according to Mendelian Laws. According to Salaman and Leslie (1923), several factors are involved and the genetical relation between them is complex, and is perhaps not fully understood. Amongst susceptible varieties, all gradations of severity of attack are known ; Arran Chief, for instance, giving an almost completely warted crop, whilst the variety King Edward VII is frequently attacked so late in the season that a proportion of the tubers may remain unaffected.

In recent years evidence of the existence of distinct biological strains of *Synchytrium endobioticam* has been published by continental workers. Braun (1942) has described a strain (" G") isolated from Thuringia which produces warts on some 58 varieties of potato immune from the official German (Dahlem " D ") form of the disease. The same worker also isolated a third strain (" SB ") from Southern Bohemia and states that, while the variety Fram is immune from all three strains, the varieties Edda, Edelragia and Parnassia are immune from " SB " and " D " strains but susceptible to strain " G " ; similarly, the varieties Primula, Sabina and Sickingen are susceptible to " G " and " SB " but immune from strain " D." Blattiny (1942) considers that there are three distinct Central European races or groups of races of *Synchytrium* : (*a*) a mountain group found around the Carpathians ; (*b*) an East German lowland group, and (*c*) a West German group which, however, may eventually prove the same as (*b*). On the other hand Hartman and Akeley (1944) have found no evidence of the existence of different strains in U.S.A., nor have they been shown to occur in the British Isles. In recording a similar lack of reason for believing in the existence of different biological strains of *Synchytrium* in Sweden Björling (1948) puts forward some interesting evidence to prove that many susceptible tubers failed to contract Wart disease if they had previously been

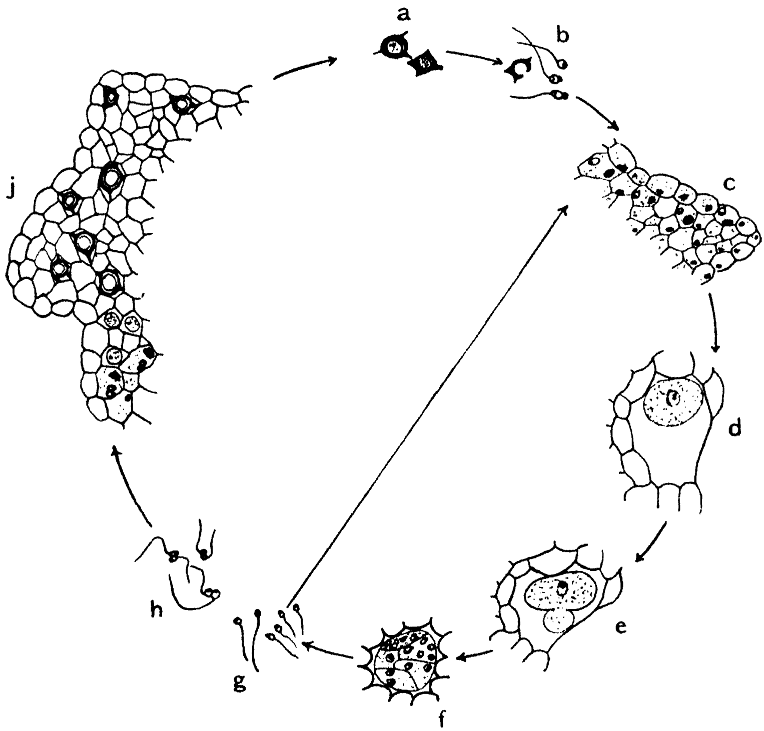

FIG. 64*a*.—Diagram representing the Life-History of *Synchytrium endobioticum*. (*Partly after* Curtis.)

(*a*) Winter sporangia in the soil.
(*b*) Germination of winter-sporangium to give rise to uni-ciliated and uni-nucleated zoospores capable of free movement in the soil water.
(*c*) Section of bud in " eye " attacked by zoospores ; three cells show the parasitic zoospore as well as the host nucleus. The zoospores have thrown off their cilia.
(*d*) The invaded cell enlarges and most of the protoplasm is absorbed by the zoospore (or pro-sorus as it is now called), which grows and forms a globular shape at one end of the cell.
(*e*) The wall of the pro-sorus bursts and liberates its contents into the empty part of the cell.
(*f*) The pro-sorus enlarges and shows both repeated nuclear and cell division. Each multi-nucleated cell is a summer sporangium.
(*g*) Zoospores liberated from the summer sporangia, which are capable of re-infecting potato cells and again giving rise to summer sporangia ; *or*
(*h*) the zoospores conjugate (*i.e.* coalesce) but, although the double zoospore (or zygote) is equally capable of causing infection, the events following infection are different.
(*j*) Section of potato " wart " showing infection by zygotes. After absorbing most of the host protoplasm these surround themselves with a cell-wall and pass into the resting state seen near the lower end of the section. These resting zygotes develop into winter sporangia by internal nuclear divisions giving rise to zoospores. The sporangium wall thickens both by the secretions of its own protoplasm and the aggregation of waste protoplasm from the host cell. Ultimately the wart decays and the winter sporangia are liberated.

attacked by the Stem-Canker fungus (*Rhizoctonia solani*, *cf.* page 295). In some cases a joint attack by the two fungi induced black necroses strongly reminiscent of the effect of *Synchytrium* attack on Wart-immune varieties. He assumes that the *Rhizoctonia* partially or wholly destroyed the cell constituents necessary for the full development of *Synchytrium*, and that in consequence about 2·5 per cent. of all varieties tested were erroneously placed in the provisionally immune category owing to the failure to develop warts in the presence of the antagonistic fungus.

EXTENT OF LOSS.—Potentially, this disease can cause very heavy losses amounting to total destruction of the crop, but since the introduction of immune varieties the actual loss sustained is negligible.

CONTROL.—The use of immune varieties and the restrictions imposed during the operation of the Wart Disease Orders have largely, but not entirely, solved the problem of control. The former can only be regarded as a palliative since the organism remains alive in the soil, whilst the restrictions quarantined not only actually contaminated land but also a far larger acreage of clean land. Nevertheless, the combined effect of these two factors on the situation in England and Wales has been startling. Thus during the period 1917 to 1946 the total number of outbreaks notified each year fell from 4823 in 1917 to 38 in 1946; the number of new records of infection similarly falling from 275 to 11 (Moore, 1948). Continuous search is being made for some means of killing the sporangia in the soil, and recently claims of success have been made in experimental tests in U.S.A. with a weed-killer (ammonium thiocyanate) applied at the rate of from half a ton to one ton per acre; but there is no experience of this substance as yet in this country. Control, so far as the grower is concerned, consists therefore of preventing the contamination of his land. Once a portion of a farm becomes contaminated with winter sporangia, their transfer to clean land follows by any means whereby soil can be so transferred, *i.e.* on boots or implements, in soil adhering to brassicæ transplants, or on turnips which are fed off to stock on grassland, by the movement of livestock from one field to another, etc. A new outbreak on land in a hitherto clean area is similarly due to the transfer of contaminated soil, most frequently on tubers (whether of immunes or non-immune varieties is immaterial), but may also be transported on other plants, *e.g.* cabbage seedlings, or on sacks used for any purpose. All affected tubers should be burned; even boiling them before feeding to stock is not a certain guarantee that living sporangia will not survive passage through the animal and ultimately find their way to the land in the manure.

CHAPTER XXIV

DISEASES CAUSED BY ARCHIMYCETES, ACTINOMYCETES AND BACTERIA

(2) Powdery (Corky) Scab (*Spongospora subterranea* (Wallr.) Lagerh.)

General Appearance.—Attacks are confined to tubers, stolons and roots, with exceptional cases of sprouts being affected from diseased tubers before planting; no signs of disease occur on the foliage or haulm, and growth of the affected plant is normal. On the tuber the disease first shows as small pimples covered by the unbroken skin. The latter, however, soon ruptures and exposes a brown mass which, under a good hand lens, will be seen to be composed of a fine brown powder justifying the use of "Powdery Scab" as the common name of the disease. As the tissues dry the brown powder readily falls out and leaves behind a smooth corky depression in the tuber flesh, which gave rise to the name "Corky Scab" commonly applied to this disease in Great Britain up to a few years ago. The small scabs may remain separate in less severe attacks, but when, as they often do, they coalesce and cover a large part of the tuber surface, the produce may be quite unsaleable. Under wet soil conditions the effect on the tubers continues until large areas of the flesh are involved; the tuber now becomes malformed and appears as though portions of flesh have been scooped out by slugs. This is the most serious "canker" form of the disease, but fortunately it is rarely seen except under badly drained soil conditions. Under the Destructive Insect and Pest Acts (Sale of Diseased Plants Order of 1936), potatoes substantially affected with Powdery Scab may not be sold for planting as seed in Scotland or in England and Wales. (Figs. 65 and 66.)

Symptoms with which Powdery Scab may be confused.—Immediately before the rupture of the skin covering the scab the disease may possibly be mistaken for Skin Spot (page 309), although in the latter disease the raised "pimples" are much smaller and flatter than the pustules of Powdery Scab. The most common source of error lies in confusion with Common Scab (page 375), and in some cases the two diseases can only safely be distinguished after microscopical examination. Powdery Scab, however, usually appears less superficial than Common Scab, for although the unbroken pustules are raised well above the tuber surface, the depressions exposed after the loss of the powdery mass of spores are more deeply embedded in the tuber flesh; the base of the depression, moreover, has a characteristic honeycomb appearance (Millard, 1921). The irregular margin of the broken skin surrounding the scab produced by *Spongospora* and the ease with which the powder can be shaken from the dry scab on to a sheet of paper are also useful means of distinguishing this disease from Common Scab. The malformations induced by the canker form of Powdery Scab may sometimes be confused with those caused by Wart disease (page 357).

DISTRIBUTION.—Powdery Scab was first described in Great Britain in 1846 by Berkeley, who, however, wrongly identified the causal organism as a member of the "Smut" fungi. The disease is especially prevalent in the north and west, occurring widely in Scotland, Northumberland, Western England and Wales, whilst the south and east of England are either free or usually show only the milder forms. This association of Powdery Scab with wetter regions is also seen in Ireland where it is most severe in the west; whilst in Russia, according to Dorojkin (1936), its distribution practically coincides with that of Blight. There is some evidence that Powdery Scab was introduced into North America from European (Belgium and the Netherlands) sources just prior to the Great War, but here also it has remained more or less confined to the wetter eastern States of U.S.A. and the Maritime Provinces of Canada. In northern and central Europe it appears to be both widespread and old-established. There is a possibility indeed that it was introduced into Europe from the original home of the potato, since it has been recorded on wild forms of *Solanum* in Peru. Abbott (1931) believes it to be endemic in that country and states that it is widespread and severe on commercial crops of the potato. Powdery Scab is not known to occur on any field crop other than the potato, although it has been artificially induced into the tomato and certain foreign

FIG. 67.—Common Scab; normal type (p. 375).

FIG. 68.—Common Scab; pitted type.

FIG. 69.—Pit Rot (page 404).

FIG. 70.—Gangrene (page 328).

species of *Solanum* (Melhus and Rosenbaum, 1916), though failure was experienced with the common weed *Solanum nigrum* (Melhus *et al.*, 1916).

CAUSE OF POWDERY SCAB.—*Spongospora subterranea* was first assigned to the group of lowly organisms known as the Myxomycetes, or "slime-fungi," by the Norwegian mycologist Brunchorst, in 1886. These organisms, amongst which is included the one causing "Clubroot" or "Finger and Toe" of swedes, cabbages and other brassicæ, can scarcely be called fungi in the strict sense, but appear to occupy a position intermediate between primitive plant and animal life. No hyphal threads are produced at any time in the life-history and the vegetative body consists of a multi-nucleated naked mass of protoplasm (the plasmodium), capable of an independent crawling movement similar to that exhibited by the primitive animal known as the amœba. On the other hand, the reproductive bodies or spores are produced in an essentially plant-like manner. Of recent years it has been generally accepted that these parasitic forms are, in fact, more nearly related to the simplest members (the Archimycetes) of the Phycomycetous fungi than they are to the often highly organised saprophytic Myxomycetes (Myxogastres); (*cf.* Ainsworth and Bisby, 1943). The primitive Archimycetes are thus separated into two Orders (1) the Plasmodiophorales, to which belong *Spongospora* and the Clubroot organism (*Plasmodiophora*). These agree in that the vegetative body (thallus) remains naked, *i.e.* never develops a limiting membrane at least until spore formation begins; the spore on germination produces a swarm-spore motile by means of two anterior flagella (cilia) of unequal length; (2) the Myxochytridiales to which belongs the Wart disease organism, *Synchytrium endobioticum* (*cf.* page 357), characterised by the formation of a membrane around the thallus immediately preceding the production of the reproductive zoospores; these vary in different families of the Myxochytridiales but never develop unequal-sized flagella for locomotion.

The features in the life-history of *Spongospora* which are likely to be of practical importance are well established, though details are still matters of controversy. The brown powder filling the scabs consists of vast numbers of "spore-balls," each about $\frac{1}{20}$ mm. in diameter and made up of a mass of tiny spherical spores, adhering for the most part by their spore-walls to each other, but with sufficient gaps to give a sponge-like appearance to the spore-ball; hence the generic name of *Spongospora*. The spore-ball thus forms a unit in much the same way as the "seed" of mangolds is a compound fruit containing the true seeds. Spore-balls, liberated into the soil from infected tubers, germinate best under conditions of ample moisture and relatively low temperature. Each germinating spore releases a minute amœba-like naked mass of protoplasm known as a myxamœba and capable of a limited amount of independent movement by the protrusion of naked branches or "pseudopodia." Under drier conditions in the soil movement ceases and the myxamœba is converted into a thick-walled cyst; in which form (as in the case of the spores) it is able to survive unfavourable soil conditions for several years (Pethybridge, 1912; Kunkel, 1915; Melhus *et al.*, 1916). On the return of optimum conditions for growth the cysts germinate and give rise to myxamœbæ in all respects similar to those produced direct from the spores. The exact sequence of events leading to infection is still in doubt, though there can be no hesitation in accepting the view that the roots, which are frequently attacked (Johnson, 1909; Pethybridge, 1912) are often badly diseased before the tubers show any sign of infection (Melhus *et al.*, 1916); these authors state that it is not uncommon to find the roots of the variety Green Mountain heavily infected at lifting time whereas the tubers are perfectly clean.

According to Kunkel (1915), infection of the tuber occurs through lenticels or directly through the tuber-skin by the solvent action of the organism on the pectin of the middle lamellæ of the corky cells of the skin. This, he says is preceded by the fusion of several myxamœbæ to form a compound vegetative body or plasmodium; the plasmodium being the infecting unit. Certainly, plasmodia have been found at an early stage of infection within the young lenticels and in the intercellular spaces below older ones or below wounds (Johnson, 1907, 1908; Wild, 1929), but there is strong evidence that infection is possible by means of single myxamœbæ (Osborn, 1911; Horne, 1930; Piard-Douchez, 1948); the last-named author describing single myxamœbæ as occurring in large numbers both between and within the living cells below the corky skin of the tuber. All, however, agree that plasmodia *are* formed by the fusion of myxamœbæ either before or after penetration, and that no reaction on the part of the tuber tissue is observable until plasmodia are formed. These plasmodia appear as plate-like, multi-nuclear bodies which fill the more superficial intercellular spaces below the skin, forcing their way between the cells by their solvent action on the middle lamellæ (Wild, 1929) and, eventually, by means of their pseudopodia, penetrating within the cells themselves. Here the parasitic protoplasm lies alongside the protoplasm of the potato cell and, so far from destroying the latter, stimulates the cell to grow to four or five times its original length in the direction of the surface ; tangential walls appear so that the new " giant-cell " is divided, with its parasitic tenant, into several portions, the pressure of which ruptures the tuber-skin and exposes the pimple of infected tissue—this being the first external sign of infection. At the same time the uninvaded cells below the region which has been infected are stimulated to divide and, by the deposition of suberin, to form a corky barrier to any deeper penetration of the plasmodia but, as Miss Wild states (1929) it is still uncertain whether this stimulation is due to the enzymic activity of the parasite or to a normal wound reaction on the part of the tuber-flesh. When the plasmodium (or more correctly the portion within each cell) is mature, it separates into a very large number of uninucleate spores corresponding to the number of nuclei present in the plasmodium and, as has already been mentioned, these spores mostly adhere by their walls, but gape apart in many places so that the compound " spore-ball," viewed under the microscope, has a remarkable similarity to a spherical sponge. The mature spore-balls are liberated into the soil by the disintegration of the scab and there await the arrival of conditions suitable for germination. Under very wet soil conditions, however, germination of the spores may occur *in situ* within the original scab, and since the protective corky layer produced under such conditions is often very thin and ineffective, the newly-germinated spores may produce myamœbæ able to penetrate deeper and begin to form the " canker " stage of the disease by successively passing through the weak cork barriers to their progress. Normally, however, the myxamœbæ, having fused to become plasmodia, extend mostly in a lateral direction (*i.e.* parallel to the skin-surface) and so easily evade the partially developed wound-cork. Later, deeper penetration occurs until, in bad cases, a great deal of the tuber may be destroyed. As might be expected, the open pustules of Powdery Scab, and still more the severe wounds produced by the "canker" stage provide an easy means for the entrance of rotting organisms of many kinds; Melhus *et al.* (1916) in particular describing *Phoma tuberosa* as a common follower of Powdery Scab and producing a hard, dry, rot (*cf.* page 330).

According to work by Ledingham (1935) which, because of its fundamental importance, must be accepted with some reserve until confirmation is available, the life-history of *Spongospora* is more complicated than has hitherto been supposed, or as shown in the diagramatic sketch (Fig. 65*a* on page 373). He considers that after incubating spore-balls in the soil for a fortnight at 65° F. these liberate biciliate zoospores not unlike those of the "Blight" disease organism, *Phytophthora infestans* (*cf.* page 336) which later become amœboid and capable of infecting root-hairs. Within the root-hairs or epidermal cells of the root are developed zoo-sporangia, either singly or in clusters by budding from the original zoo-sporangium. The zoo-sporangia exert pressure on the root cell-wall until it is ruptured and the contents of the sporangia (zoospores) are liberated into the soil. The occurrence of bi-nucleated, four-ciliated, forms among these zoospores, has naturally raised the whole question of sexuality in *Spongospora*.

CONTROL.—No commercial varieties are known which are immune from Powdery Scab, though Dorojkin (1936) claims immunity for several South American species of *Solanum*. Relative resistance to the disease is stated by Wild (1929) to depend upon the thickness of the corky skin of the tuber and hence upon the number of suberised cells resulting from the division of the cork cambium. Thus in some ten varieties she found the percentage of diseased tubers varied from 82·8 down to 1·6 while the corresponding thickness of skin varied from 53·0 μ to 118·5 μ; the thinnest skin being only some 2·87 cells thick as compared with the 5·67 cells forming the depth of the thickest skin. Since tuber-skin is undoubtedly affected by the conditions of growth, the conclusions of Wild need not conflict with the common experience in this country that varieties appearing to show resistance in one district may be badly affected in another, or perhaps in other years in the same district. The disease is

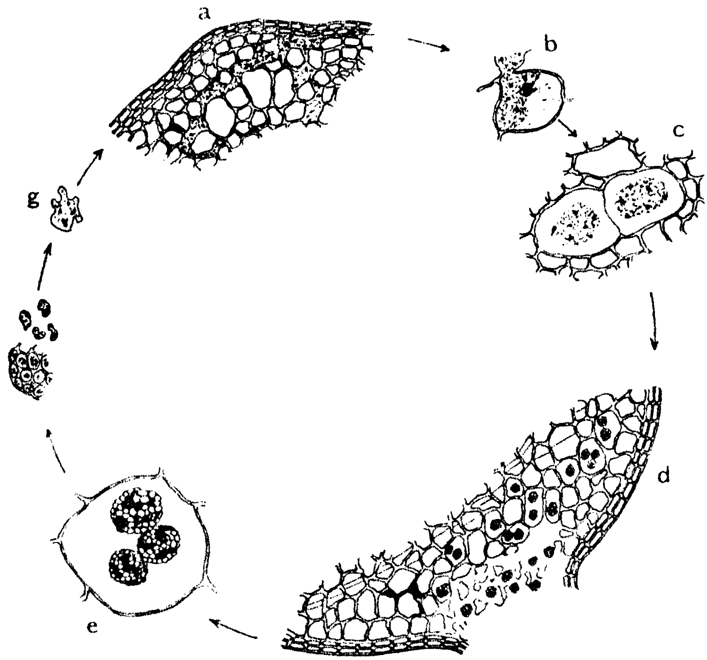

FIG. 65*a*.—Diagram representing the Life-History of *Spongospora subterranea.*

(*a*) Section of tuber showing the invading multinucleated plasmodium extending in the ntercellular spaces of the tissue.
(*b*) A cell invaded by the plasmodium, which is adpressed to the host-cell nucleus.
(*c*) The parasitised cell is stimulated to enlarge and forms a "giant-cell" the host protoplasm is absorbed and the cell, together with the plasmodium, has divided.
(*d*) Section of tuber across a scab showing the formation of "spore-balls" by the plasmodia and their release into the soil.
(*e*) Cell enlarged to show three spore-balls.
(*f*) Highly magnified portion of spores in a spore-ball, some of which have germinated to give rise to uninucleated amœba-like bodies.
(*g*) Multinucleated plasmodium which conceivably arises either by growth and nuclear division or by fusion of amœbæ, but method of formation is still unknown.

both seed-tuber borne and soil borne so that we may usefully consider first how to prevent the contamination of hitherto clean land. This may result from the use of infected seed-setts or contaminated manure, as well as by the accidental transference of contaminated soil on implements and boots. The simplest precautions should prevent the transference of contaminated soil, but more care is required in the case of manure, since Pethybridge (1911) proved that manure from pigs fed on unboiled scabbed potatoes contain living spores capable of causing infection in potatoes. No doubt this is equally true of contaminated manure from other kinds of stock, and diseased tubers should therefore be boiled before use in stock feeding. Obviously infected tubers should not, of course, be used as seed, but circumstances may compel the use of slightly scabbed setts or of tubers which are suspect in that they have been in contact with sources of infection. In such cases Pethybridge (1911) has shown that good protection is afforded by steeping the tubers (before sprouting begins) in formalin (Appendix I, page 645), or by first wetting the tubers and then rolling them in flowers of sulphur. The latter method is the more convenient and can be employed just prior to planting.

Although land should be protected in these various ways from contamination, it appears that even badly infected tubers used as seed will only cause infection on the new crop under cool damp soil conditions. Rovdo (1936) and Dorojkin (1936), for instance, report their failure to obtain infection by the use of badly infected seed in the drier potato-growing areas of U.S.S.R. This is equally true of badly contaminated soil (Ramsey, 1918) and this natural confining of infection to cool wet soil conditions is perhaps the most effective control we possess. Philipp (1932) emphasises the importance of rain and low temperatures in causing infections in Germany, whilst Dorojkin (1936) records that moist contaminated soils in Russia may show reductions of 30 per cent. of the crop in seasons when heavy rainfall occurs in May and June. In Switzerland, Miss Wild (1929) found Powdery Scab flourishing in soils with a large pore space, a high humus content combined with coarse texture, a high methylpentosan content, and a large water-holding capacity. The incidence of infection was not affected by soil reactions within a *p*H range of 5·9 to 7·6, or by its carbonate or hexosan content. These results are confirmed in part by Naoumoff (1936) in U.S.S.R., where he states that tuber infection occurred more freely in acid soil (*p*H 4·7 to 5·9) with a moisture content of 60-90 per cent. than when less acid soil of 40 per cent. moisture content was used. It seems difficult to harmonise these continental results with the views expressed in Ireland by Pethybridge (see below) on the risk involved in applying lime to reclaimed bog soils; the answer may depend on the degree of success in draining the Irish soil. In any case it would appear that, contrary to general opinion, under wet soil conditions *Spongospora* can remain active irrespective of whether the soil is markedly acid or alkaline. Good drainage is therefore of first importance in checking the disease. It is believed that the organism of Powdery Scab can persist in the soil, probably in the form of spore-balls or as encysted amœbæ, for at least three years, and Melhus, Rosenbaum and Schultz (1916) have evidence of its persistence for a five years' interval between two potato crops. An extension of the rotation to five or more years should therefore be made in order to eradicate the disease from the soil. Pethybridge (1911-1916) carried out trials with a view to testing various means of soil disinfection, and a considerable degree of control was obtained by the application of flowers of sulphur in the open drills at the rate of 6½ cwt. per acre, or 2½ oz. to the square yard. Other substances either increased the amount of scab (*e.g.* gas-lime and chloride of lime) or reduced the total crop of tubers (*e.g.* "superphosphate"), and even the sulphur dressing cannot be regarded as dispensing with the need for good drainage and extended rotations. Lime should on no account be applied, for Pethybridge (1911-1916) proved that in this way the disease was considerably intensified whether the application was made to reclaimed bog soils (which were presumably acid) or to others described as slightly calcareous.

ACTINOMYCETES

COMMON SCAB (*Actinomyces scabies* (Thaxter) Güssow) and other species

GENERAL APPEARANCE.—This disease attacks tubers at all stages of growth until fully ripened, after which no new attack need be feared. Small raised scabs or pustules are also found on the stolons and occasionally on the fibrous roots, but the crop is not reduced and plant growth is normal. The first sign of infection is the development of small scattered brown spots, usually at the lenticels or breathing pores of the tuber; these spots remain superficial but increase in size until the typical scabs are produced. If the tuber is carefully examined immediately after lifting, it is sometimes possible to see the delicate greyish white hyphal threads of the causal organism, particularly on the skin of the small unbroken scabs, but these threads quickly disappear as the tuber dries.

The form of scab lesion may vary from a mere roughening of the skin to a quite prominent raised pustule. Six types of scab have been recognised and attributed to different species of *Actinomyces* (Millard and Burr, 1926) as follows :—

(i) *Superficial Scab.*—A mere brownish roughening or abrasion of the tuber skin, attributed to *A. Loidensis* (M. & B.).

(ii) *Ordinary Scab.*—Characterised by an irregularly concentric series of wrinkled layers of cork arranged around a central core or depression. The scab surface is rough and the outline irregular ; it is most common in medium loams (Fig. 67). Attributed to *A. marginatus* and *A. coroniformis* (M. & B.).

(iii) *Pitted Scab.*—In this type there is a central " pock " or depression bounded by a ragged edge of torn skin. The scab is dark in colour and the surrounding tissue is generally stained (Fig. 68). Cork formation is slow and the interior of the depression is therefore soft and pulpy during the growth of the scab. In the more virulent forms of this type of scab the depression may be from 3 to 4 mm. deep and, coalescing, may give rise to deep cracks or furrows in which " Springtails " (*cf.* page 253) may often be found feeding. Attributed to *A. scabies* (Thaxter) Güssow, and the less virulent species *A. Setoni* (M. & B.) and *A. viridis* (M. & B.).

(iv) *Stud Scab.*—This is a distinct elevation 2 to 3 mm. above the surface of the skin and forming a raised pustule which can easily be cut off. The top is smooth, more or less circular and with vertical sides ; it is only slightly brown and surrounding tissue is not stained. The " stud " consists largely of cork cells. Apparently regarded by Jones (1927) as a form of " tumulus " scab and attributed to *A. flavus* (M. & B.).

(v) *Tumulus Scab.*—This begins as a cone-like depression distinguished from pitted scab by the firm lining of cork. Later it becomes elevated above the surface as a raised pustule distinguished from the stud type by its sloping sides. Attributed to *A. flavus* (M. & B.).

(vi) *Pimple Scab.*—The scabs are small, soft and pimple-like. It is not well defined and may be merely an immature form of one of the other types. Millard and Burr found it only in inoculation experiments. Attributed to *A. Wedmorensis* (M. & B.).

SYMPTOMS WITH WHICH COMMON SCAB MAY BE CONFUSED.—Any wounds on the tuber, *e.g.* the shallow pits caused by millepedes (page 251), will induce the formation of a wound-cork and so present some slight resemblance to Common Scab—an effect which may also be produced by excessive moisture in the soil. The only serious difficulty, however, is in distinguishing between Common and Powdery Scabs (page 367). Expert examination may indeed be necessary in some cases, but usually Common Scab can safely be diagnosed by the absence of the fine snuff-like powder within the scab, as well as by its more superficial character and angular outline; it never causes malformations such as those induced in the canker form of Powdery Scab.

DISTRIBUTION AND EXTENT OF LOSS.—Common Scab is one of the most widely distributed of diseases and has been recorded from almost every potato-growing country. According to Millard (1922), the first reference to Common Scab in this country was in 1825, and it is now known to be extremely prevalent on the light sandy or gravelly soils in the British Isles. It is usually prominent in the first two years after grassland has been ploughed up (Moore, 1943) and, normally, it is much less common on heavy or peaty land, though too much reliance on any single factor such as soil texture should be avoided. Thus, Moore (1948) reports that single samples of Majestic tubers, taken from different soil types in the east Midlands during 1945, showed the following percentages of Scab infection: chalky (2 per cent.), boulder clay (3), gravel (21), light silt (67), and London clay, black fen (97). The financial loss due to Common Scab is difficult to assess since it depends, not on any crop reduction, but on the variable degree of importance attached to what is usually merely a surface blemish; Pethybridge (1934) records a loss of from 15s. to £1 per ton on a badly scabbed crop raised from newly-ploughed pasture. In contradistinction to Powdery Scab it can be regarded as essentially a disease of dry warm seasons.

CAUSE OF COMMON SCAB.—The disease has been ascribed to a great variety of causes, most of which are only contributory in the sense that they intensify the symptoms. This is particularly true of the still prevailing views that Common Scab is due to liming, or to irritation set up by gritty particles in the soil as suggested by W. G. Smith in 1884. The persistence of these views is not surprising, since it is just under such soil conditions that the organism really responsible for scab thrives best. This organism was first isolated and its pathogenicity proved by Thaxter (1890), who also named it *Oospora scabies*; later, however, it was referred to its present genus of *Actinomyces* by Güssow (1914).

The Actinomycetes (or Actinomycetales) include a large number of forms of which only a few appear to be pathogenic to plants; some are parasitic upon animals and cause such serious diseases as "ringworm" and "wooden-tongue" or "lumpy jaw" in cattle, while still others produce similar skin diseases or respiratory maladies in man. The great majority, including the known plant-pathogens, are strongly aerobic (*i.e.* are dependent upon an ample supply of atmospheric oxygen), but one at least of the animal (and human) pathogens (*Actinomyces bovis*) which exists as a saprophyte in the teeth and at the base of the tonsils, is an anaerobe and has many characters in common with *Lactobacillus bifidus* (Skinner *et al.*, 1947). The systematic position of the Actinomycetes is still obscure. Drechsler (1919) could see no resemblance to bacteria and definitely placed them in the Fungi Imperfecti; and as late as 1943 Heald stated that while the potato scab pathogens are still considered by Bacteriologists to be filamentous bacteria, most Botanists are in agreement that they represent simple forms of the Fungi Imperfecti. An exactly contrary view is expressed in *A Dictionary of the Fungi* (Ainsworth and Bisby, 1943) where the Actinomycetes are accepted as higher filamentous bacteria, though it is agreed that some Mycologists still group them with the fungi. Dowson (1942) has pointed out that the Actinomycetes agree with the Mycobacteriaceæ and the Bacillaceæ in the fundamental property of reacting positively to Gram's stain, whereas the lower algæ, fungi and protozoa are all Gram-negative. Nevertheless this author does not include *Actinomyces* in his *Manual of Bacterial Plant Diseases* (1949) though he refers to the fact that the tuberculosis bacterium (*Mycobacterium tuberculosis*) resembles some of the "acid-fast" Actinomycetes, not only in their power to resist decolourisation by acids, but in giving rise to a small mycelium of branched cells. If the Actinomycetes are finally accepted as a homogeneous group distinct from fungi but fundamentally akin to bacteria, it would seem necessary also to accept the view of Bacteriologists that the genus *Actinomyces* should be restricted to anaerobic forms such as the animal parasite *Actinomyces bovis* ; the generic name of *Streptomyces*, adopted by Waksman and Henrici (1943), would then apply to all those common soil-inhabiting forms, including the potato-scab organisms, which are strictly aerobic, reproduce by conidia arranged in chains, and which are not acid-fast. What is doubtful is the homogeneity of the " Actinomycetes," for the most " fungoid-like " types resemble the Fungi Imperfecti more closely than they do the " bacteria-like " forms. Similarly the most " bacteria-like " forms are closer to the tubercle and diphtheroid bacilli than they are to the fungoid types (Skinner *et al.*, 1947). Until the position is cleared up it seems advisable to regard the whole group as intermediate between the true fungi and the higher filamentous bacteria, but with a closer approximation to the latter.

The name Actinomycetes, or " Ray-Fungi," accurately describes the tree-like growth of the hyphal threads of this group. These hyphæ are extraordinarily minute, much more delicate than those of ordinary fungi. They are sparsely and irregularly septate and branch repeatedly by the growth of buds from any cell in the thread, each branch itself giving rise to secondary branches in the same way. The spore-forming hyphal branches are at first even more tenuous than the vegetative ones but later the walls thicken somewhat ; in some species they grow erect but in others they remain prostrate amongst the vegetative growth. All are characterised by a spiral mode of growth which may afterwards contract into a tightly coiled spring. The direction of the spiral twist and the number and laxity of the coils are said to be constant for any given species and, together with their growth characteristics in pure culture, are used to differentiate the various species. Spore formation may occur from the tip of the hypha by the successive formation of closely spaced crosswalls or septa, or these may develop more or less simultaneously throughout the length of the hypha ; in either case the result is the production of a beaded structure reminiscent of the gonidia forms of the higher bacteria. The growth of *Actinomyces* is markedly affected by temperature, humidity and the degree of acidity of the substratum. Shapovalov (1915) showed that growth in pure culture was favoured by high temperatures, being most prolific at from 77° F. to 86° F. with spore germination at even higher temperatures. The optimum humidity is about 30 per cent. of saturation, and all growth ceases at *p*H 5·2 or below (Gillespie, 1918); at rather higher values of *p*H there is a tendency for the medium to become more alkaline as growth continues (Skinner *et al.*, 1947). According to Millard (1921) even a slight reduction in the supply of oxygen greatly reduces the rapidity and amount of growth. Cultures are extremely resistant to drought and have been found viable after being completely dried up for two years (Millard, 1923). The spores can survive long exposure to freezing or desiccation, and indeed are often produced most abundantly as the culture dries up.

Most workers agree that invasion of the potato by *Actinomyces* occurs only in the actively growing tuber. Sanford (1926), indeed, believes that the critical period for infection is limited to the first ten days of tuber formation, though Fellows (1926) and most others would extend this period up to the stage at which the thin epidermis of the tuber-skin is replaced by a corky periderm. According to Lutman (1941), very shallow scabs are the result of mycelial invasion which may occur at any junction between epidermal cells where, he says, there is no deposit of cutin; the mycelium progressing inter-cellularly by dissolving the pectin of the middle lamella. Wollenweber (1920), Fellows (1926) and Jones (1931), however, are in agreement that infection is due to the penetration of hyphal threads between the guard-cells of the stomata on the undeveloped "eyes," or between the loosely-packed, corky, cells of the young lenticels to be found scattered over the surface of the tuber. They believe that, while *Actinomyces* can invade the tuber through wounds, it cannot penetrate through unbroken suberised (corky) cell-walls of the tuber-skin. In one case Jones (1927) obtained infection when hyphal threads were in contact with the apparently unbroken cuticle of developing sprouts but considered that minute wounds might have been overlooked. Jones (1931) described the sequence of events when a lenticel is invaded as follows: the cambium layer, from which the cork-cells of the lenticel normally arise, is stimulated by the presence of the parasite to further division; but the external tissue produced is abnormal in consisting of radially elongated cells, the walls of which remain unsuberised. These unprotected cells are readily invaded by the parasite and their contents destroyed; the aggregation of dead, brown, cells forming the small brown spot which is the first external sign of scab-infection. The scab increases in surface area by the extension of the cambium laterally, and in depth by the progressive invasion of the new tissues so formed. Gradually the stimulation subsides and, with the slowing up of cell division, the last-formed cells become suberised. If this suberised layer of cells is continuous the further passage of the organism is prevented but, under dry conditions in particular, the barrier may be incomplete and deeper penetration becomes possible. This, again, stimulates division of the underlying cells with, ultimately, the formation of a second, deeper-seated, corky layer. Yet a third attempt to limit the inroads of the *Actinomyces* may be made, after which the invaded tissues appear to be too mature to react by cell division. Jones (1931) quotes Herklots as stating that suberisation is favoured by alkalinity, and suggests that the formation of the barrier of cork by the potato tissues is made possible by the known increase in alkalinity in the substratum induced by the growth of the organism; Sanford (1926) certainly found that in a mature Scab the tissues have a *p*H of 7·2 instead of the *p*H of 6·0 to 6·2 of normal potato tissue. Most workers consider the invasion by the parasite to be confined to the scabbed region of the tuber, although Jones (1931) showed that insufficiently protected sprouts and rootlets were liable to attack, and indeed that the potential loss of root-system might be seriously reflected in the fall in yield of tubers. Recently, Lutman (1945) has claimed that *Actinomyces* is capable of *systemic* invasion of all the growing parts of the potato plant, and can even be demonstrated to occur at the base of flower pedicels and to cause "blossom-drop."

Many workers have studied the influence of the environment on infection, for the conditions most favourable for the growth of the organism are not necessarily the best for infection. Scab, for instance, rarely develops on peaty soils or in those containing much humus, yet humus and dung are among the best media on which to cultivate species of *Actinomyces*. It must also be remembered that the intensity of infection depends, not only on the activity of the organism, but also on the reaction of the host plant ; and it is with these facts in mind that the influence of factors such as soil-temperature, acidity and moisture, should be considered.

Soil Temperature.—Warm summers have long been associated with bad attacks of Scab, and Jones *et al.* (1922) found that a soil temperature of 73° F. gave the highest percentage of tuber infection ; attributing to this fact the severity of the disease in the warm, southern States of U.S.A. Millard (1923), however, records the occurrence of very scabbed crops at temperatures averaging 60·8° F. (maximum, 64·4° F.) and points out that the disease is more general, and severe, in the north of England than in the south. Gäumann and Häfliger (1944) obtained the heaviest tuber infection in Switzerland at soil temperatures even lower than Millard's figures, although in pure culture the most luxuriant growth occurred at 75·2° F. They suggest that local strains of the *Actinomyces* have their own temperature relationships ; the optimum for infection being closely related to the optimum temperature for tuber growth, and therefore varying somewhat with the potato variety. Thus, tuber formation in the Swiss mountains is at its best at from 55·4° F. to 78·8° F., and the heaviest tuber-infection occurred at 50° F. for the variety Bintze and at 55·4° F. in the variety Ideal ; these being first and second " earlies " respectively.

Soil Acidity has been found by most workers to be an important factor in infection. Gillespie (1918) stated that Scab seldom occurs in soil with a *p*H of less than 5·2, and Steinmetz (1946) reported an increase in the amount of Scab, following an interval of ten years between potato crops, which was directly proportional to the rise in *p*H above 5·5 ; while plots adjusted to *p*H 6·0 and 6·5 gave unmarketably scabby crops. Millard (1923) qualifies his agreement in the importance of soil acidity by pointing out that severe attacks have been recorded in soils of *p*H 4·4 and that, although the organism may be assumed to be omnipresent in soils in this country, clean crops have been raised from soils of *p*H 7·0 ; in his view the operation of other factors, such as soil-texture, humus and moisture content, may reduce or even obliterate the effect of soil acidity. Muncie *et al.* (1944) found that while an application of powdered sulphur for one year increased the soil acidity and effected a marked reduction in the amount of

Scab, when applied for a second and third year in succession the amount of Scab again increased; this, they suggest, was the result of the organism adapting itself to the more acid conditions.

Soil Moisture.—Although there is general agreement that Scab is worst under dry conditions the relation between Scab-infection and soil moisture is not a simple one. According to Millard (1923) an effect is not seen until the moisture content is sufficient to alter the aeration of the soil, and this will vary with the soil texture. Thus, heavy rain may cause water-logging of clay soils and complete inhibition of Scab; whereas in gravelly soil there may be, as McKay (1949) has shown, an actual increase in Scab in a wet year. Indeed, in well-irrigated soils it is claimed by Starr *et al.* (1943) that infection bears no relation to abundance of soluble salts, *p*H, lime content or available phosphorus or potassium, but increases solely with the amount of water applied, and Lutman *et al.* (1936) have recorded the highest population of *Actinomyces* in Vermont, U.S.A., during winter when the soil-moisture content is at a maximum. After prolonged study of this problem in Canada, Sanford (1923, 1926, 1945) has reached the conclusion that, although improved aeration resulting from a reduction in soil moisture content will give the best conditions for Scab development, the disease can be equally severe on wet soils in which effective competition (*i.e.* antagonism) from associated saprophytes is at a minimum.

The probability that such competition exists has long been recognised, for very many species of *Actinomyces* occur naturally in soil and, since they have been found in abundance in virgin land (Jones and Edson, 1901; Lutman, 1923; Millard and Burr, 1926), the majority can be regarded as normally saprophytic. It is therefore important to discover whether more than one species is capable, under suitable conditions, of becoming pathogenic to potatoes; for if this is the case it may be expected that different species will react differently to soil conditions such as temperature, acidity and moisture. A striking characteristic of the Actinomycetes is their power to produce pigments of the most varied hue in spores, mycelium, or diffusing into the culture medium; and these colours are used, together with morphological differences in growth-forms, to distinguish the various species. Lutman and Cunningham (1914) concluded from their study of the potato pathogens that all belonged to one species which, from its power to stain the medium a deep brown colour, they named *Actinomyces chromogenus*. This "species," however, is now recognised as invalid since many forms with this property differ widely in other characters; these forms are now collectively referred to as the "chromogenus group." Wollenweber (1920) reached the conclusion that the different types of potato scab are due to the action of distinct species of *Actinomyces*, and the exhaustive study of the group made from 1920 onwards by Millard and his colleagues at Leeds

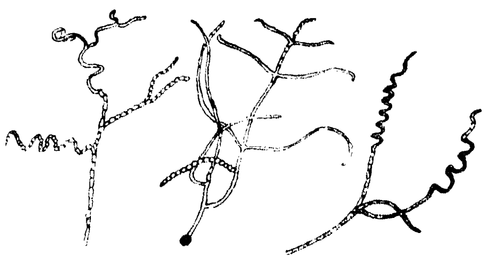

FIG. 67*a*.—*Actinomyces chromogens*. Three types of growth of the organism in pure culture. (*After* Millard and Burr.)

independently led them to the same view. Out of twenty-four forms isolated from scabbed tubers and soil, Millard and Burr (1926) described eleven species capable of producing characteristic and distinct types of Scab (*cf.* page 376). They identified the most virulent species as the one described by Thaxter in 1890 and later named *Actinomyces scabies* by Güssow (1914); a species which was afterwards shown by Millard and Beeley (1927) to induce a pitted form of scab on mangolds and beet and, as in the case of potatoes, to produce nodular scabs on the fibrous roots. Although several of Millard and Burr's pathogenic species did not belong to the chromogenus group, Taylor and Decker (1947) believe from a study of 143 "isolates" that all forms, capable of producing typical scabs, have in common the property of developing a dark ring of surface growth on separated milk. Schaal (1944), however, had been unable to find any definite correlation between pathogenicity and cultural, or other, characters; and even Taylor and Decker produced Scab in only 64·8 per cent. of tubers inoculated with one or other of 61 isolates, all of which were non-acid fast and gave the typical " pathogen " reaction on separated milk.

Pathogenicity depends on the maintenance of a fine balance between the potential parasite and such factors as soil moisture, temperature and acidity, as well as on the possible effect these factors may have on the resistance of the tuber. The interaction of environmental factors may determine which species of *Actinomyces* assumes a pathogenic rôle, for the balance of factors may differ with different species. Millard and Burr (1926), for instance, found that *A. flavus* only became pathogenic when the soil had dried out sufficiently to cause the death of the foliage, and even *A. scabies* failed to infect tubers both under the hot, dry conditions of 1921 and the cool, wet weather of 1922, but proved to be the most virulent of all the species isolated when a soil temperature of 21° C. (69·8° F.) was maintained. Millard (1923) advanced some evidence that a pathogenic species may, temporarily at least, lose its power to infect tubers after prolonged existence as a saprophyte, and suggested this as a partial explanation of the control of Scab afforded by ploughing in green manure (*cf.* below). Sanford (1926) believed that a better explanation lay in the competition or antagonism between *Actinomyces* and other members of the microflora of the soil, particularly the bacteria. Later, Millard and Taylor (1927) proved the existence of this antagonism by simultaneously inoculating soil with the pathogen *A. scabies* and the more vigorous obligate saprophyte *A. præcox*; showing that by increasing the proportion of the saprophyte in the inoculum the degree of scabbing of tubers due to *A. scabies* was reduced from 100 per cent. down to nil. Goss (1937), working in Nebraska, has produced strong evidence that the antagonism of many organisms of the microflora, in addition to saprophytic *Actinomyces*, have the same effect of reducing scabbing, while recently Bald (1947) has given specific instances of antagonism between *Actinomyces* and *Rhizoctonia* (*cf.* page 298).

The form or type of scab produced on tubers is, of course, the result of the interaction of parasite and tuber, each being in turn affected by environmental factors; it is not surprising therefore that the origin of the type of scab produced, under very diverse conditions, has been attributed to whatever factor seemed most important to the worker. In Ireland, for instance, McKay (1949) reports that over a period of six years (1941-1946) some 65 varieties showed predominantly a sunken type of scab at three centres varying in rainfall and the *p*H value of the soil. At one centre, however, this sunken type was almost exclusively replaced in 1944 by the raised type. On Millard and Burr's (1926) view this would be accounted for by the predominance, perhaps temporarily, of *Actinomyces* of the *flavus* group, over the *A. scabies* group. But trials in New York State (Anon, 1935) pointed to the degree of pathogenicity exhibited, by whatever species of *Actinomyces* was concerned, as determining the type of scab produced. Schlumberger (1929) on the other hand, in Germany, emphasises the importance of the potato variety attacked and suggests that different varieties are susceptible to different strains of the organism. De Bruyn (1939, 1947) confirms the view that different types of scab on the same tuber, in Holland, are due to different strains of *Actinomyces* but expresses the opinion that the incidence and type of scab may be so modified, by the variety of potato grown, as to influence the form of scab produced on the succeeding varieties grown on the same soil. Thus she states that the variety Bintze following Bintze was severely affected with shallow pustules, but when Bintze followed Eigenheimer nearly half the crop was healthy and when Bintze followed Jubel one-quarter remained healthy while the rest showed a deep-pitted form of scab. Noll (1939) and Stevenson *et al.* (1942) attribute the form of scab to the degree of resistance shown by the tuber and this, in their opinion, is affected by the place of origin as well as by the variety; on this view, however, one would expect to find different types of scab on the seed planted and on the progeny. Finally, Schaal (1940) disputes the importance of both strain of *Actinomyces* and potato variety and ascribes the form of scab solely to the soil reaction in which the organism was grown. Two of his isolates from soils of *p*H 5·4 and 6·8 respectively were indistinguishable when grown on media of *p*H 7·0 but, when inoculated into potato tubers, the form from the more acid soil produced shallow-blister type scabs whereas the other induced a deep and severe type of sunken scab.

CONTROL.—(a) *Varietal Resistance.*—The attempts that have been made to correlate certain tuber characteristics with varietal resistance to Common Scab infection have met with varying success. Lutman (1919) considered that resistance was determined by the thickness of the tuber-skin; colour being of no importance. He expressed the opinion that the resistance shown by all " russet " varieties was primarily due to possessing close-textured lenticels, partly buried under the tuber-skin and filled with small, corky, cells. Rieman and Hougas (1948) claim that, of recent selections by plant breeders, the " Russet Sebago " strain is significantly more Scab-resistant than the parent " Sebago " variety without, however, associating this added power of resistance with lenticel structure. Darling (1937) modified Lutman's views by correlating resistance only with tubers showing an early development of a thick, corky, skin carrying small lenticels; while McKay (1949) failed to discover any marked resistance to infection in the russeted variety Field-Marshal. Field trials in many countries have disclosed a wide range of susceptibility in commercial varieties which can be put to practical use, not only in reducing loss on contaminated land, but in the selection of possible parents for scab-resisting breeding work. Clark *et al.* (1936) in one such test in U.S.A. with 34 varieties, found five (all German varieties) with less than 1 per cent. of the Scab present on the control susceptible variety (Green Mountain). Working in Germany, Schlumberger (1937, 1938) expressed some disappointment that only four varieties reached the very low standard of commercial requirements for resistance, *i.e.* the production of 60 per cent. of saleable tubers in heavily contaminated land, yet some of these varieties have provided the basis for successful breeding work in U.S.A. In Great Britain observations over many years have confirmed the opinion that the varieties Golden Wonder and Arran Pilot usually show marked resistance; fair resistance is given by King Edward VII, Doon Star, Royal Kidney and Vanguard. On the other hand the varieties Up-to-Date and Majestic are liable to severe scabbing, while Arran Crest and Epicure are perhaps the most susceptible of all our popular varieties. McKay (1949) has tested some 65 varieties in heavily contaminated land, over a period of six seasons, at four Irish centres. He states that all varieties were badly scabbed at one or other centre, Up-to-Date and Majestic proving to be most susceptible. The variety Di Vernon was the least susceptible but still showed scabbing on 89 per cent. by weight of tubers; 20 per cent. being severely scabbed (*i.e.* scabs covered at least one-quarter of the tuber surface). Next in order of resistance were Ulster Chieftain, Edzel Blue, and Doon Early (with up to 30 per cent. showing severe scabbing). Golden Wonder usually maintained its reputation for scab-freedom but, at one centre, not only did the whole crop show the disease but 86 per cent. of the tubers were severely scabbed.

Breeding work, directed towards the production of good, commercial varieties resistant to Common Scab, may be said to have begun in U.S.A. with an expression of optimism by Darling (1937), based on the fact that semi-resistance is exhibited by some of the progeny from susceptible parents; suggesting that resistance is determined by complex factors, units of which might be present in different susceptible varieties. Reddick (1939) emphasised the importance of utilising the known resistance of certain South American species of *Solanum* in any breeding work aimed at developing commercial varieties with marked resistance to Scab infection. Thus he regarded *S. commersonii*, *S. chacoense*, *S. caldasii* var. *glabrescens*, and *S. jamesii* as likely to prove immune from attack, and worthy of consideration for breeding purposes despite their commercially objectionable characteristics of late maturity, long stolons and, in the first named species, the bitter flavour. Krantz and Eide (1948) state that while crosses between parents exhibiting equal resistance give progenies differing widely in the percentage of resistant seedlings, there is still a general correlation between the resistance of parent clones and of their hybrid progeny. Crosses between parents derived from the same resistant ancestor gave progenies which were slightly less resistant than those from parents whose resistance was derived from different ancestors. These authors consider that consistent values for grading resistance (on a numerical index basis) can be obtained by growing four plants per clone in a heavily contaminated plot for annual observation. In a summary of official breeding work for scab-resistance in U.S.A. (Tolaas *et al.*, 1947) Krantz states that the sources of resistance used were all German varieties such as Jubel, Hindenburg and Arnica. These were crossed either with each other or other higher-yielding commercial varieties. Thus the Scab-resistant variety Menominee is said to be a selection from a cross between the resistant German variety "Richter's Jubel" and the low-yielding, but resistant, U.S.D.A. Seedling 44537 (Wheeler *et al.*, 1944). The result, according to Stevenson (1947) has been to produce a number of commercial varieties already establishing a reputation for a high degree of Scab resistance; among them being Sebago (resistant both to Common Scab and to Blight), Russet Rural (Scab) and Menominee (Scab). Although breeding work for scab-resistance is not so far advanced in this country as in U.S.A., it is stated in the Report of the Scottish Society for Research in Plant Breeding (1948) that Black and Haigh have made several selections which have proved highly resistant to Common Scab and Powdery Scab.

(b) *Rotation of Crops.*—Although *Actinomyces* is so widespread in soils it is probable that many (and perhaps most) species are incapable of attacking potatoes; in fact, Nattrass (1937) states *A. scabies* is not a normal inhabitant of soils in Cyprus. Cases of infection of tubers planted in virgin soil have been slight attacks only and indicate either a greatly reduced power of infection of the normal soil *Actinomyces* or the use of imperfectly sterilised seed-tubers. Occasionally there is no increase with continuous cropping (McKay, 1949), but in the great majority of cases it is certain that scab does rapidly increase with successive crops of potatoes taken at short intervals of time (Lutman, 1923), and as rapidly decreases as these intervals increase. Under Nebraska conditions, Goss and Afanasiev (1938) even claim a marked reduction in Scab with a two-year rotation and say the incidence is negligible after a four-year interval between potatoes. Infection of tubers after much longer intervals, however, is still possible, and Lutman, Livingstone and Schmidt (1936) record some 30 per cent. infection after a lapse of nineteen years between two potato crops. These American workers do not give the system of rotation practised during this period of nineteen years, but that this is important has been shown by several investigators, *e.g.* Sanford (1933) in Canada, Berkner (1933) in Germany and Goss (1934) in U.S.A. In Northern Ireland, Cairns, Greeves and Muskett (1936) found that the normal seven-year rotation (potatoes, oats, four years ley, oats) either eliminated the scab-producing *Actinomyces* or very considerably reduced their pathogenicity. The disease is usually prominent in this country in the first two years after grassland has been ploughed up, and one severe case occurred in N. Wales in a newly broken up sixty-year-old pasture; field evidence also suggests that Scab may be worse immediately after a crop of lucerne (Moore, 1943, 1948). Miss de Bruyn (1947) makes the interesting suggestion that, since the incidence and type of Scab varies with the varieties *previously* grown (*cf.* page 386), control should be attempted by a judicious rotation of varieties, among which the resistant variety Jubel should be included. There is some evidence also, as might be expected from our knowledge of the conditions influencing infection (*cf.* page 381) that some control of the disease is afforded by early planting (Samson and Ellis, 1943)—at least in Indiana, although Noll (1940), in Germany, expresses an exactly opposite opinion.

(c) *Soil Treatment.*—The kind of artificial fertilisers used may also have a marked effect on the amount of scab developing. Acid manures, such as sulphate of ammonia, reduce the scabbing while liming may seriously increase it. The effect of lime is usually attributed to the increase in *p*H of the treated soil. This was confirmed in work carried out in Rhode Island, U.S.A. (Anon, 1945), for when Gypsum—which does not change the *p*H of the soil—was used, it had far less effect than limestone in increasing the incidence of Scab although it was applied in sufficient quantity to give double the amount of calcium oxide given to the limestone-treated control plots.

Millard (1923), however, found that lime had no effect on the amount of scab in neutral soils, but aggravated the disease in acid soils unless these were rich in humus. He considered the presence of adequate amounts of humus to be more important than the degree of acidity of the soil, and showed that excellent control of Common Scab was obtained by ploughing in some such green crop as rye, mustard or vetches. Under garden conditions the same result was achieved by digging in lawn mowings, spent hops, etc., during or just prior to planting, at the rate of ten to twenty tons per acre, or one-half to one barrow-load per four square yards. The beneficial effect of humus was at first explained as indicating a preference on the part of *Actinomyces scabies* for decaying vegetable matter so that potato tubers remained unaffected (the "Preferential Food" theory). Later, however, it was shown by Millard and Taylor (1927) that saprophytic species of *Actinomyces* increased rapidly in the humus and that the competition for the available food resulted in the starvation of the weaker parasitic species. They believed that the competition of other micro-organisms in the soil (including bacteria) would exercise a similar effect, and this view is supported by Sanford's results in Canada (1926, 1946). Soil treatment with various chemicals to kill the organism has been tested in many countries (Bolley, 1891 ; Arthur, 1897). Of these the greatest success has been obtained by the use of inorganic and organic compounds of mercury and formalin (Appendix I, page 649) and flowers of sulphur. Their efficiency appears to vary widely in different types of soil (*cf.* Généreux, 1943, 1944) and the results obtained are not commensurate with the expense, though the application of flowers of sulphur, in the drills, at the rate of one ounce per square yard, may be worth trying on a garden scale. In some cases where the separate application of humus and sulphur has failed to eradicate scab, their combined action has proved successful. Finally, the risk of recontamination of the soil with forms of *Actinomyces* pathogenic to potatoes, should not be overlooked. Morse (1912), for instance, showed that recontamination could easily result from the use of manure from farm stock fed on diseased tubers, for the organism was proved capable of surviving passage through the digestive tract of horses and cattle. Infected tubers and peelings should not be thrown on the manure pit, and should be boiled before being fed to stock.

(c) *Seed Treatment.*—It is of little use to try to eliminate *Actinomyces scabies* as a menace from the soil if infected seed-tubers are used for planting. The serious effects of planting such seed on land free from scab organisms are shown in the following table, giving results obtained in Northern Ireland by Cairns, Greeves and Muskett (1936). It will be seen that even when tubers of the varieties Kerr's Pink and Majestic were so slightly affected as to be regarded by the farmer as "clean" they produced, respectively, 29 per cent. and 87·8 per cent. (by weight) of scabbed crop. The use of obviously affected seed gave the very high infection of 52·8 per cent. and 94·0 per cent., yet most, if not all, of this infection was due to the seed, since when disinfected the incidence of scab was very greatly reduced.

The table also shows the degree of efficiency to be expected by the use of a mercuric chloride "steep," and this result was confirmed by these workers during trials extending over several years. Continental and American workers have tested many substances of which mercuric chloride (0·1 per cent.) and formaldehyde (1 in 240) have proved most efficient. By adding a small quantity of hydrochloric acid to the mercuric chloride, Cunningham (1925) in New Zealand was able to reduce the time of "steeping" from one and a half or two hours to five minutes. Similarly, by holding the temperature

TABLE XVIII

Effect on the Produce of Planting Infected Seed-Tubers

Variety	Type of Seed planted	Per cent. of Scabbed Tubers by Weight	
		No Treatment	0·1 per cent. Mercuric Chloride 90 minutes Steep
Kerr's Pink	"Clean"	29·0	0·0
Kerr's Pink . . .	Scabbed	52·8	5·8
Majestic	"Clean"	87·8	2·3
Majestic . . .	Scabbed	94·0	15·0

of the formalin and mercuric chloride at 48° C. to 50° C. (118·4° F. to 122° F.) Melhus (1918) gained a similar reduction in time of steeping. The same effect was obtained by Cairns, Greeves and Muskett with mercuric chloride by one-half to one minute steeps in solutions of higher concentration. Efficient control of scab was obtained in this way by the use of concentrations up to 2 per cent. Equally efficient control was obtained by the use of proprietary organo-mercury compounds, but with these, as with the strongest solutions of the chloride, some temporary check to plant growth occurred. In trials on Rhode Island, U.S.A., this retardation of growth particularly affected "early" varieties when seed was dipped in either organo-mercury liquids or yellow oxide of mercury (Anon, 1944). Nevertheless, Beese (1944) recommends the use of organo-mercury dips as being effective in controlling Scab at a concentration of 2 to 4 oz. in 10 gallons of water. The same worker found zinc oxide (5 lb. in 10 gallons of water) to be equally effective under conditions in which untreated seed produced 10 per cent. of commercially significant Scab;

equivalent to 1 ton per acre. Bald (1947) working in the same area of South Australia as Beese, found both organo-mercury and zinc oxide to be effective seed treatments for use with cut setts ; the zinc oxide being used the day before planting at a concentration of 5 oz. in 1 gallon of water. He states that zinc oxide is to be preferred to the organo-mercury liquids since, unlike the latter, it reduced premature rotting of the tuber and stimulated suberisation of the cut surface. It should not be forgotten that all these substances are poisonous to animals and man.

The methods for controlling Common Scab may be summarised as follows :—

(1) Increase the rotation between successive potato crops to six or seven years.

(2) Use acid fertilisers and avoid the use of lime.

(3) After a severe attack of scab, take a green crop of rye, mustard or vetches and plough in.

(4) Take precautions to prevent the manure from becoming contaminated.

(5) Use only "clean" tubers as seed and, if in doubt, disinfect the tubers with mercuric chloride (Appendix I, page 649).

BACTERIA

(1) BLACKLEG (*Bacterium phytophthorum* (Appel) Burgwitz)

GENERAL APPEARANCE.—From the middle of June onwards single plants affected with Blackleg can often be found in the potato crop. They are conspicuous by the prematurely yellowed appearance of the foliage and their stunted, rigid habit. The leaf-stalks are more or less erect, with small leaflets which either roll along the midrib or fail to expand fully. The rigid "staring" appearance may persist, but if the progress of the disease within the tissues is rapid the whole plant may become limp and wilted. The haulm becomes inky-black for a few inches above and below ground-level and it is to this condition that the descriptive name of "Blackleg" is applied. The blackened stem rapidly softens and rots so that it easily comes away in the hand if an attempt is made to lift the plant (Fig. 71). This blackened zone does not indicate the extent to which the disease has affected the tissues, for if the stem is cut across at a little higher level a brown diseased spot will be seen in each of the three main vascular bundles, whilst a vertical cut along the stem will sometimes show that the brown stain has extended even into the tip of the shoot. Similarly, many of the roots are killed and the disease can be traced along the stolons and into the heel end of some of the young tubers. An early infection of the whole of the haulms will effectively prevent any tuber formation, but it frequently happens that the disease appears later in the season or that not all the haulms are affected ; in either case there is a real danger of infection passing into the developing tubers. The disease spreads rapidly within the tuber from the heel end and reduces the tissues to a brown or black wet mass which rots away. Many affected tubers thus disappear before lifting and thoroughly contaminate the surrounding soil with the disease-producing organism ; others can be recognised, even externally, by the soft discoloured heel end, but many slightly affected tubers may escape detection during storage.

SYMPTOMS WITH WHICH BLACKLEG MAY BE CONFUSED.—Any disease in which a parasite affects the region of the conducting strands (vascular bundles) of the stems will produce somewhat similar symptoms, *e.g.* Black Scurf (page 295), Black Dot (page 331), Stalk Break (page 305) and Verticillium Wilt (page 314). Mechanical injury to a haulm may also have much the same effect, whilst the virus disease Leaf Roll, particularly in certain varieties, may easily be confused with Blackleg. All these maladies, however, are distinguished with certainty from Blackleg by the absence of the blackened, rotted haulm around ground-level. More care is required to distinguish the tuber symptoms from those found in Blight (page 334), Pink Rot (page 351) and, most of all, Watery Wound Rot (page 354).

DISTRIBUTION.—A wet-rot of the tuber which may have been the disease now known as Blackleg was first described in Germany by Reinke and Berthold in 1879, and a somewhat similar malady was studied in France by Prillieux and Delacroix in 1890, but it was not until 1899 that Frank, in Germany, connected the tuber-rot with the blackening of the haulm and so definitely identified the occurrence of the disease in Europe.

In U.S.A. Morse (1917) obtained the first record in the State of Maine in 1906, and in the same year Johnson (1907) saw what he believed to be the same disease in Ireland. It now appears to have as wide a distribution as the potato itself. There is little evidence of the incidence of Blackleg being influenced by type of soil, although Rohde (1935) states that soils deficient in potash favour the disease in Germany, whilst Klapp, Morgenweck and Spenneman (1936) have found it more prevalent in the same country in elevated situations where the soil is lacking in phosphates. In the British Isles Blackleg is more common in wet soils and in seasons with a high spring rainfall. Usually about 1 per cent. of a crop may be affected; 2 per cent. would be regarded as severe, but occasionally a figure as high as 50 per cent. of the crop has been recorded (Moore, 1943). In the State of Maine, U.S.A., 80 per cent. of all crops examined in 1935 showed 12 per cent. of Blackleg, and in one case 65 per cent. was affected. Almost as severe infections have been found in Minnesota by Leach (1931), while according to Magee (1932), the disease causes heavy losses in the coastal areas of New South Wales. It has been recorded to a greater or less extent in practically every country where the potato is grown.

CAUSE OF BLACKLEG.—The causal organism is a small, cylindrical, bacterium measuring from 1·3 to 1·8 μ in length and 0·9 μ in width (1 μ equals $\frac{1}{1000}$ mm.). It is capable of independent movement by means of delicate hair-like protoplasmic threads (flagella) arranged around the long axis, and has no resting stage in the form of spores. Normally the organism requires an ample supply of atmospheric oxygen (*i.e.* it is aerobic) but is able to adapt itself to a deficiency or absence of oxygen (*i.e.* it is a "facultative" anaerobe). The optimum temperature for growth is said to be 26° C., with a maximum at 33° C. and minimum of 4° C. (Morse, 1917). The comparative studies of the Blackleg disease by Smith (1911), Pethybridge and Murphy (1911) and by Morse (1917) showed that the causal organisms isolated and named by various workers (i.e. *Bacillus atrosepticus*, van Hall, 1902; *Bacillus phytophthorus*, Appel, 1903; and *Bacillus melanogenes*, Pethybridge and Murphy, 1911) were too closely akin in measurements and cultural characters to justify the retention of separate specific names. Since van Hall's original culture appeared to be lost, and few inoculations had been made with his organism under natural conditions, there was general agreement with Smith's (1920) suggestion that Appel's name of *B. phytophthorus* should be adopted. The Society of American Bacteriologists, however, in the process of a reclassification of bacteria (not widely adopted in this country) grouped all bacterial plant pathogens into a new Family or Tribe named *Erwiniæ*, consisting of the two new Genera *Erwinia*, with flagella arranged around the long axis (peritrichic) and *Phytomonas*, with polar flagella or none (Bergey *et al.*, 1923); the Blackleg organism thus became *Erwinia phytophthora*. Finally, by decision of the Second International Congress for Microbiology held in London in 1936, the name *Bacterium* was applied to all Gram-negative, non-sporing rods, whether motile by means of peritrichic flagella or non-motile; hence the accepted name for the Blackleg organism now becomes *Bacterium phytophthorum* (Appel) Burgwitz. What is of more direct interest to the potato grower is the view expressed by several workers (Harding and Morse, 1909; Morse, 1917; Leach, 1930 and Bonde, 1939) that *Bacterium phytophthorum*, together with other soft-rot bacteria, are all strains of *Bacterium carotovorum* (L. R. Jones) Lehmann and Neumann; an organism commonly responsible for soft-rots of many different crops, *e.g.* carrot, turnip, brassicæ and bulbs, as well as potato. In this country, Dowson (1949) agrees with these American Bacteriologists and would also include the organism *Bacterium aroideæ*) causing the soft-rot of Arum Lily. With this conclusion Rudd Jones (1950) is also in full agreement. In tests with 28 strains of coliform soft-rot bacteria, mostly isolated from rotting potato tubers, he was unable to separate *Bacterium phytophthorum* from *Bacterium caratovorum* either by differences in pathogenicity or fermentation reactions. They are therefore to be regarded as strains of one species, in which he also includes *Bact. aroideæ* on the grounds that the inability of this "species" to produce gas in sugars is not a good character on which to separate it as a distinct species; the three strains, in his view, should therefore be known as *Bact. caratovorum* (Jones) Lehmann and Neumann.

Contrary to the convictions of many careful observers, there is no evidence that *Bacterium phytophthorum* is a normal inhabitant of any kind of soil in this country. Indeed, although the rotting of badly diseased tubers must release vast numbers of the organism into the soil, it is not proved that it can normally survive through the winter. A conclusion against survival was reached in Ireland by Pethybridge (1912), in Maine and Virginia, U.S.A., by Rosenbaum and Ramsey (1918), and in Canada by Murphy (1921), all of whom raised healthy crops from clean seed planted in land which was heavily contaminated with Blackleg in the previous autumn. Morse (1917) stated that ten years' experience in the State of Maine convinced him that the sole means of infection was in the planting of diseased seed-tubers, and that the disease does not persist in the soil through the winter. Ramsey (1919) confirmed this by his failure to recover the organism from contaminated soil whether out of doors or stored in a cellar. He also noted the rapid loss of virulence in artificially infected tubers kept at 0° C. for eleven days. This is strong evidence but not necessarily conclusive. Pethybridge (1913) himself had some slight success in securing infection when soil was artificially contaminated in spring, so that the possibility of survival through a mild winter cannot be excluded. Indeed, Leach (1930, 1931, 1938) has produced strong evidence that the organism can survive the stringent winter soil conditions of Minnesota. In this country McIntosh reports (1941) that in his extensive experience he never found Blackleg in the first years of the "life" of certain commercial varieties which are now heavily infected, *e.g.* Arran Consul, and that on the other hand 3 per cent. of the disease appeared among some 2000 first-year seedlings; in both these cases he claims that soil infection alone will cover the facts. No one, however, has given the necessary proof that slightly diseased, self-planted "volunteer" tubers were not present in the soil as a source of infection for the new variety or seedling; yet this is without doubt the most common way in which the bacterium, protected by the outer layers of the tuber-flesh and skin, survives from one season to another. Pethybridge (1910) lifted apparently sound tubers from a partially diseased crop and sprouted them over winter. From these he planted only those without blemish which would have been accepted by any careful grower as free from disease; yet 94 per cent. developed Blackleg. Other examples could be given, *e.g.* Morse

(1917), in which heavy infection of the crop was traceable to the use of apparently sound, though slightly infected, seed.

There are, however, further possibilities to consider. The modern tendency to equate the Blackleg organism *Bacterium phytophthorum* with the omnivorous soft-rotting species *Bacterium carotovorum* raises wide questions of host-range, methods of over-wintering, and even the possibility of strains (producing perfectly well-known white-rots of tubers) mutating into forms possessing the enzymes required to produce the characteristic melanin of " Blackleg." All these possibilities are reinforced by Leach's (1926) discovery that the Blackleg organism can exist in a state of symbiosis in the inner tissues of the " seed-corn " maggot *Delia* (*Hylemyia*) *cilicrura* Rond (*Phorbia fusciceps*) while the same relationship has been established between the bacterium and a closely related species of insect, *Delia* (*Hylemyia*) *trichdactyla* Rond, by Bonde (1930). It is true that neither of these species has been reported on potatoes, apparently, in this country, but the American work raises problems of great interest—if only because the crop may at any time cease to be immune from attack. The symbiosis (*cf.* page 278) is between the insect and a group of not very closely related forms of bacteria, including the non-pathogenic, water, sewage and soil forms, *Pseudomonas fluorescens* Mig and *Ps. nonliquefaciens* Bergey *et al.*; the Blackleg organism is usually, but not invariably, present. The normal development of *Delia cilicrura* in Britain in the absence of *Bact. phytophthorum* is not, therefore, a valid criticism of this part of the American work. Leach (1927) appears to attach no importance to the planting of infected seed-setts as the initial cause of Blackleg in spring; nor does he emphasise the importance of his evidence that the organism normally over-winters in most American cultivated soils. What *is* stressed is the difficulty experienced by the bacterium in penetrating through the unbroken tuber-skin or through healed wounds; hence the importance of the constant nibbling by a maggot fully " charged " with the pathogen. There appears to be no selection of particular potato setts by the insect when depositing the first brood of eggs, but the second lot are said to be most frequently found in diseased, rather than healthy plants, as a result of the attraction of the fly to the rotting stem-bases. It is not suggested, therefore, that late infection of healthy tubers is likely to occur to any extent.

According to Leach (1927) the ability of an infected tuber to prevent a rapid rot of the tissues by the bacterium depends upon the rate at which a corky barrier can be developed by the potato cells, and this in turn is dependent on the presence of reserve starch in the cells. During the winter, therefore, the spread of the disease is mostly along the vascular tissues where cork formation cannot occur, and in spring the organism is only able to pass into the sprout after the tissues have been depleted of starch, and cork formation is consequently inhibited. Although the disease occurs in the region of the vascular tissue it is the soft-walled parenchyma which is mostly affected; in the intercellular spaces of these tissues the bacteria multiply and, by dissolving the pectin of the middle lamellæ, the parenchyma is reduced to a wet, slimy, mass. Not only does the organism induce enzymic changes in the attacked parenchyma so that the diseased tissue turns inky-black, but the effect is seen far in advance of the bacterium in the staining of the lignified cells of the wood to a deep brown colour. This is seen mostly in the tuber but may extend even into the apex of the plant and into the leaf-petioles. Normally thin-walled cells of the phlœm and cortex of the stem (haulm) also become converted into lignified scleroids, and protein crystals of cubical form occur in great abundance even in aerial organs where, in normal plants they are absent (Artschwager, 1920). The development of the disease is also related to external conditions, being more evident usually in early planted crops which may grow slowly at first in cold wet soil. In the wet backward spring of 1913 Pethybridge (1914) records that plots of 120 tubers of a common origin were planted in March, April, May and June, with the result that 45, 24, 8 and 4 plants respectively developed Blackleg. McIntosh (1941) planted halved tubers in dry and wet localities respectively and found that, while the former gave no disease symptoms, the latter developed 13 per cent. of Blackleg. The same author records that tubers, detached from infected plants, rarely show symptoms themselves if planted in good soil; a fact which is readily understandable if the soil is reasonably dry and warm. Not only do cool, wet, soil conditions induce a rapid development of the bacterium in the mother-tuber but lead directly to the invasion of the new tubers along the stolons. Normally this is the way in which the progeny of a diseased plant become infected, but Shapovalov and Edson (1921) showed that under irrigation (and thus presumably still more so under water-logged conditions) the mother-tuber is quickly disorganised, the bacteria liberated into the soil, and tuber infection occurs wherever the skin is abrased or, as Smith (1920) claims, through any lenticel. There is no proof that the disease ever reaches an adjoining plant. Thus the soil conditions have a direct influence on the proportion of new tubers contracting the disease from the mother-tuber, and not less on the rate of development of the disease in the newly attacked progeny; with reasonably dry, warm, soil conditions the development of the disease may be arrested, and diseased tubers lifted with no external signs of infection. Certainly many slightly affected tubers will be stored with the healthy crop, and Pethybridge and Murphy (1911) showed that great losses in the pit or clamp might occur as a result of the spread of the disease under these conditions, the infected tubers gradually rotting and releasing swarms of bacteria which then attack the sound tubers.

CONTROL.—Experience shows that the disease does not tend to increase in land successively cropped with potatoes, so that the possibility of direct infection from the soil may be ignored for practical purposes of control. Disinfection of seed-tubers by either the formalin or mercuric chloride methods (see Appendix I, page 649) is practised in some countries, notably U.S.A., but it is probably uneconomic in the British Isles unless there is also reason to suspect the presence of other tuber-borne diseases. In any case the proper place to start the control of Blackleg is the crop destined for seed. Every plant suspected of Blackleg should be dug out and care taken to remove all tubers and to destroy them. There is no evidence that the disease spreads in the field to neighbouring healthy plants, so that efficient roguing as suggested would soon eliminate the disease in all probability from potato crops in this country. Little or no work has been done to discover whether resistant varieties exist. In Scotland the varieties Arran Pilot, Arran Consul, British Queen, Eclipse, Kerr's Pink, Arran Comrade and Great Scot are most frequently affected, though only to a small extent (McIntosh, 1941). This

FIG. 71.—Blackleg-affected haulm and tuber (page 393)

FIG. 72.—Internal Rust Spot, Canker form (page 425)

FIG. 73.—Internal Rust Spot, Normal form

FIG. 74.—Frost Necrosis, internal symptoms in tuber (page 423)

does not support Stapp's (1935, 1937) belief that a correlation exists between susceptibility to Blackleg and the development of a yellow pigment in the tuber flesh. Tubers with any kind of discoloration of the skin at the heel end should not be clamped or planted. Proper ventilation of the clamp and care to prevent water-logging will help to minimise the spread of Blackleg if slightly infected tubers are accidentally included. Cut seed frequently develops a much higher percentage of Blackleg than does whole seed, especially when the soil is naturally wet. To prevent outbreaks such as this, the cutting knife should be disinfected in dilute mercuric chloride after each cut and the seed should not be planted in wet soil.

(2) Other Bacterial Rots of the Potato

(*a*) Storage Rots.—Apart from the Blackleg organism there is no evidence that any bacterium is capable of causing a disease of the potato crop in the field in this country. It is not surprising, however, that a storage organ such as the potato tuber, which is frequently transported or stored when portions of the flesh are already moribund or killed by some fungal parasite—and which is at best only protected by an easily damaged corky skin—should so often be reduced to a wet, putrid, mass by many different forms of bacteria. Most frequently this rotting appears to be due to *Bacterium carotovorum*, and this organism was isolated by Bennett (1946), and by Dowson and Jones (Moore, 1948) from material collected in a widespread rotting of tubers which occurred in this country during the autumn of 1945. In early stages the rotting tissue is delimited by a brownish band but soon the whole tuber is involved and is converted into a wet, pasty-white, mass. Bennett considered that the tubers were contaminated in the soil or soon after lifting, and that the rotting was definitely related to the degree of immaturity of the tuber; the more immature being the most liable to bacterial attack. Lack of air, a high temperature and saturated atmosphere were also contributory factors when sacks of tubers were stacked high in badly ventilated lofts and railway trucks. Among other organisms which have been found capable of causing a rot of stored tubers are *Bacterium aroideæ* (Townsend) Stapp, and *Pseudomonas marginalis* (N. A. Brown) Stapp. The former is a wound parasite responsible for the rotting of Arum Lilies and, in the potato, produces much the same type of rots as *Bacterium carotovorum*. The latter organism is the cause of "Marginal Leaf-Spot" of lettuce which it invades *via* the leaf stomata; in the potato tuber this organism induces a soft, wet, yellowish-green rotting of the parenchyma, and Dowson (1949) suggests that similar rots of tubers recorded in U.S.A. by Bonde (1939) may also be due to this organism. *Pseudomonas fluorescens* (Flügge) Migula, or a closely related form, is stated by Garrard (1945) to cause a hard, black rot of tubers, in Canada, in which the blackened pith tissues develop cavities which radiate towards the skin. This record is interesting, not only because it implicates a normal soil saprophyte, but because the rotting occurs at very low temperatures; being most rapid at 5° C. (41° F.) and only slight at 18° C. (64·4° F.). Equally interesting is Dowson's (1943) statement that *Bacillus polymyxa* (Prazmouski) Migula, a common soil organism, is capable of reducing potatoes to a yellow sticky mass in clamps where relatively high temperatures and a saturated atmosphere occur; rotting is rapid at 27° C. (80·6° F.). As Dowson remarks, this is one of the very few authentic instances of a *spore-forming* bacterium causing disease in plants. Curiously enough, although the organism is normally Gram-negative, Dowson (1949) found the reaction to be positive when the organism was isolated from the rotting tissue of potato, or in litmus milk. In all these storage rots, with the apparent exception of the rotting in Canadian clamps due to *Pseudomonas fluorescens*, bacterial activity is increased under conditions of bad ventilation which induces a high temperature and saturated atmosphere. Care should be taken to clamp only sound, dry, tubers; the clamp being effectively protected against the entrance of drainage or rain-water, and provided with adequate ventilation both at the top and base (Samuel, 1946).

(*b*) BACTERIAL DISEASES NOT KNOWN TO OCCUR IN BRITAIN.—(i) Bacterial Ring-Rot due to *Corynebacterium sepedonicum* (Spiekermann and Kotthof) Skaptason and Burkholder, was first described in Germany and, in recent years, has assumed serious proportions in Canada and the United States; it has not been recorded in this country. Affected plants appear normal during most of the growing season, but later the haulm tends to flag and the leaves wilt from the base of the plant upwards, during which they turn yellow and the leaf-margins curl inwards and show " scorch." The late wilting and the absence of blackening of the haulm—externally and internally—distinguish the disease from " Black-leg." Microscopic examination will show the presence of the bacteria blocking the wood vessels. The diseased tuber can be identified by the creamy-yellow or light-brown, crumbly rot, which develops in the tissue immediately surrounding the vascular strands ; this usually leads to the formation of a ring of disorganised tissue, or even a gap, between the cortex and the pith of the tuber. The only known method of infection is by the planting of slightly diseased " seed."

(ii) Bacterial " Brown-Rot " or " Ring " Disease is caused by *Pseudomonas* (*Xanthomonas*) *solanacearum* (E. F. Smith) Dowson ; an organism which attacks not only potato but many other members of the Solanaceæ, as well as plants of other families in tropical and sub-tropical countries (Dowson, 1949). As in the previous disease the wood cells are blocked with the bacterium, and the interruption in the supply of water to the leaves results in a complete collapse of the foliage. Internally, the disease is characterised by a browning of the vascular bundles from which a little pressure will cause the bacteria to exude in the form of drops ; these two features distinguishing " Brown-Rot " from " Ring-Rot." Similarly, the characteristic brown ring in the affected tuber is due to the invasion of the vascular tissue by the organism which, later, attacks the surrounding parenchyma and produces large cavities filled with the bacterial ooze. According to Dowson, affected tubers in Kenya appear quite normal both on the outside and when cut open, but if gently squeezed, cream-like drops of sticky liquid full of bacteria exude from the severed vascular bundles. The organism occurs in the soil and infection can take place through wounds on roots or stems, or *via* the stomata, the potato tuber is apparently invaded normally along the stolon. In Britain both potato tubers and tomatoes have frequently shown symptoms very similar to " Brown-Rot " but *Pseudomonas solanacearum* has never been isolated from such plants, and there is therefore, no evidence that the disease occurs in this country (Moore, 1943).

CHAPTER XXV

SUMMARY OF DISEASES AND CONDITIONS OF UNCERTAIN ORIGIN

(1) PIT ROT, PROBABLY DUE TO GAS ACCUMULATION IN STORAGE

GENERAL APPEARANCE.—The malady occurs only in pitted (clamped) tubers and does not develop after removal from the clamp. Affected tubers show circular dark depressions on the surface varying from one-eighth of an inch to one inch in diameter. They are scattered over the surface or may be slightly concentrated towards the rose end (Fig. 69). The circular outline is most characteristic and is only modified when two or more coalesce. In such cases the outline of the whole tuber may appear to have flattened or concave sides, this being specially obvious in round tuber varieties. When freshly removed from the clamp the surface of a tuber may show only dark circular areas which sink inwards to form depressions upon drying. When thoroughly dry the affected spots appear even firmer to the touch than the surrounding healthy tissue. The centre of each depression is usually occupied by a lenticel (breathing pore), although occasionally an "eye" occupies this position. When an affected tuber is boiled in its skin and afterwards peeled, the diseased "cup" with its underlying dead brown tissue comes away intact, so that the tuber flesh shows a series of unstained hollows; the effect on the tuber is therefore quite superficial.

SYMPTOMS WHICH MAY BE CONFUSED WITH PIT ROT.—Apart sometimes from Gangrene (page 328), no fungal or bacterial disease is known to produce symptoms resembling those described above. They are, however, almost identical with the pitting produced by over-treatment with tuber disinfectants, particularly formaldehyde and mercuric chloride (corrosive sublimate).

DISTRIBUTION.—The malady was first noticed in County Mayo, Ireland, in 1909, and has since been reported from a number of other Irish counties and from the south of England. It may be more common than is at present supposed.

CAUSE OF PIT ROT.—The identification of Pit Rot as a distinct malady, as well as the only description of its effects, are due to the work of Pethybridge (1919). Microscopical examination showed the dead tissue to be composed of compressed cells in which the starch grains were intact, but the other contents were converted into a disorganised mass of brown granulated material. In most cases this dead tissue was separated from the living flesh by a layer of cork which thus formed a complete lining to the "pit." Isolations of fungi and bacteria from diseased tissue were made by Pethybridge, but none was found capable of reproducing the symptoms in healthy tubers. Affected tubers were usually concentrated towards the middle of the long potato clamps where, it was supposed, the temperature might be higher than elsewhere; experiments in heating tubers to different temperatures, however, showed that this was not the main or direct cause. Nor was it possible to produce the symptoms by storing tubers *in vacuo* or in carbon dioxide gas, so that lack of efficient aeration was apparently not the primary cause. Pethybridge did, however, succeed in obtaining practically (if not quite) identical symptoms by prolonged treatment with mercuric chloride and ammonia fumes, whilst similar results have frequently been described by workers as due to over-treatment with other disinfectants, *e.g.* formaldehyde. The circular spread of the killing agent from the central lenticel or eye also points to the diffusion of a poison either in the form of a gas or liquid. Pethybridge concludes, therefore, that some such deleterious gas or liquid produced within the clamp is primarily responsible, and suggests the need for a study of the gases given off by tuber-rot producing organisms which might develop under bad conditions of clamping.

CONTROL.—The condition is not infectious and affected tubers produce normal plants, if any, when planted; the new crop of tubers from such plants is likewise healthy. Control begins and ends, therefore, in the proper construction of well-ventilated clamps, in which no tubers should be included which might conceivably rot with the formation of gases capable of reproducing the symptoms of Pit Rot in the remaining healthy tubers.

(2) Black Heart and other Tuber Flesh Discolorations

General Appearance.—The term Black Heart is applied to tubers which, whilst usually normal in external appearance, show a brown or black discoloration in the centre of the flesh. In slightly affected tubers the colour may become intensified after exposure to the air; badly affected tubers may also develop cavities in the blackened tissue. The malady is well known in U.S.A., where it causes heavy losses in storage and during transit in badly ventilated, overheated, railway trucks. In this country it appears to be rare, the two best authenticated cases being in Scotch seed of Arran Chief in 1920-1921 (Ministry of Agriculture, *Fungus Diseases of Crops*, 1920-1921) and two instances reported in Kent in 1931 (Salmon and Ware, 1931). Black rots, however, frequently develop in clamps and sometimes these cannot be traced to any pathogenic agent; it may therefore be more common than is at present suspected. Apart from this, some consideration must be given to Black Heart because of its possible relation to other tuber discolorations, such as the blackening observed in certain varieties after boiling and the Dutch storage disease known as Blue Spotting.

Symptoms with which Black Heart may be confused.—There is little risk of confusing this disease with pathogenic maladies except possibly Blackleg (page 393) and Pink Rot (page 351), the absence of any sign of a wet rot being usually sufficient to exclude Watery Wound Rot (page 354). Blackleg can at once be distinguished by the regularity with which it develops from the heel end of the tuber and spreads along the vascular strands (a heel end origin, however, is also characteristic of the Dutch Blue Spotting disease, but the discoloration occurs in streaks with no relation to the vascular strands). Pink Rot almost invariably originates at a wound, shows a well-marked series of colour changes after the tuber is cut, and the diseased portion has a "rubbery" consistency not found in Black Heart. There is no sharp distinction between Black Heart and Hollow Heart (page 415), and diagnosis of the former must depend upon the extent of the discoloration and on evidence that any cavity found has been produced by the rotting or shrinking of an already blackened tissue. Boyd

(1951), contrasting the symptoms of Black Heart with the internal blackening due to bruising, states that while the former usually develops first in the central medulla of the tuber and the affected part is frequently delimited by a cork cambium, in the blackening due to bruising the discoloration invariably begins around the vascular tissues (*i.e.* in a ring just below the skin) and no attempt at cell division has been observed.

Causes of Tuber Flesh Discoloration

(a) *Heat.*—Black Heart, as defined above, was first recognised in U.S.A. in tubers stored for long rail distances in trucks liable to overheating by stove-fires, and Bartholomew (1913, 1915) was able to induce the symptoms artificially by exposing tubers to a temperature of 38° C. to 45° C. (100·4° F. to 113° F.), this work being confirmed by Stewart and Mix (1917) and by MacLeod (1928). A direct effect by heat when the temperature of storage exceeds 100·4° F. is claimed by Davis (1926) at Los Angeles, and this is supported by Dastur (1931) in India. This latter author states that the symptoms appear in storage during the summer when the temperature in February and March may reach 115° F. in a dry atmosphere, this contrasting with the high humidity and moderate temperatures of the monsoon. He states that affected tubers show a black discoloration which may spread until the whole tuber is involved ; the affected portion is reduced to a pulp and the tuber emits an offensive odour, while drops of fluid exude from the skin. Very similar symptoms were found in England in the winter of 1918 when many cases were reported of the collapse of potato clamps. In one such case Paine and Haenseler (1920) recorded a temperature within the clamp of 140° F. They isolated the Blackleg organism from tubers and considered that the rotting was primarily due to this disease. The Ministry of Agriculture (1921), however, whilst agreeing that the Blackleg and other organisms accelerated the rot, were of the opinion that it was initiated by faulty clamping coupled with the inclusion of many diseased and " green " tubers which led to unusual heating. Much the same view is expressed by Kotila (1923) in cases of rotting in clamps in Michigan. Singh and Mathur (1938) believe, from their work in India, that stored tubers are most susceptible to

Black Heart midway through the dormancy period, for such tubers showed 20·2 per cent. Black Heart after forty-eight hours at 104° F., whereas with tubers in early stages of dormancy the same result was only obtained with a temperature of 118° F.; large tubers are said to be more susceptible than small ones, and still more so than actively growing small tubers.

(b) *Carbon Dioxide/Oxygen Relation.*—Although high temperatures can directly produce Black Heart, the work of Stewart and Mix (1917) showed that similar symptoms (sometimes with surface discoloration in addition) were induced at any temperature down to 32° F. so long as the air space surrounding the tubers was also restricted; the time required for symptoms to appear increasing with the lower temperature employed, *i.e.* 10-12 days at 70° F. and 23-40 days at 40° F. These results pointed to abnormal respiration as a possible cause, since at high temperatures the excessive respiration might be expected to upset the normal interchange of carbon dioxide and oxygen, whilst at low temperatures in a confined space oxygen would ultimately be used up and replaced by a high carbon dioxide concentration. This was proved experimentally by Stewart and Mix to be the case, and by absorbing the carbon dioxide as fast as it was produced they established the fact that the symptoms were due, not to the accumulation of this gas but to deficiency of oxygen supply. The work of Bennett and Bartholomew (1922, 1924) confirmed these observations in all respects. They also added the facts that whilst symptoms did not appear at low temperatures until almost all the oxygen was depleted, at the higher storage temperatures an increasing amount of oxygen remained at the time of the development of symptoms. They conclude that the temperature/time/oxygen relationship to Black Heart is a fairly strict one and state that at temperatures where Black Heart precedes oxygen exhaustion the blackening is restricted to the inner tissues, whilst it may occur at any part of the tuber after oxygen exhaustion. Kidd and West (1923) in this country produced Black Heart symptoms in tubers exposed for four weeks to a temperature of 60° F. to 68° F. in atmospheres containing from 0 to 1·5 per cent. oxygen and from 0 to 6 per cent. carbon dioxide, whereas they failed under similar conditions in atmospheres containing from 2·5 to

5·0 per cent. oxygen and 0 to 3 per cent. carbon dioxide. The physiological changes occurring in the tuber during the artificial production of Black Heart were studied by Davis (1926). He produced the symptoms at a temperature of 45° C. (113° F.) in an atmosphere free from carbon dioxide and with an abundant supply of oxygen, and found that during the sixteen hours of the experiment the internal atmosphere of the tuber accumulated over 50 per cent. of carbon dioxide and that oxygen was rapidly depleted until less than 4 per cent. remained. This was followed by increasing permeability of the cells, particularly in the centre of the tuber, the death of the tissue and the development of colour.

(c) *Potash Deficiency and/or Injury caused by Rough Handling*.—Botjes (1927) described what appears to be a related if not identical malady in Holland under the name of "Blue Spotting," later referred to by other Dutch workers as "Black Spotting." The blue patches originate at the heel end, and in severe cases most of the flesh may be streaked with bluish-black or grey areas. During storage the symptoms were sometimes associated with brown and necrotic areas in the tubers. Affected tubers were low in potash content and occurred in soils deficient in this element, the disease being largely controlled by the application of potash up to 8 cwt. per acre. Botjes's work was confirmed by Hulson (1936), who quotes Maschhaupt, in 1934, as proving the low potassium oxide content of affected tubers, and Cools as controlling the disease by the application of 5 cwt. of 40 per cent. potash salts per acre, untreated soil giving 75 per cent. of "Blue Spotted" tubers.

Botjes, however, did not regard potash deficiency as the primary cause since "Blue Spotting" was artificially produced by violently shaking tubers grown on normal soils, although even in this experiment the effect of shaking was more pronounced in tubers from potash-deficient soils; soft-fleshed varieties were said to be more liable to suffer from "Blue Spotting" than harder kinds. The effect of potash is to produce hard strong-walled tissue and to facilitate the production of starch. A deficiency in this element, therefore, induces the formation of weak-walled tissues poor in starch and easily injured by rough handling, such injuries being, according to Botjes, the immediate cause of the development of the blue symptoms. The same inferences were drawn by Miss de Bruyn (1929) who continued the investigations in Holland, and demonstrated the connection also between the occurrence of symptoms and low tuber specific gravity (usually indicating a low starch content). She, however, attached much importance to a correlation she found between " Blue Spotting " and the occurrence of necrotic areas below the skin, and on the edge of the outer phloem of the tuber, these areas having similar anatomical features to " Spraing " (page 427). McIntosh (1935) is of the opinion that bruising, particularly internal bruises, due to rough handling of tubers, may be the direct cause of much of the internal blackening of tuber flesh sometimes found in consignments of potatoes ; heat, frost and even age are, however, also known to produce similar symptoms. In his experiments 80 per cent. of tubers dropped from a height of 3 feet on to a wooden floor showed surface cracks, and from 20 to 40 per cent. developed blackened internal areas after six weeks' storage, these being most pronounced in uncracked tubers which, it is believed, sustained the most severe internal bruising. Boyd (1951) agrees that bruising may be a direct cause of internal blackening of the tuber flesh and relates this reaction to bruising with the degree of flaccidity of the tissues. Although, as might be expected, susceptibility to bruising increased with the degree of maturation of the tuber, Boyd found no great difference in the susceptibility of different varieties. Salmon and Ware (1931) reported the occurrence in two crops in Kent of a blackening of the tuber flesh usually seen only after boiling ; in both cases it was associated with potash deficiency in the soil and with subsequent rough handling of the tubers. It is not without interest to note that, in an ever-increasing number of cases of plant diseases, a discoloration of the storage tissue is associated with a deficiency of some one chemical element, *e.g.* Black Heart of sugar-beet and Brown Heart (Raan) of swedes, which are attributed to boron deficiency, and Marsh Spot of peas due to manganese deficiency.

(d) *Enzymic Activity.*—It is probable that these discolorations, whatever their immediate cause, are all chemical in origin and are accelerated (*i.e.* catalysed) by the action of enzymes present in the potato cells, these enzymes acting upon easily oxidisable substances with the formation of pigmented end-products. The potato, in common with many other plants, contains such a substance in the aromatic compound called catechol (or other compounds with a similar di-hydroxyl grouping in the ortho position), and this slowly undergoes oxidation in the presence of air with the formation of a peroxide. This autoxidation is, however, greatly speeded up by the action of an enzyme, also present in the tuber, and known as oxygenase. The peroxide so produced is acted upon by yet another enzyme, peroxidase, with the formation of nascent oxygen ; this active form of oxygen facilitates still further oxidation of catechol and similar compounds and results in the production of dark pigmented ortho-quinones. The three substances (*a*) catechol, (*b*) oxygenase and (*c*) peroxidase, together form an enzyme system in the tuber and are collectively known as oxydase. It is due to the occurrence of oxydase in many plant tissues (*e.g.* apple, pear and potato) that a brown or even black colour develops when the cut, crushed or otherwise injured tissues are exposed to air, and this no doubt affords a partial explanation of the association of the injuries caused by rough handling with the Dutch " Blue Spotting " disease.

In the potato the tendency of the flesh to discolour is increased by the presence of another enzyme system consisting of the enzyme tyrosinase and an easily oxidised amino-acid called tyrosin. Tyrosinase has many affinities with oxygenase and is able to catalyse the oxidation of the tyrosin to form carbon dioxide, ammonia and a reddish orthoquinone (similar to the end-product of oxidase reactions). The orthoquinone continues to autoxidise and the colour gradually darkens to inky-black (melanin). Similar if not identical enzymes occur in certain " toadstools " and insects, and it is probable that the production of black discolorations in potatoes affected by such diseases as Blackleg and Pink Rot is accentuated by an enzyme of the nature of tyrosinase, possibly secreted by the causal organisms. Apart from organic enzymes, many inorganic catalysts are known which intensify the production of melanin in plant tissues, and this is the basis of Bechhold and Erbe's " copper-strip " method of diagnosing virus diseases in potato tubers (page 443). For this specific purpose the method is unreliable, but the great variability in colour development shown by different varieties, and by different tubers within the one variety, indicates an equal diversity in the enzyme systems in the tissues.

The rate at which discoloration occurs depends upon the temperature (inasmuch as this controls the activity of enzymes) and on the concentration of the oxidisable substrate (*e.g.* catechol and tyrosin). As the temperature increases there is a parallel increase in enzyme activity so that between 0° C. and 10° C. the rate of oxidation may be doubled or trebled. The activity is still greater at higher temperatures up to 35° C. to 45° C., after which destruction of the enzyme itself begins and is complete at temperatures in the neighbourhood of 60° C. It is not surprising, therefore, that Black Heart in potatoes develops most rapidly at the optimum temperatures (35° C. to 45° C.) for enzyme activity. The occurrence of the malady at low temperatures in oxygen-free air is less easy to understand, but is explained by Bartholomew (1915) as due to the increase in the oxidisable substrate (tyrosin) consequent upon the death of the tissues by asphyxiation.

BLACKENING ON BOILING.—There is a similarity between the Black Heart developing in storage and the blackening seen in the tubers of some varieties after boiling. One apparent difficulty, of course, lies in the fact that enzymes are destroyed by boiling, and there are other problems which must also await the result of research before the nature of pre- and post-boiling discolorations are properly understood. It may, however, be pointed out that the enzyme tyrosinase merely initiates the reactions leading to the final production of melanin, whilst oxygenase similarly only accelerates the oxidation of catechol; in both cases the reaction continues without the aid of the enzyme. Merkenschlager (1929) explained the extensive occurrence of blackening, after boiling, in the 1928 potato crop in Germany as being due to an abnormally large development of tyrosin in the tubers, so that there was an almost immediate development of melanin by the action of the enzyme tyrosinase as the temperature was raised in cooking. If this view is accepted, it would account for seasonal complaints involving varieties reputed to be "good boilers." Robinson (1941), on the other hand, disputes the importance of melanin since this substance is stable in acid solutions at *p*H 3·0, under which conditions the tuber discoloration disappears. She is of the opinion that blackening of potato tissues on boiling is associated with a high tuber-content of ferrous iron which is probably hydrolysed to the hydroxide on boiling, and thereafter is gradually oxidised to the black ferric oxide as air reaches the tissues. The close relationship between pre- and post-boiling blackening of tubers is indicated by Cowie (1941) and by Wallace and Wain (1943). The former examined samples from forty fertiliser experiments and found post-boiling blackening to occur only in tubers grown on potash deficient soils with a relatively high nitrogen content. Under these conditions, the amino-acids increase partly at the expense of the protein and this may result in an abnormal distribution of iron in the plant and a high concentration in the tuber. Wallace and Wain conclude from the results of their trials that typical blackening on cooking may arise from (1) a deficiency of potash accentuated by high nitrogen content of the soil, and (2) a deficiency of phosphate; a non-typical discoloration may also result from calcium deficiency. They point out that, if blackening is the direct result of an accumulation of iron, this may occur in different ways in the cases of potash and phosphate deficiencies. With potash starvation there is no evidence that the intake of iron by the plant is increased, but it is known that iron tends to become immobilised in the plant by excessive oxidation and accumulates especially in the nodes. With phosphate deficiency, however, there may be an increased absorption of iron and increased mobility within the plant, since phosphate acts as a precipitant of iron. These two effects of phosphate deficiency may therefore be expected to result in a high total iron content of the tissues. Since iron is more readily soluble in soils with increasing acidity, and acid soils provide conditions where both phosphate and calcium are likely to be deficient, these facts should be taken into account when acid soils are being ploughed for potatoes. The work of McIntosh (1928), Lauder and Robertson (1931) and Smith and Robertson (1933), showing that groups of varieties can be segregated according to the rate at which the tuber flesh becomes discoloured when suitable oxidisable substances are added, may be regarded as a measure of enzyme activity, and may have some bearing on the well-known fact that certain varieties become discoloured on cooking whilst others do not. They include, for instance, the varieties King George and Majestic amongst the kinds which are rapidly discoloured in the oxygenase and tyrosinase test (page 66), and these varieties are also liable to discolour on boiling. On the other hand, they found the reaction slight in King Edward, and this variety enjoys a reputation for retaining its colour even after several "steamings." Salaman (1926) also states that the variety King Edward is deficient in catechol and suggests this as a reason for its good boiling properties. Recent work has suggested that storage conditions may directly affect the liability of tubers to blacken on boiling. Thus Wager (1947) found that late-lifted tubers stored at low temperatures (46·4° F.) showed an increased liability as storage proceeded; any effect of higher temperature was indirect in stimulating the production of pigments only in the presence of other, unknown, factors. Tottingham *et al.* (1947), after a nine-years study of tuber-blackening at Wisconsin concluded that climatic factors in some way exerted an effect on the tendency to blacken; that potash alone among soil minerals was important in reducing blackening, and that the trouble could be prevented by exposing tubers for three or four days to a temperature of 100° F. Rieman *et al.* (1944) also implicate climatic factors, which are left undefined, as being principally concerned in influencing the formation of substances which darken the tuber on boiling. The conditions of storage also affect the rate at which these blackening substances develop but, in the authors' view, the *tendency* to respond to these stimulating factors by the production of blackening substances is inherited; the tendency to give white flesh on boiling being dominant to the tendency to produce a grey flesh. This grey or black producing pigment has been stated by Lewis and Doty (1947) to have a colourless, fluorescent precursor, containing a carbohydrate and a nitrogenous group (an amino-acid or a peptide) but neither tyrosine nor tryptophane.

CONTROL OF BLACK HEART.—Although it appears that discolorations in tuber flesh may arise from several different causes, a few principles, consistently applied, should eliminate the trouble in many varieties and reduce the liability even in those kinds particularly susceptible to discolorations. The risk of growing the potato crop on soil deficient in potash or phosphate has been illustrated and can easily be guarded against. Diseased and "greened" tubers should not be clamped and the clamp should not be covered finally until the tubers are dry. Care is needed to see that the clamp is nowhere more than 4 feet high so that air can reach all the tubers; above all, efficient ventilation must be provided. Although not strictly a matter of control, it is worth remembering that tubers affected with Black Heart should not be used as seed. According to MacLeod (1929), the germination, vigour and yield of a crop grown from affected tubers were in each case proportional to the degree of freedom from symptoms in the seed used.

(3) Hollow Heart, Cracking, Second Growth and Glassiness due to Unfavourable or Irregular Growth Conditions

(a) *Hollow Heart.*—This is characterised by the development of an irregular cavity in the centre of the tuber; the flesh immediately bordering the cavity may be brown or black but the discoloration does not extend into the surrounding tissue. In some cases the cavity may be invaded by saprophytic fungi, with the production of a more or less flocculent mycelium. Large tubers are most affected and therefore the trouble may be looked for in varieties such as Gladstone, Majestic, Arran Banner and Great Scot, which produce large tubers in rich soil. The condition is due to resumed growth following a check, and is therefore to be expected when heavy rains follow a dry early growing period. It is the cause of serious loss in the Middle West of U.S.A., where it is said to be most prevalent in large tubers from widely spaced plants producing only one or two stems each. The use of complete fertilisers and planting of large setts close together in the row are suggested as the best method of control (Werner, 1927; Moore and Wheeler, 1928).

(b) *Growth Cracks.*—This closely related condition was fully described by Powell-Jones and Moore (1935, 1936) in Yorkshire material. The variety Red King was severely affected by extensive cracking, the fissures often radiating from a common centre, but occasionally a single furrow girdled the tuber. A secondary effect was the development of a wet rot in 15 per cent. of the cracked tubers in storage. These authors state that the condition was especially severe in the variety King Edward following sulphuric acid spraying against Blight (Appendix I, (page 647). Cracking is reported as serious also in Nebraska (Peltier *et al.*, 1932) and in Maine (Bonde, 1935), whilst it is reported from Ireland by Murphy (1936). All these workers agree that, as in the case of Hollow Heart, with which it is often associated, this condition is the result of renewed growth following a check. Murphy also states that it is aggravated by boron deficiency in the soil, and by the presence of certain virus diseases. According to the same author, cracking may also occur during or after lifting, when it is due to over-turgidity of the tissues, a condition likely to happen, for instance, when frost kills the foliage but allows root action to continue. The condition was reproduced experimentally by storing freshly dug tubers in moist sand at 0° C. to 2° C. for six weeks, when cracking first appeared in a tuber dropped 2½ feet on to a wooden floor, and later on developed spontaneously in others when they had lost from 4·2 per cent. to 7 per cent. of their water. The association of cracking with injuries produced by dropping the tubers had been pointed out by Peltier *et al.* (1932), whilst Macmillan (1931) found that when naturally over-turgid tubers lost 6 per cent. in weight they ceased to crack. It should not be overlooked that cracking of tubers may also be due to some pathogenic agency, e.g. *Actinomyces scabies* (page 375), *Corynebacterium sepedonicum* (page 402), or the Tuber-Rot Eelworm (page 236).

(c) *Second Growth.*—As the name implies, this condition also is one of renewed growth of already mature tubers and is believed to be induced by warm wet autumn weather, following on a dry period. It may take the form of a prolongation of the major axis so as to produce an unusually elongated tuber, or of protrusions from an eye (gemmation), or the newly formed secondary tubers may be separated from the primary one by a length of stolon (chain tuberisation, Fig. 22). Murphy (1936) regards these forms as indicating a progressive decrease in the capacity for growth of the primary tuber, for in the case of prolongation of the axis the whole rose end proliferates, in gemmation the whole of an eye, and in chain-tuberisation only a single bud from an eye. McIntosh (1927) and Murphy (1936) have listed varieties showing each form of second growth. Amongst them may be noted Arran Pilot, British Queen, King George, Puritan, Catriona, and occasionally

FIG. 75.—Frost Necrosis affecting vascular tissue of tuber (page 423).

FIG. 76.—Frost Necrosis; external symptons on tuber (page 423).

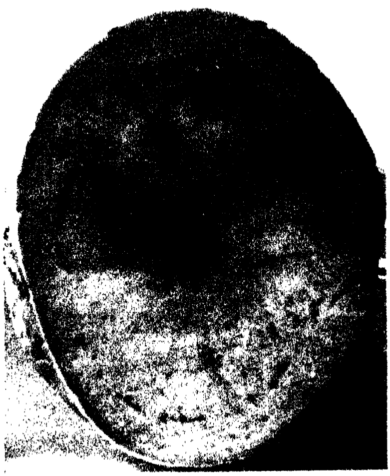

FIG. 77.—Net Necrosis of tuber (page 428).

FIG. 78.—Jelly-End Rot (page 417).

Golden Wonder, as showing axis prolongation ; gemmation is seen in British Queen, King George and Majestic, and chain-tuberisation in Up-to-Date and Rhoderick Dhu, amongst British varieties.

Little work seems to have been done on the value of secondarily produced tubers for planting as seed, although there is a prejudice against their use. According to Whitehead (1935) this is only justified on the grounds that the detaching of the tubers exposes wounds which induce rots during storage for, in his trials, there was no significant difference in yield from planting setts of equal weight from primary and secondary tubers. It should be remembered, however, in considering these results that the trial was carried out with tubers from the 1933 crop in North Wales. This season was remarkably dry, the foliage was not cut down by Blight, and the variety (Kerr's Pink) continued to grow after the heavy October rains. It is probable, therefore, that second growth of the tubers was the result of new assimilation by the leaves. It may well be that different results would be obtained in cases where the new growth was the result of depletion of food from the primary tubers after the death of the foliage.

(d) *Glassiness* or *Jelly-end Rot.*—This condition, often associated with second growth, was first described from Victoria, Australia, by Penman (1929). When tubers showing second growth by prolongation of the axis, or by gemmation, were cut a high proportion showed a translucent area darker than the normal flesh. This area occurred almost always at the heel end but sometimes extended through most of the tissue. The condition was attributed to the resumed growth of the tuber after a severe drought in which the foliage had been killed ; all such growth, therefore, must be at the expense of the starch in the already mature tuber. Murphy (1936) reports the occurrence of the malady in Ireland and states that the stem end of the affected tuber shows a progressive soft rot, in advance of which the flesh is yellow, glassy and devoid of starch. The rot eats away a large part of the original tuber and then stops and is sloughed off as though cut away by a knife. According to this writer, the tuber first loses a considerable amount of water (and sometimes also carbohydrates and nitrogen) as a result of the drought. This terminates the dormancy of the tuber and sets up renewed growth at the rose end, with a consequent evacuation of the food reserves of the original tuber and rotting of the stem end. (Fig. 78.)

(e) *Premature Tuber Formation and "Little Potato."*—Our present knowledge of this condition which, in some seasons may cause serious "misses" to occur, has been summarised by Moore (1943). The immediate cause of the "miss" is the failure of the seed-tuber to produce the normal green shoots above ground but, instead, forms clusters of tiny new tubers around the sprouts, either singly or in short chains. The malady is more common in early than in late varieties; in small tubers rather than in large ones, and in tubers of any size which were immature when lifted. Dutch workers (Botjes, 1924; and Wellensiek, 1929) have contributed most of our knowledge of the factors involved in the production of what the Dutch farmer knows as "Blind Tubers" or "Submarines." Both these workers agree that unfavourable soil and storage conditions are mainly responsible, but whereas Oortwyn Botjes attaches great importance to the degree of atmospheric humidity, Wellensiek considers that this requires no special attention so long as tubers are stored under optimum temperature and light conditions. "Little Potato" has been shown to be due partly to the *repeated* removal of sprouts rendered necessary when tubers are stored for a long period under rather warm conditions, *e.g.* between 9° C. (48·2° F.) and 13° C. (55·4° F.)—though not usually at temperatures below 5° C. (41° F.). This, in itself, will not induce the premature tuber formation unless the tubers are afterwards planted in soil at a temperature below 10° C. (50° F.); both factors are apparently necessary for the symptoms to occur. Moore (1943) quotes Kohler (1937) as having reached the same conclusions on comparing the incidence of premature tuber formation in Germany with the temperatures prevailing between November and May over a period of fifteen years. It was prevalent only when an exceptionally mild winter was followed by a return to cold conditions in April and May. It did not occur after a mild winter followed by a warm April to May period, and cold conditions at planting time failed to give rise to it after a cold winter. Sprouting tubers in the light is a sure way of preventing the trouble or, if this is not possible, the tubers should be stored under cool conditions with all the light available; too early planting should be avoided in a cold, backward spring. However, it is not certain that all possible causes have been studied, for Small (1934) has described premature tuber formation as severe in Jersey in one instance after applying a heavy dressing of naphthalene salts to the soil immediately before planting a field with sprouted tubers of International Kidney.

(4) Malnutrition Diseases

Although the potato plant responds in vigour and yield to correct manuring, it is only in extreme cases of malnutrition that the converse effect is so great as to justify the term "disease" being applied to it. A very excessive nitrogenous manuring, for example, may result in luxuriant foliage and no tuber formation at all; but, however unsatisfactory this result may be to the commercial grower, the plant must at least be described as healthy. On the other hand, the stunted growth and yellowish green foliage of potatoes grown on poor, thin or sandy soils deficient in nitrogen, clearly show the inability of the plant to make headway against unsuitable soil conditions; it is obviously in ill-health.

It should be remembered that deficiency of an element implies a shortage of that element within the plant and not necessarily a shortage in the soil. A chlorosis (pallor) of foliage may be caused by an actual deficiency of iron in the soil, or by the iron present being inactivated or immobilised by excess of calcium (lime). Magnesium deficiency in the soil is reported from the eastern states of U.S.A. (Brown *et al.*, 1933) as causing severe loss in potatoes by chlorosis followed by the death of the foliage, but in this case the symptoms are intensified by excess of nitrogenous manuring and mitigated by applying magnesium compounds containing calcium, *e.g.* magnesium limestone. The problem of manuring is, in fact, much the same as in the feeding of stock, being essentially one of proper balancing of food rations. In manuring, the factors to be taken into account are (1) the present composition of the soil and (2) the particular requirements of the crop to be grown, the successful balancing of manures depending upon the accuracy with which these two factors are known.

In this country a number of diseases have been attributed to a deficiency of a chemical element in the soil. Of these, potash deficiency is by far the more serious and well substantiated. *Potash deficiency* has been described from many European countries as well as from Great Britain, where it appears to comprise many, if not all, the symptoms known as "Rust." The foliage becomes stippled with minute necrotic spots so that a "bronzed" appearance results; the surface of the leaves may be raised into corrugations and the leaflet tips and margins curl downwards. Marginal necrosis of the leaflets usually follows, so that the whole plant appears to be suffering from drought or scorch; root and tuber development is poor. Large *et al.* (1946) state that in Devon the condition is usually more severe in the middle of the field; is more prevalent on dry or sandy soils and under semi-drought conditions, although it is also common in wet weather. The "scorch" was more severe on soils of high or average *p*H, and high or normal lime content, and on crops of moderate growth. Early crops showed more scorch in mid-August than did the later sorts; Arran Banner being more affected than Majestic. These authors say that a top dressing of extra muriate of potash, hoed in before earthing the crop, strikingly reduced scorch and gave an increase in yield of 0·6 to 6 tons per acre. Beaumont and Large (1944) have pointed out that scorch or "rust" due to potash deficiency is often responsible for the apparent failure of spraying against Blight to result in an increase in yield; in two centres in Devon the foliage dried up owing to the effect of potash deficiency and reduced the yield which, of course, could not be remedied by spraying against the Blight which subsequently attacked the crop. An effect upon the tuber flesh which is attributed to potash deficiency has been described under "Black Heart" (page 409). A deficiency of *boron* in the soil is the cause of the upward curling of the leaflet margins characteristic of some potato varieties, according to O'Brien and Dennis (1936). The authors conclude, on not very satisfactory evidence, that the varieties Gladstone, Catriona and Di Vernon exhibit this non-parasitic of Leaf Roll. The symptoms vary from a slight marginal upward curling of the leaflets to a definite roll almost indistinguishable from true Leaf Roll (page 437); they are most conspicuous in dry seasons and largely disappear after heavy rain. O'Brien and Dennis also state the condition is characteristic of certain Scottish soils and control was effected by an application of boron in the form of commercial borax at the rate of from 10 to 20 lb. per acre. Potatoes are, however, very susceptible to the toxic effects of excess borax, and this substance should be spread on the soil as evenly as possible before the drills are drawn; for convenience of application it should be mixed with artificial manures which do not react with the boron, or with dry sand. Potatoes on Fen soils and the black sands of the Midland counties of England are said by Davies (1939) to show a general pallor in the tips of the foliage accompanied by a brown spotting between the veins. This is attributed to a deficiency of *manganese* in the soil and should therefore be controllable by the application of manganese sulphate as in similar disorders of other crops. Wallace and Hewitt (1948) found that potatoes were frequently planted, during the late war, under much too acid conditions. At *p*H 4·0 most of the plants failed to grow; those which produced foliage showing typical symptoms of *calcium* deficiency, *i.e.* leaves near the tips of shoots remained small, upward rolled and somewhat chlorotic; they tended to fall off. Tubers remained firm but failed to grow when planted. Much the same effects were found to occur in Scotland by Hunter and M'Gregor (1945) though brown, dead patches also appeared on the foliage, mostly marginally and at the leaf-tip, but later between the veins also. Here, again, a deficiency of calcium was diagnosed, aggravated by *magnesium* shortage, and considerable improvement was effected by the application of ground, shell, lime. With still greater magnesium deficiency, these authors describe severe symptoms including stunting, extensive dead patches between the veins and bright yellow margins; upward rolling of leaves only occurred in early stages. Analysis showed that the foliage contained only one-seventh the normal amount of magnesium. The treatment suggested was to apply dolomitic limestone (thus supplying both calcium and magnesium) or to alternate farmyard manure with dressings of other suitable salts of magnesium.

(5) Necrotic Diseases of the Tuber

The occasional occurrence of rusty-brown spots in the flesh of otherwise sound tubers has long been a source of annoyance to the housewife when preparing potatoes for cooking. Until recent years all such cases were regarded as of similar though obscure origin. They have been studied under a variety of names, *e.g.* " Eisenfleckigkeit," " Trockenfäule " and " Buntwerden " (Frank, 1898) ; " Maladie des Tache en Couronne " (Swellengrebel, 1906) ; " Internal Disease " and " Sprain " (Horne, 1910). The last named, however, distinguished the " Spot " or blotchy type of symptom in " Internal Disease " from the streaks seen in tubers affected with " Sprain " ; while Paine (1918, 1923) described two types of spotting, one of which he equated with " Sprain " and " Internal Rust Spot " and the other with the " Net-Necrosis " of Schultz and Folsom (1921) in America. Quanjer (1926) and Atanasoff (1926*a*) also regarded " Sprain " and " Internal Rust Spot " as synonymous and as distinct from " Net-Necrosis." Burr (1928, 1929) grouped " Sprain " and " Internal Rust Spot " together as necroses primarily of the parenchyma, and distinguished " Net-Necrosis " or " Phlœm-Necrosis " from a necrosis of the xylem which he named " Corky Bacteriosis " ; described as forming complete circles around the primary xylem bundles and partial rings, involving several xylem groups, when secondary thickening had occurred. The more recent recognition that certain types of tuber necrosis are associated with specific virus infection, still further emphasises the need for a re-examination of the ætiology and histology of these various tuber necroses. So far as this country is concerned, the official view stated by Moore (1934) is usually accepted, and the name " Spraing " (the Scottish term for " Sprain ") is confined to necroses in which the brown, necrotic tissue takes the form of arcs of circles (thus probably assuming synonymity with Quanjer's (1931) " Concentric Necrosis "), while the name " Internal Rust Spot " is retained for necroses not forming arcs or circles but, rather, having an indefinite shape. There are, however, difficulties in attempting to summarise the present position of knowledge owing to uncertainty of the precise symptoms covered by names in use in different countries.

(a) *Necroses regarded as due to Soil Deficiencies.*—A malady in South Africa and known as Internal Brown Fleck is attributed to a deficiency of phosphorus in the soil, associated with high acidity. The symptoms are stated by Van der Plank (1936) to comprise rusty-brown lesions up to 1 cm. in diameter and occurring both in the pith and the outer cortical tissue of the tuber. They are arranged irregularly but sometimes there is a tendency to a radial pattern. There are no external tuber symptoms and none in the foliage. Control is effected by the application of lime as early as possible before planting, followed by the use of superphosphate. The value of the lime appears to lie in the neutralising of the acidity of the soil and is not now regarded as evidence of the disease being caused by calcium deficiency. Nevertheless, a somewhat similar disorder in Holland is stated by Van Schreven (1934) to be directly due to calcium shortage. This malady is known as medullary necrosis and is characterised by the occurrence of rusty spots in the pith region of the tuber, and is sometimes accompanied by a diffused brown discoloration of the rest of the flesh. The condition is said to occur in poor sandy sour soils in Holland and has been noted as severe in the variety King Edward.

(b) *Necroses due to Unsuitable Temperatures or to some Unknown Unsuitability of the Soil*—(i) *Drought and Heat Necrosis*.—Murphy (1936) described a disease of the tuber as occurring in Ireland in very hot dry light soils, particularly when the plants are dying from drought and the crop is left undug. Under such conditions the vascular tissue of the tuber may be killed as well as the surrounding soft flesh, the colour passing through golden-yellow to brown. It is most marked in the outer phloem of the vascular ring and the cortex, especially at the two opposite ends of the tuber. The malady may also take the form of groups of yellow or brown dead cells, varying from specks to half an inch in diameter, occurring in any part of the flesh and sometimes developing in storage.

(ii) *Frost Necrosis*.—Much of the descriptive work of tuber necrosis due to low temperatures was done before the full significance of other factors was understood, and it is possible that some of the tuber damage ascribed to frost is really due to other causes. There is no doubt, however, that tubers kept at low temperatures for long periods are liable to severe damage owing to the death of portions of the tissue. Very briefly, the sequence of events is as follows: vegetable sap contains salts in solution and hence only freezes when the temperature falls below the freezing point (32° F.) of water. Moreover, the temperature required to freeze the sap is directly proportional to the concentration of salts in solution and, by one of the compensations of nature, the sap becomes increasingly concentrated as the temperature falls by the loss of water into the intercellular spaces and the conversion of starch into sugar. A sharp severe frost which results in a rapid fall in temperature prevents such adjustments on the part of the cell and is therefore more dangerous than even a lower temperature only gradually acquired. Applying these facts to the potato in storage, the first effect on the tuber as the temperature approaches 32° F. is the conversion of starch to sugar—the potato becomes "sweetened." With continued fall in temperature water passes into the intercellular spaces where it may freeze without permanent damage to the tuber. The point at which the actual tissue freezes is said by Wright and Harvey (1921) to be from 29·66° F. to 28·13° F., but this does not occur until still lower temperatures have first been reached and the tissues have again warmed slightly up to the freezing point. Any rough handling, however, of these superchilled tubers at once causes the tissues to freeze solid. These writers also found that the freezing point of tubers becomes steadily higher during the winter and that early varieties freeze at a higher temperature than late sorts. It follows, therefore, that the danger from frost is higher with these early maturing varieties and increases as spring approaches. The cells are killed at the low temperatures but the damage only becomes visible as the tuber warms and so allows enzyme action to discolour the tissue. According to Wright and Taylor (1921) the effect of maintaining tubers of seven varieties at 28° F. for forty-eight hours was negligible, whereas after seventy hours 31 per cent. showed necrosis. In this country, Wallace (1935) found necrosis in tubers kept at 26·6° F. for twelve hours and at 21·2° F. for only three hours, the symptoms including a shrinkage of the tissues and browning or blackening just below the tuber skin and sometimes reaching the surface. He found that even when the exposure was not sufficient to produce any marked symptoms, either external or internal, the crop produced by such tubers, when used as seed, was 10 per cent. below that of normal tubers ; there was, however, no significant increase in this loss in the case of tubers showing severe injury as a result of exposure to low temperatures. Apart from this loss of value as seed, there is the added danger of increased susceptibility to Dry-Rot (McIntosh, 1944) and of putrefactive bacteria gaining entrance and causing secondary rotting (Figs. 74, 75 and 76).

(c) *Necroses associated with Certain Types of Soil and/or otherwise of Unknown Origin*—(i) *Internal Rust Spot* (usual form).—The modern use of this name is restricted to the type in which groups of cells are killed to form brown spots varying from specks to small, irregular, blotches distributed throughout the tuber flesh (Fig. 73); the spots do not appear to form a connected system as would be the case if the vascular tissue were necessarily involved. According to Burr (1928, 1929) the attacked parenchyma cells become brown, thickened and lignified. An encircling cork cambium develops at an early stage some two or three cells away from the diseased tissue; this corky layer may be from 4 to 10 cells thick in cortical spots but only from 2 to 3 cells thick in the pith. Only the inner-most cells of the cork are suberised and, when this is incomplete, the diseased tissue may extend through the gap to form a "streak." In contrast to this, "Corky Bacteriosis" affects only the xylem, the cork cambium arises in the parenchyma cells immediately abutting on the affected xylem, and the whole corky layer rapidly becomes suberised. The malady occurs in this country mainly in sandy loam soils poor in organic matter, potash and lime, whilst Ghirenko (1932) states that in Russia it is almost completely absent in acid soils (*e.g.* pH $=4{\cdot}3$ to $5{\cdot}8$) and attains its most severe form when the soil is neutral. O'Brien and Dennis (1936) attempted to control the disease by applying borax to the soil but without success. The lesions can be seen when the crop is lifted and do not appear to increase in number or severity with storage. The disease is believed to be non-parasitic but the cause is still unknown; it is not transmitted through the seed-tuber.

(ii) *Internal Rust Spot* (canker form).—This disease is more localised in distribution than the type just described and has been the subject of considerable studies in Yorkshire. It is still uncertain whether this is a very intense form of ordinary Internal Rust Spot or an entirely distinct disease. According to Burr (1931) the malady is not restricted to such sandy soils as are poor in lime as well as in organic matter but occurs also when the lime content is normal. At lifting time the spots may be scarcely visible but develop later in storage and may result in a breakdown of the tissue to form cavities, with subsequent rotting (Fig. 72). The disease does not pass from the mother tuber to the newly formed crop and cannot be transmitted by any artificial means from tuber to tuber. It is, however, clearly contracted from the soil, and Paine (1923) and Burr (1931) attribute the cause to soil bacteria. The former writer named the supposed organism *Pseudomonas solaniolens*, but Burr was unable to confirm the pathogenicity of this bacterium and considered the organism he had isolated (*Bacillus rubefaciens*) to be the responsible agent. There is some doubt as to the specific disease under investigation by Paine and Burr respectively, but there is evidence that *Bacillus rubefaciens* is capable of inducing tuber lesions not unlike those of the canker form of Internal Rust Spot. The fact that the disease often occurs on land contaminated with Common Scab (page 375) led Burr to try the effect of ploughing in some winter-green crop such as rye or mustard as a means of control, with, it is said, fair success. In a later paper, Burr and Millard (1938) tabulated the reaction of a number of varieties to the canker form as a result of trials carried out in Yorkshire. The most susceptible varieties are said to be Eclipse, Golden Wonder, Bishop, Kerr's Pink, Great Scot, Gladstone and Arran Cairn, in the order given. Doon Star and Majestic are stated to give saleable crops if sold off early, whilst the most resistant varieties proved to be Arran Consul, Arran Chief and King Edward.

(iii) *Skin Necrosis*.—This name has been given to a tuber disease of unknown origin described by Moore (1943) as occurring from time to time since 1931, when it was first noticed on Royal Kidney tubers grown on various types of soil in south Lincolnshire. Since then it has been seen on a number of varieties in different counties, and has also been observed in tubers from Jersey and in seed-tubers from Ireland. There seems no reason to regard any one type of soil as particularly liable to induce the malady for, in one instance, only one of three fields of the same soil type, and similarly manured, developed Skin Necrosis when planted with seed potatoes of the same origin. Superficially, the symptoms are said by Moore to resemble Blight, but the injury is confined to the skin and a cortical zone not more than ⅛th in. thick, which is brown and dead. The necrotic areas of the skin are dark coloured or black, irregular in shape, often slightly sunken, with an uneven surface and have well defined margins (Fig. 58). The necrosis may occur on any part of the tuber though, in one case, in which extreme drought may have been a factor, the necrosis always began at the " heel " end. At first sight Skin Necrosis might be mistaken for " Sun Scald," but the latter has always been associated with tubers dug in an immature condition and left exposed to a hot sun. Moore remarks that, in a general way, the symptoms recall those described by Atanasoff (1922) as found in tubers of certain varieties affected by " Stipple Streak," *i.e.* virus " Y " (page 461). However, there is no confirmation of Atanasoff's observations and it is likely that the tuber necroses to which he referred were the result of infection with other types of " Mosaic " or " Top Necrotic " viruses, *e.g.* viruses " X," " A," " G " or " F " (*cf.* pages 500, 501, 506 and 538). In any case, tubers with Skin Necrosis sprout normally and give a good crop of sound tubers. Whatever the cause of Skin Necrosis, there is at present no evidence that any pathogen is responsible. Frequently the necrotic areas are quite sterile, though at other times several species of fungi (including *Phoma*, *Fusarium*, and *Cephalosporium*) have been isolated.

(d) *Necroses believed to be of Virus Origin*—(i) *Spraing.*— This disease is often confused with Internal Rust Spot but can be distinguished by the fact that, instead of irregularly shaped spots or blotches, the lesions occur as wavy streaks or as parts of concentric circles; the name indeed is a Scottish dialect word meaning a streak or stripe. These lesions are to be seen at lifting time and do not increase much, if at all, in storage. Although they may occur throughout the tuber flesh some usually reach the surface, at which point there may be external signs of injury; in such cases arcs or rings, which are slightly raised, may be visible on the surface, sometimes completely encircling the tuber. The ring glints in the light with a suggestion of brown or purplish colour shining through the skin. In storage, the skin over the raised ring sometimes cracks (Anon, 1944*a*). Occasionally the ring of dead tissue may completely cut off part of the healthy flesh and this can then be lifted out as a " plug " to form a surface pit in the tuber. Although the malady is said to be less common in this country than Internal Rust Spot severe losses have occasionally been recorded, *e.g.* 75 per cent. of a crop of Arran Pilot in

Cardigan in 1937, and 60 per cent. in Berkshire in Arran Banner in 1941 (Moore, 1943). Spraing appears to be widely distributed on the Continent, and in Holland is known as Concentric Necrosis ; it occurs in light sandy or gravelly soils and is worst in dry seasons. Atanasoff (1926), however, states that in Holland it is found in soils rich in organic matter but is always absent from heavy clays ; he does not consider water shortage to be a determining factor. According to Pethybridge (1912, 1913), Atanasoff (1926) and Quanjer (1926), the disease is not transmitted from mother tuber to the progeny, but there is no doubt that it can be contracted from the soil. Grieve (1934) failed to find any evidence of a bacterial agent and confirmed Atanasoff's statement that it can be transmitted from diseased to healthy tubers by means of *grafts* ; he therefore supports Quanjer (1926) in attributing the disease to a soil-inhabiting virus. No methods of control are known, but Burr and Millard (1938) have given a table of varietal reactions based on trials in Yorkshire. According to this, Arran Cairn, Gladstone and Arran Chief were the most susceptible varieties tried and could not be grown profitably even on land not badly affected with the disease ; the malady is very common in Arran Pilot in Scotland (Dennis and Foister, 1942). (Figs. 79 and 80.)

(ii) *Net Necrosis*.—This disease affects the sugar-conducting tissue (phloem) which forms the inner and outer boundary of the vascular ring of the tuber. Hence, when a tuber is cut across either the long or the short axis, the lesions show as a more or less complete double ring of spots or short streaks (Fig. 77). These streaks are usually more pronounced at the heel end, and since the vascular strands form a loose open network below the tuber skin, the lesions also appear as a network when the heel end is cut obliquely ; it is this appearance which has given the name of Net Necrosis to the disease. The condition was first described in U.S.A. by Schultz and Folsom (1921) in a number of American potato varieties and in the European varieties Beauty of Hebron and Up-to-Date. They suggested a connection between Net Necrosis and the virus disease Leaf Roll (page 437), and reported that affected tubers invariably produced thin wiry sprouts well known under the name of " Spindling Sprout." Gilbert (1927, 1928) advanced good evidence of Net Necrosis being a first-year symptom only of Leaf Roll ; necrotic tubers thus gave rise to Leaf Roll plants but such plants showed no necrosis in their new crop of tubers. Elze and Quanjer (1929) confirmed Gilbert's work with the American variety Green Mountain, but were only able to induce Net Necrosis in European varieties by partially burying Leaf Roll seed-tubers in such a way that the eyes at the rose end grew into rootless shoots whilst those at the heel end formed roots and tuber-bearing stolons; under such conditions the mother tuber was forced to function as a stem and necrosis developed in the primary vascular strands.

In Great Britain, Net Necrosis has only been recognised within recent years, possibly because of confusion with other necrotic disorders of the tuber, *e.g.* Internal Rust Spot (page 425), Spraing (page 427), or even frost necrosis (page 423). McIntosh (1937) reported it as common in Scottish stocks of the variety Golden Wonder and, later (Anon, 1939*a*) the malady was found also to occur in the varieties Arran Consul and Kerr's Pink. In all these varieties it was commonly, though not invariably, associated with current-season ("primary") infection with the virus disease Leaf Roll (page 437), *i.e.* it occurred in 91 out of 724 known cases of primary Leaf Roll infection. In England it has been seen in isolated instances in the varieties Golden Wonder, Arran Victory, Majestic, King Edward and Dunbar Cavalier; in which last variety a stock was said to show 90 per cent. infection (Moore, 1943, 1948). Both in this country and in U.S.A. (List, 1947) doubts have been expressed as to whether the Leaf Roll virus, by itself, can cause Net Necrosis in the tuber, and it has been suggested that these symptoms occur only when Leaf Roll is superimposed upon an already existing infection with virus "A" (page 506), but this theory would appear to ignore the fact that Net Necrosis occurs in varieties such as Up-to-Date, Kerr's Pink and King Edward which are "field immune" from infection with virus "A" (page 588). Prior infection with virus "X" (page 501) is similarly ruled out for, although practically all stocks of Up-to-Date, Kerr's Pink and Green Mountain contain virus "X," the variety King Edward is field immune.

It may be well, for the present, to suspend judgment on the degree to which Net Necrosis is dependent even upon infection with the virus of Leaf Roll, for in America other forms, indistinguishable from the Leaf Roll Net Necrosis, have been attributed either to viruses of the "Yellows" type or to the direct effect of the feeding of the insect responsible for transmitting the virus. Thus Folsom (1946*a*) describes Net Necrosis as occurring in some of the small tubers, strung out "necklace" fashion, on the stolons of the variety Green Mountain infected with "Yellow-Top" (page 469). This is a virus disease which Folsom regards as identical with one or more of a group of such diseases, including "Purple-Top," "Witches' Broom," "Apical Leaf Roll" and "Aster Yellows." List (1947) also attributes a form of Net Necrosis to Aster Yellows; while another form appears to be definitely associated with "Psyllid Yellows" (page 471), which is accepted by Smith (1937) as due to a virus, but is considered by Leach (1940) and Sanford and Grimble (1944) to be a non-virus, systemic disease produced by a toxin injected into the potato foliage by the tomato psyllid, *Paratrioza cockerelli* Sulc, while feeding (*cf.* page 257). It is interesting to note that the symptoms of Aster Yellows on potato (Younkin, 1943*a* and *b*); Yellow Top (Folsom, 1946*a*) and Apical Leaf Roll (Schultz and Bonde, 1929) all include a rolling of the upper foliage closely resembling the primary symptoms of true Leaf Roll; indeed the two last-named diseases can only be separated by the fact that foliage rolling in "Apical Leaf Roll" is confined to the upper leaves in the progeny, however remote, of infected plants (page 469).

Net Necrosis, associated with primary Leaf Roll, is essentially a storage disease which may, or may not, be visible at lifting time but which develops slowly or rapidly according to the temperature at which the tubers are kept during storage. Folsom and Goven (1943) and Folsom (1946*a*) found that storage at constant temperatures of 45° F. to 50° F. led to a considerable increase in the amount of necrosis, whereas at temperatures of 33° F. or 70° F. it was largely inhibited, even when the tubers were later transferred to storage at optimum temperatures for the development of tuber symptoms; under suitable conditions the percentage of tubers affected will continue to increase until, at least, the end of January (Folsom *et al.*, 1940). Not only is Net Necrosis definitely a varietal reaction, but it appears to have no relation to the susceptibility of the variety to contract Leaf Roll. Even those varieties most liable to develop Net Necrosis usually only show it in a proportion of tubers formed on a primary-infected Leaf Roll plant. Thus it was reported in Florida (Anon, 1939*a*) that when a crop of "Spaulding Rose" tubers, containing 37 per cent. Net Necrosis, was separated into necrotic and unaffected samples the latter produced 44·7 per cent Leaf Roll plants and the former 84·2 per cent. Clearly, therefore, many non-necrotic tubers were actually infected with Leaf Roll and, apparently, many necrotic tubers gave rise to normal plants. The ratio of necrotic to symptomless tubers, produced on primary Leaf Roll infected plants, varies also with the season, for the most sysceptible variety, Green Mountain, is reported by Bonde and Simpson (1943) as showing a ratio of 1 in 4·31 in 1941 and 1 in 2·82 in 1942. (Fig. 77.)

(iii) *Pseudo-Net Necrosis*.—This name, which really means "false" Net Necrosis, is a survival of faulty diagnosis, for the symptoms are not very similar to true Net Necrosis. The disease forms brown necrotic spots in the outer pith and inner cortex of the tuber and thus these spots are arranged in obvious association with the vascular strands. Consequently an affected tuber cut either along the long or short axis will display something approaching the double necrotic ring noted in Net Necrosis, but an oblique cut will clearly show the absence of any connected mesh. Quanjer, Thung and Elze (1929) state that symptoms develop in tubers during storage, the incidence being increased by a rise in temperature from 10° C. to 20° C. (30° F. to 68° F.), especially in tubers from sandy soils. The variety President is said to be very susceptible and to show external symptoms in the form of necrotic spots on the skin. These writers agree with Atanasoff (1926) as to the virus origin of the symptoms, since they were able to transmit the malady both by juice inoculation and by means of the aphid *Myzus persicæ*. They do not accept Atanasoff's view, however, that Pseudo-Net Necrosis is a tuber symptom of Aucuba Mosaic, since it could be found in cases where no Aucuba Mosaic occurred in the foliage, and was absent in typical Aucuba Mosaic material received from Murphy in Ireland. These divergent views have been clarified to some extent by the work of Clinch, Loughnane and Murphy (1936) on Aucuba Mosaic (page 449), in which Pseudo-Net Necrosis is definitely ascribed to viruses named "F" and "G," the latter being also responsible for the foliage symptoms known as Aucuba Mosaic.

CHAPTER XXVI

DETERIORATION OR DEGENERATION OF POTATO STOCKS

(1) INTRODUCTION.—Degeneration describes the progressive decline in yield of tubers, both in weight and size, which usually occurs when seed is continuously saved from the preceding crop. It differs from the otherwise similar reduction in crop which results from the planting of obviously diseased tubers, for no amount of care in selecting unblemished, healthy-looking seed will serve to retard degeneration in the stocks over a number of years. Degeneration differs also from purely constitutional maladies, such as "wildings" and "bolters" are supposed to be, in that constitutional disorders are not infectious. The occurrence of degeneration in the absence of any tuber symptoms, together with the recognition that each new variety in turn showed a progressive falling off in yield and had to give way to some still newer product of the plant breeder, led to the belief that degeneration might be due to continuous vegetation propagation. This was considered to weaken the stamina of a variety, and sooner or later to necessitate a return to sexual reproduction, *i.e.* to the use of true seed.

According to Salaman (1921), this theory, in which degeneration is explained on the ground of progressive senility in the vegetatively reproduced stocks, was first advanced by Parmentier (1786) and remained a lively source of controversy up to the years immediately prior to the Great War of 1914-1918. Yet, one only needs to quote such cases of vegetative propagation as the banana, vine, Jerusalem artichoke, many plants in our herbaceous borders and the couch grass of the fields to realise that such continuous propagation from vegetative organs does not necessarily reduce stamina and require rejuvenescence. Further, since all plants of a given potato variety, wherever it may be grown, originated from a single plant derived from a true seed, they must all have undergone the same number of vegetative propagations and, consequently, should all degenerate simultaneously. That this

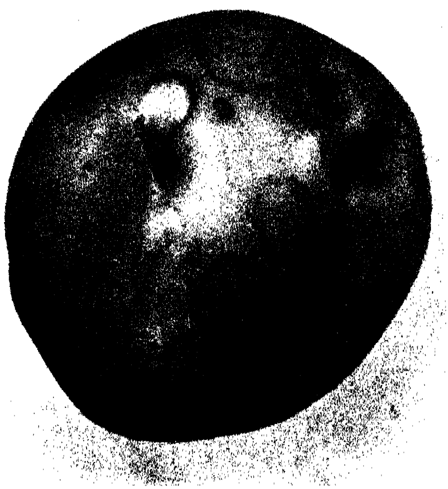

FIG. 79.—Spraing; external symptoms on tuber (page 427).

FIG. 80.—Spraing; internal symptoms in tuber.

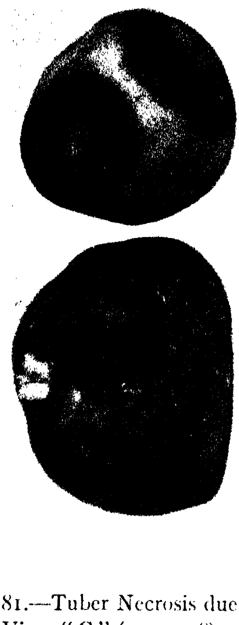

FIG. 81.—Tuber Necrosis due to Virus "C" (page 538).

FIG.—82.—Top Necrosis; experimentally induced by graft (page 538).

is not the case is known to all potato growers, who must frequently have seen degenerate and vigorous stocks of the same variety growing in the same field.

(2) LOCALITY AS A FACTOR IN DEGENERATION.—In all varieties the rate of degeneration is in some way linked up with the locality in which the crop is grown, for a variety will degenerate, or "run out" as it is sometimes called, quickly in some areas whilst remaining vigorous in others, *e.g.* Magnum Bonum is credited with retaining all its original vigour in certain mountainous districts of Scandinavia, whereas it has long since gone out of cultivation in this country. Indeed, it may be assumed that the occurrence of vigorous and degenerate stocks of the same variety in the one field usually indicates that one or other of the crops is of recent introduction. The importance of locality was almost as quickly recognised as the fact of degeneration itself, and Salaman (1949) quotes R. Maxwell as stating in the *Practical Husbandman* for 1751 that the decline in potato yields in Galloway necessitated a renewal of stocks from England and Ireland. Indeed the literature of one hundred and fifty years ago contains references to the need for obtaining seed-tubers from some locality where degeneration did not appear to occur, such as the moss lands of Lancashire, the moors of Yorkshire or the limestone hills of Denbighshire, and the Hebrides of Scotland. Whether the recognition of Scotland as the main source of vigorous stocks of potatoes for planting is rightly attributed to the use of "ware" tubers from Scotland to make up a shortage of seed in Lancashire in the middle of the eighteenth century, or to the more romantic desire of Scottish migrants to bring their own seed potatoes with them when starting life anew in the south of England, is of no particular importance. What *has* proved of the highest importance to potato culture in general, and to Scotland in particular, is that this imported seed cropped much better than the southern seed, and the buying of Scotch seed potatoes became established as "good farm practice."

(3) IMMATURITY OF "SEED" AS A FACTOR IN DEGENERATION.—Not unnaturally, perhaps, this gave rise to a new theory of degeneracy based on the supposed immaturity of Scotch seed. In point of fact the growing season in Scotland, even in the most northerly potato-growing counties, is not

noticeably shorter than in England; nor is the seed raised earlier or in any more immature condition than is customary elsewhere. Yet this view persisted into our own times because of the undoubted fact that immature seed in England usually did give increased vigour to the succeeding crop. When, however, trials were carried out in districts where degeneration of fully matured seed was at a minimum, *e.g.* Craibstone in Aberdeenshire (Profeit and Findlay, 1923) and on the seaboard of Anglesey (Whitehead, 1930*b*), no advantage could be traced to the use of seed raised in an immature condition; whilst Brown and Blackman (1930) found evidence that very immature seed was somewhat *less* valuable than fully matured seed in producing vigorous crops, even in the Midlands and south of England. Degeneracy is, therefore, not necessarily a concomitant of maturity in seed stocks.

(4) VIRUS DISEASES AS A FACTOR IN DEGENERATION—(a) *Infectious Nature of Degeneracy.*—From the earliest recognition of degeneracy in potatoes, it was always associated, apart from loss in cropping power, with the occurrence of curly, wavy or crinkled foliage and with a tendency for the leaf-stalks to become brittle. This "Leaf-Curl," as it was called, was regarded merely as the expression of degeneracy and not as its cause. Even as late as 1916 Hutchinson duly noted the higher percentage of "curled" plants in the degenerate progeny from matured seed as compared with the percentage found in the progeny from immature seed, but the difference in disease incidence was not included as one of the causes of the difference in yields, this still being attributed to differences in maturity as such.

However, proof of the infectious nature of "curl" had already been obtained by the classical researches of the Dutch scientist Quanjer (1913, 1916), although it was not until the end of the Great War of 1914-1918 that his work became generally known. Quanjer distinguished between two forms of "curl." In one form the leaflet margins rolled upward to become spoon-like and this he called "Leaf Roll"; in the other there was no rolling, but the leaf blades became mottled with a pattern of light and dark green areas to which he gave the name "Mosaic," because of its resemblance to the Mosaic disease of tobacco. He was unable to find any parasitic organism constantly associated with either form of "curl," but they could be transmitted to normal plants by grafting, and hence were to be regarded as diseases of the virus type and so related to the cause of tobacco mosaic, a conclusion which has been fully established by all later work. Quanjer proved that natural transmission of these diseases occurred in the field; but it was another Dutch worker, Oortwyn Botjes (1920), who established the fact that "greenfly," or aphides, were the responsible agents of natural transmission of Leaf Roll. This was afterwards confirmed in U.S.A. by Schultz and Folsom (1921), who also proved the complicity of aphides in the field-transmission of "Mosaic."

(b) *Correlation between Virus Disease Incidence and Degeneracy.*—Evidence rapidly accumulated to prove that potato crops suffered both in weight and numbers of tubers with increased infection with virus diseases (*e.g.* Murphy and McKay, 1924), but since a quite similar relation could be found whatever disease occurred in the crop, something more was required to establish virus infection as the sole or main cause of *progressive* degeneracy. The additional proof was furnished by the work of Brown and Blackman (1930) in several centres in England, and by that of Whitehead (1930*a*) in Wales. The former workers could find no evidence of degeneration being influenced by purely physiological factors, such as early lifting or protection from overheating, whereas there was a general relation between the amount of virus disease present in new seed, once-grown and twice-grown seed on the one hand, and the falling-off in cropping power on the other. The latter worker determined the increase in virus infection in two varieties, year by year, over a period of six years. By comparative yield trials with such once, twice, thrice, etc., up to six times grown seed he found that, *in the absence of other diseases*, the yields from the different plots only differed significantly when there was a significantly different percentage of virus diseases present, the correlation between the two being of a very high order (*i.e.* 0·83 with Kerr's Pink and 0·97 with Great Scot). It seems certain, therefore, that virus diseases are to be regarded as, for all practical purposes, the sole cause of progressive degeneration in potato stocks; but this does not mean that stocks free from virus infection are thereby immunised against seasonal losses due to other parasites, or to unfavourable soil or weather conditions. Degeneration may theoretically become progressive by (*a*) a gradual intensification of the effects of a virus disease in the progeny of an affected plant, (*b*) the gradual increase in the number of infected plants in a crop owing to the infectious nature of virus diseases, or (*c*) a combination of the two. These questions are discussed more fully in the next two chapters, but in practice it may be assumed that the term "progressive degeneration" implies an increase in the number of infected plants in a crop.

(5) VIRUS DISEASES IN THE POTATO PLANT.—From the earliest work of Quanjer until about 1930, almost the sole approach to the problem of degeneration and its control lay in a study of the symptoms produced in the plant. Thus Quanjer (1921, 1923), Murphy (1921) and Schultz and Folsom (1923) segregated "Mosaic" into a number of distinct types of symptoms readily recognisable in the field and these, with but slight modification and additions, still remain the recognised terms with which to describe the virus diseases associated with potato degeneration. From the appearance of the affected plant alone, in a specified variety, we may therefore identify the diseases Leaf Roll, Mosaic, Aucuba Mosaic, Interveinal Mosaic, Crinkle, Rugose Mosaic, Streak (or Leaf-Drop Streak), Curly Dwarf, Marginal Leaf-Rolling Mosaic, *Calico*, *Spindle Tuber*, *Yellow Dwarf*, *Witches' Broom*, *Apical Leaf Roll*, *Yellow Top*, *Purple Top*, *Psyllid Yellows*, and *Giant Hill*. Of these, the diseases shown in italics have only been identified with certainty overseas.

The characters by which these diseases may be recognised are described in the following pages of this Chapter, but it is important to remember that the descriptions are of *symptoms* and not of *causes*. The isolation of the different causal viruses was a later and more difficult development, which is outlined in Chapter XXVII, and it is now known that some diseases (*e.g.* Mosaic) can be produced by each of three different viruses having quite different methods of transmission in the field, whilst other diseases (*e.g.* Crinkle, Interveinal Mosaic) are due to the combined effect of two viruses. Without such extensions of our knowledge of viruses as are given in Chapter XXVII, and of the conditions under which they may produce disease, there can be no systematic attempt to improve the standard of health of commercial stocks of potatoes.

For this reason the problems of controlling the virus diseases described below are referred for full discussion to Chapter XXIX.

Nevertheless, all Certification schemes are based on visual inspection of the growing crop, and a useful purpose is served by the grouping of symptoms into recognisable "diseases" which can themselves be arranged into less severe, and more severe, types according to the probable effect on the plant. In the following pages, therefore, the potato virus diseases are discussed from the clinical or symptomatic aspects, under the four headings: (A) Leaf Roll; (B) The Milder Forms of Mosaic; (C) Severe Forms of Mosaic; and (D) Virus Diseases only recorded with Certainty from Overseas.

(A) Leaf Roll

External Appearance.—Both tubers and sprouts are usually of normal appearance, but in cases where net necrosis (page 428) occurs the sprouts are thin and spindling. There is little evidence that the disease is localised in any part of the tuber, and any of the sprouts almost invariably give rise to a diseased shoot. Growth after planting is slow, and the delay in appearing above ground, together with the rather pale green colour of the foliage, are sometimes sufficiently pronounced as to arouse suspicion before the first signs of rolling appear in the lower leaves. It is this upward rolling of the leaflets of the *lower* leaves around the midribs which remains the most reliable symptom of the disease throughout the season. The rolled leaves are leathery in texture and rattle when shaken; the exposed under-surface may become almost silvery or may show a yellowish or reddish colour. As the leaf matures, brown dead spots develop and the leaf turns brown and may die back from the tip. The general appearance of the diseased plant is a stiff, erect or "staring" habit, with the pallor of the foliage accentuated by the exposure of the under-surfaces of such leaves as are rolled (Fig. 83). The degree of rolling and the number of rolled leaves on a plant varies from plant to plant, but is also to some extent a varietal character, *e.g.* it is usual to find most of the leaves rolled in an affected plant of the variety Lochar, whereas Arran Comrade commonly shows rolling only in the lower third of the foliage, and diseased Up-to-Dates may escape detection because only one or two of the lowest leaves are affected. Diseased plants may be more or less stunted or may be fully as large as healthy neighbours ; it is not known whether this difference is one of response by the plant (indicating differences in the ability of the plant to outgrow the influence of the virus), whether it represents a difference of virus strain, or a dosage effect only. Growth is stopped but there is no premature death of the affected plant. Leaf Roll plants give only a small crop and the tubers are either clustered close to the stem or are borne on much shortened stolons ; the mother tuber usually remains hard and unrotted throughout the season. In most varieties there is a reduction in the amount of " ware " tubers produced, due both to the small number of total tubers and to the reduction in size of the individual ; in Up-to-Date, however, the whole crop may consist of two or three large tubers. McIntosh (1937) has recorded the fact that, in Scotland, Leaf Roll is most prevalent among the very slow-sprouting varieties such as Golden Wonder, Arran Consul, President and Bishop, possibly owing to the succulence of the young foliage—as compared with the more mature leaves of quicker-growing varieties—at the time the plants become infested with the insects (aphides) which transmit the disease ; an exception is the very susceptible, but quick-sprouting variety, British Queen.

Plants infected in mid-season may show some rolling of the leaflets of the *upper* leaves only (the so-called " primary " symptoms), but this is unreliable as a means of detecting current season infection. More usually no symptoms at all are to be seen until the progeny is grown on in the following year, when the full or " secondary " symptoms develop. Tubers infected through the sprouts, in storage, also develop full secondary symptoms when planted (Murphy, 1923), as do plants which become affected within about one month after appearing above ground (Whitehead and Currie, 1930) ; facts which may be of importance in determining the responsibility for an outbreak of disease in late-planted crops in the south of England. Ordinarily, there is no masking or diminution of the symptoms of Leaf Roll in the field, though rare instances are known of diseased plants failing to show rolling owing to the exceptional vigour and consequent shading effect of the surrounding healthy plants. The virus of Leaf Roll has not been recorded as occurring, in nature, in any plant except the potato. Hovey and Bonde (1948*a* and *b*) showed, however, that *Physalis angulata* L. reacts severely some ten days after being experimentally infested with the aphid *Myzus persicæ* carrying the Leaf Roll virus ; the symptoms including severe stunting with chlorosis and mottling of the leaves. To this species Kirkpatrick (1948*a* and *b*) has added *Physalis floridana* and *Datura stramonium* ; the former showing symptoms which develop quicker and are more reliable than in the case of *P. angulata*, while the symptoms in *Datura* are the slowest to develop and the least reliable.

SYMPTOMS WITH WHICH LEAF ROLL MAY BE CONFUSED.—Growers should distinguish between Leaf Roll and the symptoms of Blackleg (page 393), Black Scurf and Stem Canker (page 295), Verticillium Wilt (page 314), Black Dot (page 331) and Root Eelworm (page 205). The virus disease known as Marginal Leaf-Rolling Mosaic (page 457) may be distinguished from Leaf Roll by the shallow boat-like appearance, due to the fact that only about a quarter of an inch of the leaf margin becomes upwardly curled ; the leaf edge is also wavy and the whole surface usually shows a blotchy mosaic. Le Clerg (1945) has reported the occurrence of a non-infectious form of leaf rolling in first-year seedlings, it is found in both crosses, reciprocals and inbred progenies. The symptoms, which are definitely inheritable, involve the successive rolling of leaves from the base to the top of the plant ; often with the development of purplish-red coloration. In the previous year (Le Clerg, 1944), he described an inherited, but non-infectious, rolling in the first tuber propagation in the field from seedlings. In this case the symptoms were markedly influenced by environmental conditions of storage and growth, and the condition seems to be the American equivalent of what is known in this country as " Varietal Rolling " ; a source of anxiety to all concerned in the eradication of true Leaf Roll from our crops. Thus, a rolling of leaf margins occurs in the lowest leaves of Sharpe's Express and throughout the foliage in the variety Gladstone, particularly in warm dry seasons. In the latter case all stages from a slight marginal curl to a pronounced rolling along the midrib may occur in the crop, though most of the symptoms will disappear after heavy rain ; the rolling is not restricted to the lower leaves as in most cases of true Leaf Roll. According to O'Brien and Dennis (1936), the rolling in such varieties as Gladstone, Catriona and Di Vernon may be due to boron deficiency in the soil (page 420), but the evidence is inconclusive and requires confirmation. Finally, any injury to the stem or haulm will impede the movement of carbohydrates from the leaves and will induce an upward rolling of their margins ; such injuries, therefore, should be looked for before attributing the rolling of the foliage to the virus disease.

INTERNAL CHARACTERS OF LEAF ROLL.—The chief internal sign of injury caused by Leaf Roll is the death of the food-conducting strands (phlœm) forming part of the vascular bundles (veins) of the leaves and haulm, death being indicated by the disintegration of the protoplasm and nuclei, and by the thickening of the walls of the phloem cells. The thickening is due to the deposition of a lignin-reacting substance, first in the angles between adjacent cells and then extending gradually over the whole cell-wall. This condition is known as "phlœm-necrosis," and Quanjer *et al.* (1916) showed it to be a reliable test for Leaf Roll. The necrotic cells, which occur only in the primary phlœm, can readily be identified by the yellowish-red colour produced when a section through the node of an infected stem is immersed in a solution of 1 per cent. phloroglucinol in 50 per cent. alcohol for one minute and then transferred to 50 per cent HCl (Sheffield, 1943 ; Wilson, 1948). The underground parts of an affected plant, however, do not usually exhibit phlœm-necrosis, although some varieties show it in the tubers as a first-year symptom of Leaf Roll (Net Necrosis, page 428). Necrosis of the phlœm in the haulm of some varieties (*e.g.* President) is so severe that the cell cavities are almost completely obliterated, whereas in a variety such as Arran Comrade it may even be difficult to demonstrate at all (*cf.* page 537).

Even before necrosis (or death) sets in, there is serious interference in the transport of carbohydrates through the phloem, with the result that sugars and starch accumulate in the cells of the leaf where they are manufactured. This in turn produces an abnormal turgidity in the mesophyll cells of the leaflet and causes it to assume the rigid, leathery, upwardly rolled appearance characteristic of the disease. Some of the excess sugars are used up in respiration, for the Leaf Roll plant respires at a much greater rate than the healthy one (Whitehead, 1934), and part of course is also utilised in the growth of the young foliage. The fact that neither the excessive wastage of the sugars by respiration nor the reduced rate at which they are formed in Leaf Roll leaves (Barton-Wright and McBain, 1931-32) can prevent an inordinate accumulation of sugars is a measure of the extent of interference with translocation. Indeed, Whitehead (1927), found the movement of sugars to the tubers to be so slow during the night that some sugar and all the reserve starch remain in the leaf until new carbohydrate formation begins again the following day, thus causing an excessive accumulation of starch as well as of sugars in the diseased leaf. Murphy (1923) had already observed that much of the starch remained in a Leaf Roll leaf even after it had been continuously covered for seventeen days, and he made use of this fact as a test for Leaf Roll in doubtful cases. A *lower* leaf is cut off, kept in the dark for some forty hours and then killed by plunging into boiling water. It is then decolorised by placing in methylated spirits and finally covered with a weak solution of iodine. If the leaf is infected with Leaf Roll it at once turns a deep bluish black colour owing to the action of the iodine on the starch within the cells. If healthy, little or no starch will be left in the tissues and the leaf will merely be stained the colour of the iodine. Even when some depletion of starch has begun in a diseased leaflet, this will be restricted to the basal part, whereas a healthy leaflet clears from the tip backwards towards the base. The test is not infallible, but is extremely useful even in material sent for diagnosis by post.

Barton-Wright and McBain (1931-32) have shown that the main carbohydrate changes occurring in Leaf Roll leaves consist in the conversion of starch to hexose, hexose to sucrose, and sucrose back to starch, the series forming an almost completely closed system with only a small outlet of *hexose* towards the tubers. In healthy leaves, on the other hand, they find hexose to be the first sugar formed by photosynthesis. The hexose is either converted to sucrose and so transported to the tubers, or is changed temporarily to starch and then reconverted to sucrose for transportation. This difference in the kind of sugar translocated is associated with a difference in the path taken for, according to Barton-Wright and McBain (1931, 1932), the hexose of Leaf Roll plants is transported *via* the ground tissue and not at all through the phlœm as in the case of the sucrose of healthy plants. Quoting Appleman and Miller's (1926) view that the high rate of respiration of immature healthy tubers as compared with mature ones was correlated with differences in the sucrose/hexose ratio, Whitehead (1934) suggested that this might be equally true of the high rate of respiration of Leaf Roll infected potatoes as compared with healthy ones at all stages of growth (except immediately following the break in dormancy). This was independently shown to be the case by Pfankuch (1934) who found that the ratio of total sugar to reducing sugars was greater in diseased tubers than in healthy ones, and that the mg./per centage " invert sugar," calculated on a glucose content of 1000 mg./per cent. was 435 for Leaf Roll tubers and only 145 for healthy tubers. Barton-Wright and McBain (1933) have also studied the nitrogen metabolism of healthy and Leaf Roll leaves. They find that the total nitrogen content of diseased leaves is less than that of healthy ones and there is evidence that synthesis of nitrogenous compounds proceeds at a lower rate. Translocation is likewise impeded in much the same way as with carbohydrates, and nitrogen compounds accumulate in the petioles. Nevertheless, Barton-Wright and McBain believe there is no fundamental difference induced in the sequence of nitrogen metabolism as a result of Leaf Roll infection and do not agree with Schweizer (1926, 1930) that the disease is essentially one of disturbed nitrogen nutrition.

The composition of the tuber is also affected by the disease. McLean (1926*a* and *b*) showed that in many varieties the total dry matter content of Leaf Roll tubers was some 4 per cent. less than that of healthy tubers, *i.e.* falling on the average from about 22 per cent. to 18 per cent. The water-retention power, on the other hand, was higher in the diseased tuber, and such tubers remained hard in contrast to the softened, flabby condition of healthy tubers towards the end of the storage period. The same author also found that, when planted, the diseased seed-tuber depleted both nitrogen and carbohydrates at a much slower rate than did healthy ones. Even when most of the reserve food has disappeared from the diseased seed-tuber this persists, largely as a reservoir of water, until the end of the growing season in many cases ;

there being no autolysis of cell-walls as in healthy seed-tubers. The ascorbic acid content of Leaf Roll tubers was found by Smith and Paterson (1937) to be abnormally high and they utilise this fact as a test of the disease (see Indophenol Test, page 67). According to Bechhold and Erbe (1936) the enzymes in " degenerate " tubers are preponderantly of a reducing type whereas oxidation occurs more freely in healthy tubers. This belief was earlier (1934) used by these workers in diagnosing " degeneracy " by inserting a strip of clean copper into the tuber, which was then incubated at 37° C. for eight hours and finally left at room temperature for a further sixteen hours. In healthy tubers the copper diffuses into the surrounding tissues and assists the normal enzymes in catalysing the catechol to form melanin (page 411), whereas in " degenerate " tubers the oxidising capacity of the tissues is inadequate for much melanin production and diffusion of copper is, for some reason, inhibited. Thus the effect is to cause extensive blackening of tissues in healthy tubers in contradistinction to diseased ones, in which only the narrow band of tissue in direct contact with the metallic copper becomes blackened. There is no doubt of the wide differences of enzymic reactions shown by individual tubers, but this is not correlated with degree of " degeneracy," and Pethybridge (1934) has pointed out that, at least as far as Leaf Roll is concerned, the " copper-strip " test is of little value. Yet another test for the presence of Leaf Roll, for which some evidence has been advanced, is that of the fluorescence of cut surfaces of infected tubers when exposed to ultra-violet light. McLean and Kreutzer (1944) found that a white fluorescence was characteristic of Leaf Roll and that a yellowish one was usual for Spindle Tuber (page 467) infection. In this country Allan (1945) confirmed fluorescence as specific to Leaf Roll, and states that, while it is confined to the vascular bundle in current-season tubers, the fluorescence extends throughout the pith in tubers after storage. Harris (1947), however, can find no correlation between fluorescence in tuber tissue and any virus disease and, indeed, it can scarcely be expected that a test, originally devised for the diagnosis of Bacterial Ring Rot (page 402) by Iverson and Kelly (1940) and Harvey (1941) should be specific for virus diseases; the more so since, according to Flint and Edgerton (1941), fluorescence can be demonstrated in potato tissue affected by various types of "breakdown." Claims that the method is useful in identifying potato varieties have also been made (page 67).

INHERITANCE AND TRANSMISSION.—Murphy and McKay (1925) as well as Elze (1931) have presented some evidence of an occasional inheritance of Leaf Roll through the true seed. The disease can also be transmitted from an infected to a healthy plant by grafting haulm, sprouts or (less successfully) tubers; it cannot be transferred by mere contact of foliage or by inoculating the sap expressed from a diseased plant into a healthy one. Whitehead (1923) suggested the possibility of transmission occurring below ground-level through the medium of soil animals, and this was confirmed by Elze (1927); the evidence, however, is inconclusive and the question remains an open one. However that may be, there is overwhelming evidence that, in nature, Leaf Roll is mainly spread in a crop by the agency of aerial sucking insects, of which the aphid, *Myzus persicæ*, is by far the most important (page 260).

DISTRIBUTION.—Leaf Roll probably occurs wherever commercial potato crops are grown, but it is of interest to note that in grafting experiments with some 59 potato varieties collected in Peru, Dennis (1939) obtained only doubtful evidence of the presence of the Leaf Roll virus. The best seed-producing districts of northern Scotland and Ireland appear to be relatively free from the disease, but heavy infections may occur in southern areas in Ireland, in south-east Scotland, and in most of the "ware" growing districts of England and Wales. It is one of the most important causes of degeneracy in commercial potato crops.

VARIETAL RESISTANCE.—This may be genetical in origin and so inherited; it will reveal itself either in resistance to infection or in a tolerance of the virus when the plant is infected, so that the effect on the yield is small. On the other hand a form of resistance is common in varieties due to habit of growth, palatability, or to some other factor which minimises the risk of aphid infestation; this could more properly be described as resistance to infestation by aphides and may be subject to considerable variation according to the environmental conditions. Finally, from the growers point of view, the risk involved in a selection of varieties to grow may be indicated (Table XIX) in a list of varieties most frequently found to be heavily infected. Such a list, however, does not necessarily measure the relative susceptibility of varieties, for the differences may be due to different degrees of exposure to infection, to the length of time the variety has been on the market, or even to its popularity.

Direct resistance to infection, *e.g.* by graft or controlled insect infestation, does not appear to have been demonstrated in any variety or seedling, and success in breeding has, in the

TABLE XIX

Varieties sometimes badly attacked	Varieties attacked to a less extent
Arran Cairn	Ally
Arran Consul	Arran Chief
Arran Comrade	Champion
Arran Crest	Eclipse
Arran Pilot	Epicure
British Queen	Flourball
Dunbar Cavalier	Great Scot
Dunbar Yeoman	King Edward VII
Duke of York	Ninetyfold
Golden Wonder	Royal Kidney
Katie Glover	Shamrock
Kerr's Pink	Witchhill
King George V	
Majestic	
May Queen	
President	
Sharpe's Express	
Up-to-Date	

main, been measured (1) by the proportion of plants escaping infection under natural conditions as compared with a standard "susceptible" variety and (2) by the degree of tolerance, *i.e.* the effect of the virus on the plant when infected. Köhler (1938, 1940) classified 24 German varieties according to the degree of field resistance shown to the Leaf Roll virus and to virus "Y"; some being resistant to both. He considered that some relationship existed between the factors responsible for resistance in these two viruses. Müller (1939) found by selfing varieties that they were heterozygous for resistance, reciprocal crosses between them being identical and intermediate in tolerance between that shown by the two parents. Differences in tolerance of the virus when infected are well known in commercial varieties. Whitehead (1930) and Whitehead and Currie (1931) distinguished between susceptibility of foliage and tubers to infection in commercial varieties. They considered that the rate of degeneration of a crop is the resultant of three forms of susceptibility, *i.e.* (i) the liability of the foliage to contract infection; (ii) the liability of tubers to contract infection from the diseased foliage and (iii) the effect of infection on the yield. The loss in yield was found to be less influenced by seasonal factors than either percentage foliage or tuber infection, so that an estimate of susceptibility based on loss in yield would have the wider applicability to other localities and seasons. These three ways of expressing susceptibility are shown in Table XX, in the case of four varieties

TABLE XX

Ways of Expressing Susceptibility (from 1924 Trials)

Variety.	Per cent. Infected.		Per cent. Loss in Numbers.	Crop from Progeny Weight.
	Plants.	Tubers.		
Crusader . . .	100	100	84·1	95·7
Up-to-Date . .	100	98	39·6	14·2
Majestic . . .	87	60	53·0	65·2
Great Scot . .	60	45	29·7	45·3

exposed in 1924 to equal, and heavy, chances of infection. A plant was known to have been infected by the occurrence of one or more diseased plants developing in the progeny in 1925, while the proportion of diseased to healthy progeny from a diseased plant indicated the tuber-susceptibility. The variety Crusader showed all three forms of susceptibility in an extreme manner; Up-to-Date was very susceptible as regards foliage and tuber infection but the effect on the yield was very small (14 per cent.), while the varieties Majestic and Great Scot were far less readily infected in field tests but infected plants suffered a severe loss in yield. Botjes (1941) also found the loss in yield from infected Up-to-Date plants to be very small (5·3 per cent.) as compared with 84·6 per cent. loss in the variety President; he regards Up-to-Date and Bintje as the most resistant and Duke of York and President as the most susceptible of British varieties (*cf.* page 547).

There is no proof that the aphid vector exercises any selection between varieties in the field, but there are many facts suggesting that this may be the case. Thus reference has already been made (page 438) to McIntosh's (1937) opinion that very slow-sprouting varieties may provide an abundance of succulent foliage at the time of initial infestation by aphides, and that this may account for the prevalence of Leaf Roll in such varieties in Scotland. Bald *et al.* (1946) imply some form of insect selection by their use of an " index " formula of resistance which integrates the percentage of virus infection found, with the proportion of plants in the crop infested by aphides; from this index they calculated that, under the conditions of South Australia, the variety Bismark has from seven to eight times *less* likelihood of becoming infected than the variety Up-to-Date. A similar explanation is implied in the field resistance shown in Ireland by the varieties Skerry Champion, Shamrock and Matador (McKay and Clinch, 1944). These varieties are readily infected by graft or by sprout infestation by aphides but, in the field, Skerry Champion is almost immune and the disease is rarely seen in either of the other two varieties. In a field test of susceptibility, using 6 plants each of a number of varieties, S. Champion had 0 in 6 infected and Shamrock 1 in 6, while of the rest, Arran Cairn, Golden Wonder, and President each had 5 in 6 and Champion 4 in 6 infected. Locke (1948) attempted to measure resistance by the difference in the rate of increase of the disease in field crops of different varieties growing in Maine, U.S.A.; he states that Katahdin showed most resistance to Leaf Roll with an increase of only 16 per cent.; the next variety (Sequoia) giving a 26·7 per cent. increase. Since 1938 intensive breeding for resistance has been in progress in Maine, U.S.A., obviously with considerable success. Stevenson *et al.* (1943) report that, in a year (1941) when the standard susceptible variety (Green Mountain) showed an increase of Leaf Roll from 0·5 per cent. to 90·5 per cent., some 300 (or 5·4 per cent.) of their seedlings remained free from infection. Many of the most promising seedlings are derived from the variety Katahdin, which has the additional advantage of apparent immunity from Net Necrosis (page 428). In this country attention has been directed mainly at breeding for resistance to viruses of the Mosaic type, but in 1940 the Scottish Plant Breeding Station reported (Anon, 1940) a very high degree of resistance to Leaf Roll in two varieties and in their first generation seedlings.

EXTENT OF LOSS.—Very heavy losses from Leaf Roll have been recorded, *e.g.* Murphy (1921) gives the loss in Canada at 66 to 82 per cent., and Cotton (1921) reports a loss of from 36 to 75 per cent. in trials carried out in many districts of Great Britain. The loss in marketable tubers is even higher, since one effect of the disease is to increase the proportion of seed and chats in the crop ; it is, however, not progressive in the sense that the progeny of a Leaf Roll plant show a still further decline in yield in the following year. The effect of the disease varies considerably in different varieties as can be seen from Table XXI ; from which it follows that equivalent losses in yield in different varieties will require very different degrees of Leaf Roll infection in the crop. Thus, Bonde *et al.* (1943) found in the seasons 1938 and 1939 the variety Irish Cobbler showed no significant loss until a crop infection of from 20 to 30 per cent. was recorded, whereas 12 per cent. infection gave a significant loss in Green Mountain. The effect is also less severe when the crop is well cultivated than under poor conditions, and in moist, good-growing, seasons as compared with dry hot summers (Whitehead, 1924).

TABLE XXI

Mean Yields (lb.) from Normal and Leaf Roll Plots, each of 20 plants

Variety.	Normal.		Leaf Roll.			
	No.	Weight.	No.	Per cent. Loss.	Weight.	Per cent. Loss.
Arran Crest . .	119	32·9	29	75·6	1·50	95·2
Herald . . .	204	43·75	69	66·2	1·05	97·6
Great Scot . .	133	37·6	114	14·3	19·00	49·5
Arran Consul . .	187	46·2	65	65·3	6·31	86·4
Arran Banner . .	140	46·3	98	30·0	17·81	61·6
Kerr's Pink . .	195	45·56	101	48·2	13·25	70·9
Field Marshal .	170	43·9	145	14·7	32·5	26·0

(B) THE MILDER FORMS OF MOSAIC

These diseases are all characterised by a more or less pronounced mottling of the foliage produced by the contrast between yellow, or light-green, areas and the normal green of the variety. There is little or no necrosis (*i.e.* dead, brown,

FIG. 83.—Leaf Roll, var. British Queen (page 437).

FIG. 84.—"Severe Mosaic"; var. Golden Wonder (page 458).

spotting) of the foliage but necrosis of the tuber may occur in certain varieties. Typically, there is little obvious effect in the vigour of growth.

(i) *Aucuba Mosaic*

EXTERNAL APPEARANCE.—This disease was apparently first observed by Orton (1914) in Germany and U.S.A., and later was recorded in Canada by Murphy (1921). It was, however, first named and adequately described by Quanjer (1919, 1921) in Holland. The name recalls the similarity of the conspicuous round yellow spots which develop on the lower leaves of affected potatoes, with the well-known variegation of the leaves of *Aucuba japonica*. There are no other foliage symptoms to be seen on naturally infected potatoes in the field, and the vigour does not appear to be affected. The tubers of some varieties, however, show a necrosis of the tissues (see below) which is visible externally as irregularly shaped brown patches, developing later into sunken dry brown areas somewhat resembling the effects of Blight (Clinch, Loughnane and Murphy, 1936).

SYMPTOMS WITH WHICH AUCUBA MOSAIC MAY BE CONFUSED.—Both the regular outline of the disease spots and their scattered or haphazard distribution serve to distinguish Aucuba Mosaic from the marginal variegation sometimes seen in certain potato varieties, *e.g.* King Edward VII. The yellow discoloration produced by frost may easily be confused with the disease but the spots are rarely as vivid as in Aucuba Mosaic, and according to Murphy (1921) are usually yellowish white in colour. The American disease known as " Calico " (page 466) appears to have somewhat similar symptoms, but the yellow areas are much larger and may occupy upwards of 95 per cent. of the leaf surface. The " Yellow " or " Aucuba " Mosaic of the tomato has very similar symptoms but has no other connection with the potato disease.

INTERNAL APPEARANCE.—Clinch (1932) has made a cytological study of diseased leaves and she finds the chlorosis to be due to loss of chlorophyll and disintegration of the chloroplasts, which results in the release of quantities of oil droplets within the cells. There was also an accumulation of starch in the pallid spots, and later (1936) she and her colleagues showed that starch translocation was impeded. There is no record of phlœm necrosis occurring as in the case of Leaf Roll, but necrosis does develop in the parenchyma cells of both cortex and pith in the tubers of certain varieties (Clinch, Loughnane and Murphy, 1936). The necrosis begins near the heel end of the tuber and does not affect either the vascular tissue or the " eyes." It occurs internally as groups of mis-shapen dead cells with brown granular contents and swollen brown and disintegrating walls, surrounded by a zone of translucent tissue containing little or no starch, and in which incipient cork formation is observed. The centre of the spot is occupied by a small group of cells filled with large starch grains. The necrosis develops during storage, and is favoured by darkness and high temperatures, and particularly by a turgid condition of the cells. This tuber necrosis is identified by these workers with " Pseudo-Net Necrosis " (page 431), and was found to occur in the varieties British Queen (in which the yellow mottling of the foliage was preceded by a wilting and drying-out of the tips of lower leaves), Champion, Dunbar Yeoman, Great Scot, Majestic, President and, occasionally, Roode Star ; to these may be added Arran Signet, Dunbar Standard, Gladstone, Redskin and Ulster Monarch (Clinch, 1941). Tuber necrosis was not found in affected plants of Arran Banner, Early Regent and Arran Crest, and only in Arran Victory, Irish Chieftain and Up-to-Date, when the Aucuba Mosaic was due to a less common virus named " F," or to a combination of viruses " F " and " A " (see below).

INHERITANCE AND TRANSMISSION.—Elze (1931) believes he has evidence of inheritance of Aucuba Mosaic through the true seed, but this has not as yet been confirmed. It is carried in the tubers and can be transmitted artificially by graft and juice inoculation. The question as to whether Aucuba Mosaic is transmitted by natural means in the field, *i.e.* by leaf contact or the action of insects, depends upon the viruses responsible for the production of the Aucuba symptoms. These viruses have been isolated by Clinch, Loughnane and Murphy (1936) and named " G " and " F." The characteristics of these and other viruses are described in Chapter XXVII, and it is only necessary here to say that the most common form of Aucuba is that induced by virus " G," which apparently cannot be transferred to healthy plants either by leaf contact or by such potato insects as have been tested. A less common form of

Aucuba is caused by virus " F," in which case it is a subsidiary feature of Interveinal Mosaic (page 456) and is likewise incapable of transmission in the field. Rarely, however, virus " F " and a virus known as " A " are able, in combination, to cause an intense form of Aucuba Mosaic which *is* capable of being transmitted under field conditions by the aphid *Myzus persicæ*. All cases, therefore, of field transmission of Aucuba must be regarded as the " Double Virus " Aucuba of Murphy (1936). In the varieties Irish Chieftain, President and Golden Wonder the Double Virus Aucuba induced is a particularly brilliant yellow variegation which begins on the lower leaves and gradually extends almost to the top of the plant; it is even more intensified in the second generation (Clinch, Loughnane and Murphy, 1936).

PREVALENCE OF AUCUBA MOSAIC IN DIFFERENT VARIETIES.—The disease is most common among first early varieties and particularly so in stocks of Ninetyfold and Early Regent. It has also been reported (Anon, 1925) in Epicure, Fiftyfold, Duke of York, British Queen, King George V, Catriona, Majestic, General and President. So far as is known, the loss in yield is negligible.

(ii) *Common Mosaic*

EXTERNAL APPEARANCE.—As the name implies, the characteristic feature of this disease is a more or less distinct mottle of interlocking light and dark-green areas covering the leaf surface. Typically the leaves are free from brown, necrotic, lesions and the leaflets are fairly flat (*i.e.* neither wrinkled, blistered nor distorted); growth is normal and there is no obvious loss of vigour. For Certification purposes such a plant is said to be affected with " Mild Mosaic " or, if the mottling is so faint as to require a background of white paper to reveal it, it is regarded as a " negligible mottle " and ignored; the name " Mosaic " therefore covers all grades of mottle from the barely perceptible to the very obvious. The intensity of this mottling appears to depend upon (1) the particular virus (*i.e.* viruses " X," " A " or " Y," Chapter XXVII) or virus complex causing the symptoms, (2) the variety of potato affected, and (3) the environmental conditions (especially temperature) under which the plant is growing (Dickson, 1922). Mechanical injury to a haulm usually intensifies any mottling of the foliage, which possibly explains some instances of plants in which mottling appears to be restricted to a single shoot, as well as explaining the frequency with which plants at the ends of drills show Mosaic. Apart from the intensity of the mottling, some plants may obviously be severely affected ; some dwarfing may occur and irregular brown, necrotic, areas may develop on the foliage. Clearly such a Mosaic must be described as " Severe," although the symptoms do not include the blistering and distortion characteristic of Crinkle (page 459) or Rugose Mosaic (page 464). The disease is, in fact, an extreme example of infection with a virulent strain of virus " X," and in any scheme of Certification of potato stocks such a plant is classed as " Severe Mosaic." There is no field test which can be applied to determine the particular virus, or virus strain, responsible for " Mosaic " in most varieties, *e.g.* Majestic ; though as will be seen later (page 588), certain varieties such as King Edward or Epicure are " field immune " from viruses " X " and " A," and a mottle therefore will probably be due to virus " Y " while a quite similar mottle in the variety Kerr's Pink, on the other hand, is almost invariably the result of virus " X " infection. All tubers from a plant showing symptoms of Mosaic will give rise to diseased plants, as will tubers which contract infection through the sprouts in storage. There is no reliable evidence as to whether symptoms may develop during the same growing season in which infection occurs, but, unless sprout infection is suspected, it is usual to assume that mid-summer symptoms are the result of infection of the mother plant in the previous year. As in the case of Leaf Roll, the infected seed-sett frequently, but not invariably, remains intact throughout the season.

SYMPTOMS WITH WHICH MOSAIC MAY BE CONFUSED.—The mildness of the mottling and the absence of distortion in the foliage are the best criteria in distinguishing this disease. Variegations and Aucuba Mosaic are easily recognised by their sharply contrasting yellow and green areas on the leaf surface. A yellowish mottling is also characteristic of Interveinal Mosaic (page 456) and Marginal Leaf-Rolling Mosaic (page 457) ; the yellowish zones lying between the veins of the leaf in the former disease and along the margins in the latter. Frost injury has been found in Ireland to simulate Mosaic

FIG. 85.—Severe effects of Virus "Y"; var. King Edward (p. 462).

FIG. 86.—"Crinkle"; var. Irish Chieftain (page 459).

symptoms (McKay and Clinch, 1945); a strong mottling developing about ten days after sharp frost. Under field conditions, even with supposedly healthy stocks grown for seed, the effect of frost is probably to accentuate the symptoms of a virus already present; the authors state, however, that the frost mottle occurred also in virus-free plants growing under glass.

INTERNAL CHARACTERS OF MOSAIC.—The light-green areas of the leaf show a reduction in the size of intercellular spaces and of cells both of the palisade tissue and mesophyll, which results in the pale areas being thinner than the darker tissues. These latter dark areas are normal, *i.e.* there is no hypertrophy as compared with entirely healthy leaves. There is an increase in the number of hairs on the surface of the pale areas whilst chloroplasts are reduced in number and in colour as compared with healthy tissue (Dickson, 1922). Miss Clinch (1932) also records a tendency for an abnormal accumulation of starch in the cells of the pale zone as well as of tannin and fat. There is no necrosis of the phloem or other cells, but K. M. Smith (1924) noted the occurrence of abnormal structures within the cells which have since become known as "X" bodies (*cf.* page 475). Tuber necrosis has been obtained in some varieties when the mosaic-producing virus "A" has been introduced by means of grafts, but there is no record of similarly necrotic tubers being found in the field.

INHERITANCE AND TRANSMISSION.—Infected tubers are the only known means whereby the disease can persist from one season to the next, although the possibility of transmission through the true seed has not received the attention its importance deserves. Stelzner (1942), however, believes he has confirmed the presence of viruses "X" and "Y" in the embryo of potato and *Datura* though they are inactivated during the ripening, storage, and germination of the seed; a claim which must be received with some caution since *Datura* is regarded as immune from virus "Y" (Smith, 1937). Mosaic can be transmitted to healthy plants by artificial means, such as grafting tubers, sprouts or haulms, or by inoculating the sap expressed from a diseased plant into a healthy one. In storage, Mosaic (virus "X") is transmitted by sprout contact (McIntosh, 1944), but not by means of the cutting knife nor by rubbing the cut surface of the tuber with virus sap (Bawden *et al.*, 1948). Transmission in the field may occur through contact of diseased and healthy foliage in the case of virus " X," (Loughnane and Murphy, 1938), or the same virus may spread underground from one plant to another by some means as yet unknown (Roberts, 1946, 1948). Mosaic due to viruses " A " and " Y " may be transmitted under field conditions by certain insects (page 506 *et seq.*). As in Leaf Roll the aphid *Myzus persicæ* appears to be far the most consistent vector of the insect-transmitted Mosaic viruses, but much remains to be discovered before the problems of field transmission of this and similar diseases can be regarded as solved.

Distribution and Loss caused by Mosaic.—This is perhaps the most widespread of potato virus diseases ; practically all stocks of some varieties (*e.g.* Kerr's Pink, Golden Wonder and Up-to-Date) appear to be infected. Indeed, there is probably no variety grown which does not, in some stocks, show a mild form of mosaic symptoms, even though it may require careful examination with the help of a sheet of white paper in order to discern the mottling ; such cases are usually described as a " negligible mottle." Nevertheless, it is a great mistake to assume that they are negligible in regard to their possible effect on some adjacent variety in which the symptoms become more pronounced ; or even negligible in the varieties showing the mildest of symptoms when another virus is superimposed (pages 459, 519). That the more severe forms of Mosaic are responsible for a large reduction in yield has long been apparent, but information on the loss caused by " Negligible Mottle " or " Mild Mosaic " (due in most cases to the less virulent strains of virus " X ") has had to await the production of sufficient quantities of completely virus-free plants to act as a standard of yield. The following Table XXII, summarises the results obtained by various workers in determining the loss in yield of potatoes affected with strains of virus " X " of different degrees of virulence.

All these workers agree that the loss in yield is directly related to the severity of symptoms displayed, except in the case of negligible mottle due to the least virulent of strains of " X." It has been pointed out by Bawden *et al.* (1948) that constitutional differences in vigour occur even in the produce of a single plant. Differences in yield due to infection with an avirulent strain of a virus may be intensified, or neutralised by these constitutional effects and this, it is suggested, may account for the results of Clinch and McKay (1947) and of Bawden *et al.* (1948) in which infected plants gave higher yields than plants completely free from virus; Bald (1944) noted one similar instance in Australia, while Black and Haigh (1948), in Scotland, also obtained higher yields from plants

TABLE XXII

Symptoms.	Variety.	Per cent. Loss (weight).	Author.	Remarks.
Negligible Mottle	Majestic	13	Scott (1941)	Controls—S.S. seed probably containing an avirulent strain of "X"
Mild Mosaic	Majestic	34	Scott (1941)	Controls—S.S. seed probably containing an avirulent strain of "X"
Border-line Severe Mosaic	Majestic	43	Scott (1941)	Controls—S.S. seed probably containing an avirulent strain of "X"
Negligible Mottle	Up-to-Date Great Scot	12 12	Bald (1943)	Controls—Virus-free
Mosaic	Great Scot	45	Bald (1943)	Controls—Virus-free
Latent "X"	Various	9 to 22	Schultz and Bonde (1944)	Controls probably with avirulent "X." Latent "X" includes our Mild Mosaic
Negligible Mottle	Various	12	Smith and Markham (1945)	Inoculated virus-free half-tubers
Latent "X"	Majestic	Nil or increased yield	Clinch and McKay (1947)	Inoculated virus-free half-tubers. Latent "X" symptomless or Negligible Mottle
4 strains "X" of increasing virulence	Majestic and A. Banner	10 to 24 nil to 21	Bawden *et al.* (1948)	Inoculated virus-free half-tubers with X^m, X^b, X^v, or X^n viruses

infected with the mildest strains of "X" in preliminary tests against virus-free plants. In a continuation of their 1947 work Clinch and McKay (1949) found that two avirulent strains of "X" caused reductions of 12 and 8 per cent. in the crop of one clone of the variety Up-to-Date but, when similarly inoculated into another clone of this variety, no effect on the yield was produced. They conclude that, so far as cropping power is concerned, different clones of the same variety may react differently to infection with the same mild strain of virus "X," and that this reaction may be considerably affected by environmental conditions.

(iii) *Interveinal Mosaic*

EXTERNAL APPEARANCE.—It is only after considerable experience that this disease can be distinguished in the field from common Mosaic. The leaf-blades are flat or slightly undulating in their margins and the foliage has a characteristic grey-green colour. This is partly due to the type of mottling, which is more regularly disposed than in common Mosaic and consists of yellowish-green areas between the veins bordered by the dark-green zones of the veins themselves, the effect being to give somewhat of a striped appearance to the leaf-blades. There is no necrosis and little or no reduction in vigour.

INTERNAL CHARACTERS.—There appears to be no fundamental difference between common Mosaic and Interveinal Mosaic in their effects upon the plant cells, according to the studies of Clinch (1932), and similar " X " bodies (page 475) are to be found within the cells. In grafting experiments with Interveinal Mosaic material Clinch, Loughnane and Murphy (1936) produced a tuber necrosis similar to but rather more severe than that found in Aucuba Mosaic (page 449). This effect on the tubers occurred in all the varieties in which they had already recorded it when Aucuba Mosaic was used, as well as in Arran Victory, Up-to-Date and Irish Chieftain, which do not show tuber necrosis with Aucuba caused by virus " G." Although, as in the case of this latter disease, it is still unknown to what extent the tubers are affected in naturally infected plants, a causal connection is usually assumed between the naturally occurring Pseudo-Net Necrosis of tubers (page 431) and one or other of the two virus diseases, Aucuba Mosaic or Interveinal Mosaic.

INHERITANCE AND TRANSMISSION.—The disease is normally carried in the tuber and it has been artificially transmitted to healthy potato plants by grafts (Quanjer, 1923; Murphy and Loughnane, 1936), whilst it has been successfully transferred by juice inoculation to tomato, tobacco and *Solanum nigrum* (Quanjer, 1923) and to *Datura stramonium*, *Nicandra physaloides*, tobacco and *Nicotiana rustica* by Murphy and Loughnane (1936).

According to K. M. Smith (1933, 1937), Interveinal Mosaic is due to a single virus " X," but Loughnane (1935) regards it as a complex of this virus and virus " F " (*cf.* page 487), and all recent studies by this worker and his colleagues are believed by them to confirm the dual nature of the disease. Neither of the two viruses is insect transmissible, alone or together, and there is no evidence of the direct transmission of Interveinal Mosaic by means of insects in the field. Loughnane and Murphy (1938), however, present evidence of the complex being spread by leaf contact, which is not surprising since each of the viruses is easily inoculable by needle to potato (pages 500, 501). There is a further possibility of field transmission by means of the aphid *Myzus persicæ*, since Clinch, Loughnane and Murphy (1936) have succeeded in so transferring virus " F " in the presence of virus " A." Virus " A " is not a constituent of Interveinal Mosaic, but if the two viruses " F " and " A " are transmitted to plants already infected with virus " X " it is possible that a form of Interveinal Mosaic would result.

PREVALENCE AND LOSS DUE TO INTERVEINAL MOSAIC.—The disease was first named from material of the variety Duke of York by Quanjer, but has now been identified in a number of other varieties, *e.g.* President, British Queen, Majestic, Arran Banner, Arran Victory, Champion and Great Scot. There is no available information as to the extent to which stocks of these or other varieties may be infected with the disease, or the effect the disease may have on the yield.

(iv) *Marginal Leaf-Rolling Mosaic*

EXTERNAL APPEARANCE.—This disease, at least in its typical form, is only known to occur in the three varieties Catriona, Katie Glover and Arran Chief. Symptoms are seen only in the foliage, the leaves showing a mottling of light and dark green areas in the centre of the blade and a very pale or yellowish margin. The margin is also extremely wavy and undulating, and usually curls upward to give a shallow boat or " punt " effect, with the exposed lower surface of the margin appearing grey-green in contrast to the darker green of the upper surface. The characteristic marginal curling may occur in any of the leaves but is most common in the upper part of the plant, and this, together with the undulating edge, serves to distinguish the disease from true Leaf Roll or the physiological curling of the margin referred to on page 439, in certain varieties. When, as often happens, the margin of the leaf fails to curl upward the symptoms are those of typical Crinkle. Indeed, Marginal Leaf-Rolling Mosaic is sometimes regarded as merely a varietal form of typical Crinkle. (Fig. 86.)

INTERNAL CHARACTERS.—One objection to accepting the disease as ordinary Crinkle is the accumulation of abnormal amounts of starch and, presumably, of sugars in the marginal chlorotic part of the leaf, resulting in the upward marginal curling. There can be no doubt, therefore, of carbohydrate transportation being impeded although phlœm necrosis has not been recorded. It is probable that the degree of marginal rolling is determined by the excess of sugars in the cells and therefore by the environmental conditions for photosynthesis. It is not known whether " X " bodies occur within the cells.

INHERITANCE AND TRANSMISSION.—Nothing is known as to the means, if any, of natural spread of this disease in the field. All tubers from an affected plant will themselves produce plants with more or less typical symptoms, and as the final upward curling of the margins may occur at any time during the season, an impression is given of a rapid spread of the disease within the variety which may not be justified. If other varieties contract the disease from one of the three varieties Catriona, Katie Glover and Arran Chief, the symptoms produced must be quite different, and there is no evidence as to whether such transmission, in whole or in part, does occur to other varieties. Nothing indeed is known of the constituent virus or viruses producing Marginal Leaf-Rolling Mosaic. It cannot be identified with Quanjer's Marginal Leaf Roll (1923), since no mottling was described by Quanjer as occurring in this disease. Nor does it appear to be identifiable with the American disease known as Leaf-Rolling Mosaic in which the leaves are described as rolling along their midribs (Schultz and Folsom, 1923) and differing mainly from Leaf Roll in remaining flaccid.

EXTENT OF LOSS.—There is no reliable information as to the extent or nature of the loss due to this disease, but it seems probable that it is similar to that caused by Crinkle.

(C) SEVERE FORMS OF MOSAIC

For Certification purposes the severer forms of Mosaic, from which heavy losses in yield can be expected, are distinguished from the milder types already described. Severe

Mosaic diseases give rise to plants of reduced vigour, usually dwarfed, and with necroses in some form (spotting or streaking of the foliage. The leaves are often reduced in size and show puckering or distortion of the leaf-blades. A plant showing some of these symptoms will certainly be counted among the " Severe Mosaics " by any Inspector, though doubts may arise with robust plants, vividly mottled, but showing little or no necrosis of the foliage. Such " border-line " cases, which usually result from infection with a severe, but non-necrotic, strain of virus " X " should also be regarded as " Severe Mosaic " if the standards of certification are to be maintained.

(v) *Crinkle*

EXTERNAL APPEARANCE.—Crinkle is one of the common " severe mosaic " diseases, and there is usually a marked reduction in vigour. The leaf-blades show a conspicuously heavy, blotchy mottling and are much distorted (Figs. 84, 86). This distortion is due to a blistering of the surface and/or to a twisted or undulating margin. Typically, the margins and leaf-tip do not curl downwards although individual leaflets may do so ; these symptoms should be compared with those described for Mosaic (page 451) and Rugose Mosaic (page 464).

INTERNAL CHARACTERS.—The microscopical characters of Crinkle have been studied by Clinch (1932), who considers the effects of the disease to be similar to, but more pronounced than, those described by her for Interveinal Mosaic (page 541) ; there is a further similarity in that " X " bodies within the cells are most abundant in plants suffering from prolonged effects of the diseases and are inconspicuous in young diseased plants. The occurrence of tuber necrosis in certain varieties is reported by Murphy (1938) as being diagnostic of Crinkle, but there is no evidence of the extent to which it is found in naturally infected material of the disease.

INHERITANCE AND TRANSMISSION.—Like other virus diseases, Crinkle is tuber-borne ; there is no evidence as to whether it can be inherited through the true seed produced by an infected plant. Murphy and McKay (1932) have shown that the full symptoms of Crinkle can be transmitted by grafting stems or " core " grafting tubers. These authors proved that typical symptoms of Crinkle are produced by a combination of the viruses " X " and " A " and the complex nature of the disease is now generally accepted. Nevertheless, the more virulent strains of the former virus (" X ") alone can undoubtedly give rise to symptoms indistinguishable from those produced by the combination, and it is uncertain to what extent the disease in the field should be attributed to one or to double infection. Clearly, this is important in any discussion of field transmission. In any case in which Crinkle is due to virus " X " alone, the only known method of transmission in the field is by contact, whereas when virus " A " also is implicated this unit virus can be transmitted to plants already infected with virus " X," with the result that Crinkle will develop in its progeny when planted. The double-virus form of Crinkle can also be transmitted by sap inoculation (Bawdon, 1936).

PREVALENCE AND LOSS DUE TO CRINKLE.—If, as is assumed in this book, the name Crinkle is used in the sense in which it was originally coined by Murphy (1920, 1921), as purely descriptive of the *symptoms* displayed by an affected plant, it must be accepted that the disease occurs in typical form in many varieties. The later view expressed by Murphy and McKay (1932*b*)—when the disease in certain varieties was proved to be due to the combined effects of two viruses " X " and " A "—that the name should be confined to such cases of dual infection, has obvious advantages as can be seen from the discussion above on the field transmission of "Crinkle." Inevitably, however, it entails the segregation of a group of varieties which simulate Crinkle in the field, but which are now known to be " field immune " from virus " A " and have never been found to contain this virus under field conditions. Thus, what is believed to be true Crinkle (" X "+" A ") can be found in Golden Wonder and Langworthy, President, King George, Irish Chieftain, Catriona, Champion, Myatt's Ashleaf, Skerry Blue and Ulster Monarch among others. Similar symptoms in Kerr's Pink are probably due to virus " X " alone, and in Epicure or King Edward to virus " Y." The variety Golden Wonder, until recent years, was almost wholly infected with Crinkle, but stocks showing only mild symptoms of Mosaic are now on the market. Reliable evidence as to the loss in yield caused by Crinkle is difficult to obtain. However, Table XXIII, compiled from the " Guides to Experi-

FIG. 87.—Variety Majestic; *Left*—Normal ("carrying" virus "X") (page 501); *Right*—Leaf-Drop Streak; Virus "Y" (page 461).

ments at Craibstone" (1936-1939), illustrates the loss caused by a disease referred to as Crinkle, but which may be a form of Simple Mosaic in the variety Kerr's Pink, and what is probably the complex form in the varieties Langworthy and Golden Wonder.

TABLE XXIII

Percentage Loss due to "Crinkle" at Craibstone

Year.	Kerr's Pink.	Langworthy.	Golden Wonder.
1935	35	32	36
1936	19	16	26
1937	43	46	51
1938	38	42	41

In the first two varieties the loss is attributable solely to the presence of the disease, but in the Golden Wonder trial the figures represent the combined effect (1935, 1936) of contrasting the yields from sprouted, well-manured tubers free from Crinkle and those which were unsprouted, unmanured and were infected with the disease. On the other hand, in the years 1937-1938, the results are the *nett* differences obtained when Golden Wonder tubers without Crinkle but well sprouted and well manured were contrasted with others free from the disease but unsprouted and unmanured. The table is also of interest in showing the effect of season on the loss, for in each variety the loss was considerably reduced under the growing conditions of 1936. The disease "Crinkle" is not recognised in U.S.A., where the symptoms produced by a combination of virus "A" with Latent "X" (healthy potato virus) is known as "Mild Mosaic." According to Schultz and Bonde (1944) this form of "Mild Mosaic" is responsible for a reduction in yield of some 25 per cent.

(vi) *Leaf-Drop Streak* (*Streak*)

EXTERNAL APPEARANCE.—This disease is now generally regarded as the first-year reaction of the plant to infection with virus "Y," although in at least two varieties (Gladstone and Katahdin) the symptoms may be reproduced exactly in the following year also (Bawden and Kassanis, 1947). Typically, the field symptoms are well marked and unlikely to be confused with other diseases of the "severe mosaic" group. Shortly after infection occurs, black necrotic spots appear on the inoculated leaf and a blotchy mottling develops which spreads during the first month throughout the foliage. Brown or black streaks appear on the lower side of the veins of the leaves and these extend down the petioles into the stem. The petioles become very brittle and the leaves fall off (or hang suspended by only a thread of tissue) in succession from the base towards the top of the foliage, to describe which the name "acropetal necrosis" has been coined. The youngest leaves do not fall but usually show a corrugation of the surface between the veins and an undulation of the margins, in addition to a diffused or blotchy mottling. The final appearance of the infected plant in the field recalls that of a palm tree with its bare stem surmounted by a tuft of young leaves at the apex. (Fig. 87.) No tuber symptoms have been confirmed in any variety (but *cf.* page 427). Unfortunately the typical foliage symptoms are not shown by many commercial varieties, some of which may exhibit only varying intensities of mottling or may even "carry" the disease with few or no symptoms. According to Salaman (1932), potato varieties react as follows when infected with the streak-producing virus (virus "Y," *cf.* page 507).

(a) *Mosaic or "Crinkle" with Veinal Necroses and Leaf-Drop Streak*—Arran Banner, British Queen, Up-to-Date, King George V, Majestic and President.

(b) *Veinal Necroses and Leaf-Drop Streak* only—Arran Consul and Arran Crest.

(c) *Mosaic and Veinal Necroses* only—Abundance, Arran Chief and Great Scot.

(d) *Veinal Necroses* only—International Kidney and Sharpe's Express.

(e) *Mosaic or "Crinkle," sometimes with small necrotic spots*—Arran Victory, Duke of York, Epicure and King Edward VII (Fig. 85).

(f) *No symptoms*—Di Vernon and Kerr's Pink.

Even if virus "Y" is assumed to be a simple, stable, entity, it is obvious that it may produce a wide range of distinct diseases according to the variety of potato infected. But

Salaman, even in 1937, had already found an attenuated form of the virus in *Schizanthus* and, ten years later, Bawden and Kassanis (1947) showed that many distinct strains exist and express themselves in a wide range of reactions. Thus Majestic, King Edward VII, Doon Star and Arran Banner, react with necrosis and Leaf Drop Streak to some strains of the virus, and with Common Mosaic to others. Gladstone and Katahdin proved to be necrotic to all strains and Arran Pilot was necrotic to none. Hence, not only does the same strain produce different reactions in different varieties of potato but, with each variety, there is an equally wide range of type and severity of symptoms with different strains of the virus. Further, these workers showed that the reaction differed according to the stage of development of the tissues when invaded. Thus, the varieties Majestic and Up-to-Date showed the normal Leaf-Drop Streak when infected in the field, and in most cases the usual second year symptoms of Severe Mosaic (*cf.* Rugose Mosaic, page 464) developed in the progeny; but occasionally an "eye" on a tuber had obviously escaped infection during the previous autumn and winter and grew without symptoms until, in turn, the shoot became infected, with the result that this shoot (alone among the "Mosaic" shoots) developed Leaf-Drop Streak. Hence, the authors conclude, in these varieties at least the tissues react necrotically only if well developed at the time of infection, while Mosaic characterises tissues infected soon after initiation. Also Hansen (1941), after stating that some tubers on a plant showing Leaf-Drop Streak may escape infection, records the occurrence of occasional shoots developing normally from infected tubers, and only succumbing after several weeks of apparently healthy growth. This he explains as due to a localisation of the virus in the tuber, resulting in the production of initially healthy shoots into which, as they mature, the virus can only penetrate very slowly; he does not suggest that the symptoms which finally develop in these initially healthy shoots differ from the Rugose Mosaic shown by the remaining shoots of the tuber.

Inheritance and Transmission.—There is no evidence to show whether this disease is inherited through the true seed. Stelzner's (1942) claim to have found the virus in the embryos of potato and *Datura* requires confirmation since *Datura* is usually regarded as immune from infection with " Y " ; in any case Stelzner says the virus is inactivated during the ripening, storage, and germination of the seed. Certainly very similar symptoms have several times occurred in first-year seedlings, but in all such cases the streaking and leaf-fall appear to be due to some constitutional weakness not transmissible by graft or other means to a healthy plant. Streak is perpetuated through the tubers, the plants arising from them usually exhibiting the symptoms described below as Rugose Mosaic. The method of transmission in the field to healthy plants, so far as is known, is wholly by means of aphides, of which the most efficient vector is *Myzus persicæ* (*cf.* page 260). Experimentally, it can also be transmitted by graft or by juice inoculation, neither method of course operating in nature, nor is there any evidence that Streak can pass over to a healthy plant by mere contact or natural bruising of the foliage (Smith, 1943). According to Murphy (1938), all cases of Streak in the field are due to virus " Y," but, as shown above, not all cases of " Y " infection result in Streak.

PREVALENCE AND EXTENT OF LOSS.—Streak must be regarded as one of the most serious diseases affecting the potato, the yield both in number and size of tubers being greatly reduced. The records of its distribution open up several interesting problems. It is regarded as the most important cause of deterioration of stocks, particularly in the varieties Majestic and King Edward, in the eastern and south-eastern parts of England, whereas it is much less common in the west and north-west. In Ireland it is also stated to occur rarely, whilst in Scotland, according to Cockerham (1939), the disease is localised in the south-west ; the problems are discussed further on page 465 and in Chapter XXIX (page 575).

(vii) *Rugose Mosaic*

EXTERNAL APPEARANCE.—A typical infected plant is stunted, sometimes prostrate, with the leaves markedly corrugated between the veins, distorted, and with downwardly curling margins and leaflet-tips. Mottling may be difficult to see and the leaf surface may be so stippled with minute necrotic spots as to give a brownish, rusty appearance to the foliage. The petioles may be brittle and, in consequence, some of the oldest leaves may fall off.

SYMPTOMS WITH WHICH RUGOSE MOSAIC MAY BE CONFUSED.—The disease is usually separated with ease from others except Crinkle or the effects of mineral deficiency, particularly potash. As regards Crinkle, the heavy mottling and wavy margins of the leaves are the best criteria. Potash deficiency in the soil gives a similar stippling and rusty appearance to the foliage but there is usually no distortion, nor is the plant markedly stunted ; these characters, together with the occurrence of the symptoms in all plants over a wide area of the crop, will usually indicate the direct effect of the soil.

INHERITANCE AND TRANSMISSION.—It is not known whether the disease is transmitted through the true seed, but all affected tubers produce plants showing either typical Rugose Mosaic or a still more dwarfed appearance known as Curly Dwarf (*cf.* below). Rugose Mosaic is now generally believed to be merely a " second-year " form of Streak and there can be no doubt that Streak plants do give rise to this condition. There is no proof, however, that all such cases of Rugose Mosaic arise in this way. Indeed, whereas Streak is due to virus " Y " the virus content of Rugose Mosaic plants is often given as a combination of viruses " Y " and " X," but this may merely reflect the almost universal occurrence of the latter virus in commercial stocks. On the other hand, only virus " Y " of this complex is aphis transmitted (the most effective vector being *Myzus persicæ*), so that the full development of Rugose Mosaic may possibly only occur when this virus is inoculated by the aphid into a plant already infected with virus " X." Rugose Mosaic is particularly common in south-western Scotland and in the east and south-east of England where Streak, due to virus " Y " is almost as serious a disease as Leaf Roll. Streak is relatively rare in most parts of Scotland, Ireland and Wales, but Severe Mosaic, including Rugose Mosaic, is by no means uncommon ; a lack of relationship which may conceivably be due either to late-season transmission of virus " Y " which fails to produce Streak symptoms in affected plants, or to confusion between true Rugose Mosaic and the severe symptoms of virulent " X," or " X "+" A," infection.

EXTENT OF LOSS.—Rugose Mosaic is to be classed as one of the " severe mosaics," for although no precise figures as to loss are available, there can be no doubt that it is considerable.

According to Bald (1945) the loss in yield is proportional to the diminution in leaf area, measured during thirty days after the beginning of tuber formation; it is expressed in the size and weight of the tuber rather than in the number produced.

(viii) *Curly Dwarf*

EXTERNAL APPEARANCE.—The name of this disease is a sufficiently accurate descriptive term. The plant is dwarfed either by a reduction in length of the stems, or more usually by the procumbent habit of the matted trailing stems. Mottling may or may not be visible but the leaves are invariably distorted and corrugated; the disease is unlikely to be confused with any other condition of the potato plant.

INHERITANCE AND TRANSMISSION.—There is no evidence of transmissibility through the true seed but affected tubers give rise to similar dwarfed plants. Curly Dwarf is one of the most degenerate forms taken by virus-infected potatoes, but it is uncertain whether all cases are due to the same virus complex. Usually it is regarded as an extreme form of Rugose Mosaic, and, if so, it may be assumed that the virus "Y" constituent is transmissible in the ordinary way by *Myzus persicæ*, although no evidence of this has been reported. However, according to Salaman and Le Pelley (1930), the varieties Arran Victory and Arran Chief assume the Curly Dwarf form in the second year after infection with virus "E" (Para-Crinkle, page 498). In any case there can be no doubt that Curly Dwarf is a reaction in which variety plays a large part. It is common in degenerate stocks of Irish Chieftain, Skerry Blue and Edzell Blue, but rarely occurs in the more popular commercial varieties. Affected plants give a negligible yield composed wholly of chats.

(D) VIRUS DISEASES ONLY RECORDED WITH CERTAINTY FROM OVERSEAS

(1) POTATO CALICO (Solanum Virus 10: K. M. Smith, 1937).—The symptoms differ from Aucuba Mosaic (page 449) principally in the large area covered by the yellow spots, which in this American disease often leaves little of the normal green visible. Its infectious nature was demonstrated by Porter (1931) who found it to be perpetuated in the tuber, and transmissible either by tuber-core grafts or by inoculating

healthy leaves with unfiltered sap from infected plants. It has not been transmitted experimentally by means of insects.

(2) Spindle Tuber (Solanum Virus 12 : K. M. Smith).—Affected plants are somewhat dwarfed and with an upright "staring" habit. The leaves tend to be greyish-green in colour with some rugosity (surface corrugations), while the leaflets are abnormally narrow with a tendency to overlap, even in varieties usually showing an "open" growth. The chief effect, however, is on the tubers, which are elongated with tapering ends and prominent eyes and "eye-brows." The affected tuber may have an unusually smooth and "tender" skin and the flesh cuts more easily. Many insects, including grasshoppers (Goss, 1928); aphides (*Myzus persicæ* and *Macrosiphum gei*, according to Schultz and Folsom, 1925); the tarnished plant bug, *Lygus pratensis*, various beetles and the larva of the Colorado Beetle, *Leptinotarsa decimlineata* (Goss, 1931), have all proved capable of transmitting this disease which, incidentally, can also be passed to healthy tubers by the cutting knife (Schultz and Folsom, 1925; Goss, 1926) and by the contact of freshly cut surfaces of diseased and healthy tubers (Goss, 1926). A very similar tuber spindling of some wilding types in British varieties is known, but there is no evidence that this condition is connected with any virus infection. According to Fernow (1923) the disease originally described in Dutch material by Quanjer (1923) as Marginal Leaf Roll is identifiable with Spindle Tuber.

(3) Yellow Dwarf (Solanum Virus 16 : K. M. Smith).—Was described in U.S.A. by Barrus and Chupp (1922). Typically the stems are spindly, with necrotic pith, and with internodes so shortened that the plant may assume a dwarfed, rosette, appearance. The stem growing points may die back and the flowers either fail to open or wither. A characteristic feature is the upward rolling of the leaflet margin accompanied by a downward arching of the mid-rib; a mild mottle may also be visible on the yellowish foliage. The tubers, which may fail to grow, are deformed and often show external cracks; when cut open the flesh exhibits scattered, small, necrotic spots in the pith and internal phlœm region of the vascular bundles. Late-infected plants frequently show no symptoms and this, together with the failure of tubers to grow, may possibly be related to the marked reaction of the infected plant to differences

of temperature. Thus high air temperatures of 24° C. to 28° C. (75·2° F. to 82·4° F.) cause the most severe symptoms to develop, while at 16° C. (60·8° F.) the symptoms are masked. Similarly the high soil temperature of 75·2° F. to 82·4° F. may result in the failure of infected tubers to emerge above ground, or in the early development of symptoms in those that do grow (Goss and Peltier, 1925; Walker and Larson, 1939). Yellow Dwarf is transmitted by the clover leaf-hopper, *Aceratogallia sanguinolenta* Prov., and, with difficulty, by sap inoculation (Black, 1937).

(4) WITCHES' BROOM (Solanum Virus 15: K. M. Smith).—This disease was first described in U.S.A. by Hungerford and Dana (1924). The symptoms agree closely with those found in Wildings (page 75) in this country, and the development of yellowish or chlorotic leaf margins in the American disease is reminiscent of forms of marginal variegation seen in some "undesirable variations" in British seed stocks. Murphy and McKay (1932*a*) equated Witches' Broom with Wildings from Irish and Scottish sources but this has not yet been confirmed by other workers; there can, however, be no doubt of the existence in this country of a transmissible disease, closely similar to Witches' Broom, and easily confused with Wildings. Witches' Broom differs from the Wilding type first in the fact that flowering is stimulated rather than retarded and, most important of all, in being infectious. The Wilding condition is perpetuated in the tuber but is not transmissible to a healthy plant. Witches' Broom, on the other hand, is transmissible by tuber-core or stem grafts, and Kunkel (1943) has also succeeded in transmitting the American disease from potato to tomato and tobacco by using Dodder to serve as a link between these plants and the source of infection; he failed, however, by these means to transfer the disease from potato to potato. Witches' Broom is said to spread under field conditions, but no insect vector is known. Current season infection in American varieties results in "primary" symptoms in which prolific branching occurs only in the young "tops"; the leaves are dwarfed and sometimes develop purplish centres with yellow or chlorotic margins. The tubers, as with Wildings, are very small in size but very numerous, and may be produced at intervals (necklace fashion) along a stolon; on being cut open, diseased tubers may show Net Necrosis (page 428).

The temperature relations seem to have similarities with Yellow Dwarf, for Kunkel (1943) grew normal-looking plants from infected tubers, not more than three-quarters of an inch in diameter, by exposing them for six days to a temperature of 36° C. (96·8° F.); symptoms also were largely masked in plants maintained at this temperature under glass.

(5) APICAL LEAF ROLL (Solanum Virus 17: K. M. Smith).—Has been described from U.S.A. by Schultz and Bonde (1929) as resembling Witches' Broom, but differing in being taller and more vigorous, though with fewer shoots and producing fewer and larger tubers. It still more closely resembles the current-season symptoms of Leaf Roll (page 438), from which it can be distinguished, however, by the persistence of rolling only in the uppermost leaves in the progeny of infected plants. The disease is said to be transmissible by tuber-grafts but, since the original description, little or no investigation appears to have carried out; no insect vector is known (*cf.* Net Necrosis, page 428). Schultz is stated by Folsom (1942) as accepting a close resemblance between this disease and "Yellow-Top," and K. M. Smith (1937) equates these two diseases.

(6) YELLOW TOP (Solanum Virus 17: K. M. Smith).—This disease was first described in America (Maine) by Folsom (1926). The symptoms include distinct dwarfing, a stiff leaf-texture, premature death and Net Necrosis in the tubers. Sometimes there is extreme chlorosis or distinct leaf-rolling and, on some occasions the many small tubers are produced, "necklace" fashion, along a stolon. The whole top of the plant has a yellowish hue and this, and the prolific development of aerial tubers in the leaf axils, serves to distinguish the disease from Leaf Roll. Yellow Top certainly spreads in the field (Folsom, 1942) but the insect vector, if any, is unknown. Folsom regards Yellow Top as probably identical with one or more of a group of closely related diseases of the "Yellows" type, *i.e.* Apical Leaf Roll, Witches' Broom and Purple Top (Aster Yellows). Kunkel (1943) definitely identifies Yellow Top with Witches' Broom.

(7) PURPLE TOP (*Callistephus* Viruses 1 and 1A: K. M. Smith).—This usually minor disease of the potato in U.S.A. can at times constitute a serious problem (Folsom, 1942). The symptoms as described by Severin and Haasis (1934)

include the production of slender, purple sprouts, on some of which terminal, leafy, aerial tubers may develop. In the growing plant the shoots are purple and carry aerial tubers in their leaf axils. The leaves have upwardly rolled margins and the petioles and mid-ribs are arched downwardly; the maturing leaves turn yellow, dry, and both leaves and stems become brittle. These symptoms were produced by Severin and Haasis in the course of transmission studies of the California Aster Yellows disease by means of the insect vector—*Macrosteles divisus* (Uhl) = *Cicadula sexnotata* Fall, but the authors report that they were unable to recover the virus from the infected potato by means of this insect. Kunkel (1931) had failed to transmit the eastern or New York form of Aster Yellows to potato and, later, he (Kunkel, 1932) and Severin (1932) reported a similar failure to transmit the eastern disease to Celery whereas the western form of Aster Yellows was readily transmitted to celery by the leaf-hopper *Macrosteles divisus*; these differences, among others, led to the eastern and western forms of Aster Yellows being regarded as due to distinct strains of the same virus. Kunkel (1937) has demonstrated the readiness with which the virulence of the virus is affected by changes in temperature (*cf.* page 567), and it is interesting therefore to note that Purple Top in potato has now been transmitted by *Macrosteles divisus* carrying the *eastern* strain of the virus (Epps, 1943; Younkin, 1943*a* and *b*), the latter author, however, describes the disease in the potato variety Green Mountain as causing a yellowing, dwarfing and upward-rolling of the youngest leaves, with the production of axillary shoots and aerial tubers. There was also a form of necrosis in the stem bases and roots, and Net Necrosis developed in some tubers. In the meantime Leach (1939) reported the production of Purple Top in potatoes by the use of *M. divisus* collected from wild plants, though Folsom (1946*a*) regarded the symptoms so produced as closely resembling Yellow Top. In the following year Severin (1940) identified a naturally occurring potato disease as Purple Top, and in 1946 Leach and Bishop confirmed that this naturally occurring disease was due to Aster Yellows virus transmitted by the leaf-hopper *M. divisus*. The reader will have realised that the symptoms ascribed to Purple Top have been regarded as characteristic of one or other of the various diseases described under (3) to

(6) above, but Leach and Bishop (1946) add characters which are certainly confined to Purple Top. They state that the disease is never seen in young plants, the first symptom—a purple colour, of varied tint, in the foliage—developing at, or after, flowering and this is followed by wilting some two or three weeks later. Two further statements are unique for any virus disease, and suggest similarities with the condition Psyllid Yellows described below. Thus Leach and Bishop assert that Purple Top is not perpetuated in the tuber, while Folsom (1942) suggests the possibility that two forms of Purple Top exist, one of which is perpetuated in the tuber and the other is not. In the tuber-transmitted form, Folsom states that tubers from primarily infected plants either fail to grow or give rise to only weak plants ; the tubers produced by such weak plants will, however, produce almost normal plants and tubers the following year.

(8) PSYLLID YELLOWS (Solanum Virus 18 : K. M. Smith).—This malady was first described on potato and tomato from Utah by Richards (1928). The symptoms on potato include, first, an upward rolling of the young leaves, the margins of which turn yellow ; in some American varieties with pigmented tubers, the rolled leaves develop a brilliant reddish or purple colour. Older leaves later roll upward, become yellow, necrotic, and die. Axillary buds form a profusion of aerial tubers or rosettes of bright-coloured and distorted leaves. Tuber formation is reduced and, instead, some stolons produce aerial shoots. Shapovalov (1929) thought the condition was perpetuated in the tuber, but Richards and Blood (1933) were not able to confirm this statement. They showed, however, that the malady was closely associated with the feeding of the nymphs, only, of the tomato psyllid *Paratrioza cockerelli* Sulc., but reached no conclusion as to whether the toxic saliva of the psyllid was responsible, or that the insect merely served to transfer a virus to the plant. On this rather doubtful evidence K. M. Smith (1937) has accepted the virus nature of the malady, but this is strongly opposed by some American workers (Leach, 1940 ; Carter, 1941). Although it is not usual for a salivary toxin to produce systemic effects in a plant, cases of this are certainly known, and the evidence in favour of Psyllid Yellows being due to a systemic toxin, is strong. Richards and Blood (1933), for instance, showed

that the symptoms varied with the number of feeding nymphs and that if the insects were removed there was no further development of symptoms and the plant tended to recover. If, in spite of this evidence, the malady is still to be regarded as due to a virus, it must also be accepted as one of the few cases of the inheritance of a virus by an insect (*cf.* page 556) for Richards and Blood state that the ability to produce Psyllid Yellows symptoms is confined to the larval stage but is nevertheless inherited by the insect without any necessity to feed on an affected plant.

(9) GIANT HILL.—The symptoms described are similar to those seen in " Bolters " which, like Wildings, are regarded in Scotland as of genetic or constitutional origin and not as caused by any virus. In America, also, most attempts to transmit the condition known as Giant Hill have failed, but Dana (1926) has stated that he succeeded once in transmitting it by means of a core-graft.

CHAPTER XXVII

VIRUSES IN RELATION TO POTATO DEGENERATION

(1) INTRODUCTION

SINCE Pasteur's classical researches on the relation of bacteria to disease, no single discovery has so stimulated investigation as has the discovery of the existence of viruses. So far as plant diseases are concerned the initiative came from Holland when Mayer (1886) discovered the contagious nature of the Mosaic disease of tobacco, and showed that the cause was an organism capable of passing through the pores of a filter-paper. This was followed in 1892 by Iwanowski's demonstration that even a fine-pored Chamberland filter, of unglazed porcelain through which the smallest known bacterium was unable to pass, was no barrier to the Mosaic organism. Finally, Beijerinck (1898) advanced evidence of the ability of the pathogen to diffuse through agar-jelly without losing its power to reproduce the disease. This result (although never confirmed) led him to postulate, as the cause of the disease, an infectious living fluid—*Contagium Vivum Fluidum*—which startled the scientific world, and released an investigational fervour as infectious as the pathogen. The similarity of this plant disease with certain animal maladies was quickly appreciated and the non-committal name of "virus" or "poison," already in use, was adopted to designate any infectious agent capable of passing, unharmed, through a bacterial filter. Virus particles, with perhaps one exception, are less than 1/6000 mm. (1/152,400 in.) in diameter, and are therefore below the limit of vision with the highest magnification of the ordinary optical microscope. Some of the larger animal-viruses were photographed by Barnard (1932, 1935), using the shorter wave-lengths of ultra-violet light ; a method which, however, did not permit of any measurement of the particles. The first measurement of a plant virus (tobacco Mosaic virus) was made the following year by Bawden *et al.* (1936) when, by X-ray analysis, the virus particles were shown to have a width of 15·2 mμ. (mμ. = one-millionth of a millimetre) and a minimum length of ten times the width. Many measurements of virus particles have since become possible by means of the electron microscope in which light rays and lenses are replaced respectively by a beam of electrons and a magnetic field. The first plant virus to be photographed and measured by this latest instrument of precision was also tobacco Mosaic virus (Kausche *et al.*, 1939), who confirmed the width of the particle as 15 mμ. and the length as varying from 150 mμ. to 300 mμ.; other viruses are now known which are, however, isodiametric. Minute as they are, however, these particles possess some, at least, of the attributes of living organisms and are capable of inducing such serious diseases as small-pox, measles, mumps, influenza, typhus, yellow fevers, and infantile paralysis in man; foot and mouth disease, swine fever, louping ill, rabies and distemper in farm animals, and a vast number of diseases affecting plants.

The form taken by a virus *within* an infected cell is still unknown, but as early as 1903 Iwanowski drew attention to the occurrence of amorphous (amœboid) and crystalline plates among the cell inclusions, which he believed to be specific to virus infection though not the cause. Since then other forms of inclusions have been described, including "raphide-like" spikes, crystalline spindles and long, coiled inclusions of a fibrous nature (Henderson Smith, 1930; Sheffield, 1931; Kassanis and Sheffield, 1941) and a causal relationship has been abundantly confirmed between virus infection and all these varied cell inclusions. Much controversy has ranged around the nature of this relationship but before this can be discussed, however briefly, we must assemble the outstanding facts regarding the structure and occurrence of these cell inclusions. (*a*) The crystalline plates are true three-dimensional crystals usually in the form of more or less perfect hexagons, colourless and transparent and with a relatively high refractive index. When viewed edgeways through crossed Nicol prisms they are strongly birefringent with straight extinction, but show no birefringence when viewed through the flat surface; these being characters shared by other, undoubted, crystals. These inclusions were only known to occur in the cytoplasm of plant cells infected with viruses, though long known in the *nuclei* of infected animal cells. In 1939, however, Kassanis showed that the nuclei of plant cells infected with tobacco Severe Etch contained similar crystalline plates which behaved with most stains in much the same way as the nucleoli. Since then they have been described in the nuclei of cells infected with tobacco Mild Etch (Bawden and Kassanis, 1941), and in one only of the strains of tobacco Mosaic virus (Woods and Eck, 1948). The occurrence of two nuclei in cells infected with a virus had been noted by Sheffield (1936) and Salaman (1938), and in 1941 Sheffield observed that nucleic inclusions occasionally caused a direct division of the nucleus into two, followed by the liberation of the crystalline inclusion into the cytoplasm and the formation of new crystals in the " daughter " nuclei. There seems to be no record of any type of crystalline inclusion body (either in the nucleus or cytoplasm) in cells affected with any potato virus. (*b*) The fibrous inclusions have an interest of their own in being the only crystalline form in which viruses have been precipitated *in vitro*, whether " pure " or combined with other substances. Bernal and Fankuchen (1937), who drew attention to this fact, also pointed out that the fibrous forms are " two-dimensional " in the sense that while the elongated constituent particles are arranged parallel to each other, and at a fixed interval to give a regular pattern, there is no regularity of particle arrangement in the direction of their length ; the fibrous bodies therefore belong to a type of " liquid " or " para " crystals having the essential characteristic of birefringence. They have been found both in the nucleus and cytoplasm of infected cells. (*c*) In contrast to the crystalline inclusions, the amorphous (amœboid) types are found only in the cytoplasm. They are either structureless, irregular bodies, or globular to elongated forms resembling rather compact masses of protoplasm in being translucent, granular, and usually vacuolated. Henderson Smith (1930) and Sheffield (1934) were not able to find confirmatory evidence of the existence of an external membrane as claimed by Goldstein (1926) though certain facts suggested that such a membrane might well occur. The aggregation of discrete particles to form the amorphous " X " bodies, as they were appropriately called by Goldstein (1926), was observed by Sheffield (1931), and they were shown to be carried passively in the cytoplasmic stream, picking up extraneous particles such as oil-drops and mitochondria *en route*, and being temporarily indented after collisions with the nucleus or other cell bodies. Similarly, different " X " bodies would temporarily unite, and later separate again, and so give rise to the earlier belief that they are " amœboid " in nature. In size the " X " bodies range from about 3 mμ. to 30 mμ. according to the size of the containing cell, and although very sensitive to changes in osmotic pressure they resist changes in *p*H ; remaining unaffected at a *p*H as low as *p*H 2 (Bawden, 1950). As with the crystalline inclusions, the " X " bodies react to all the usual protein-stains ; they can, however, be differentiated from the nucleus by means of Feulgen's reagent which stains red the desoxypentose nucleic acid characteristic of chromosomes but has no effect on the ribose-type of nucleic acid found in the " X " bodies.

It must not be assumed that cell inclusions invariably accompany virus infection, for that is by no means the case and in the great majority of virus diseases they have not as yet been demonstrated. Thus they occur abundantly in association with many strains of potato virus " X " but very sparsely with potato virus " Y," and only a new staining technique has recently disclosed their presence in potato Leaf Roll (Bald, 1949) ; they have not been found in any other potato virus. When they do occur there is evidence that they are to be found in all tissues in which the presence of the virus can be demonstrated except the primordial meristem (Clinch, 1932 ; Sheffield, 1942). Indeed, Goldstein (1926) claims to have seen them even in this tissue, but this is discounted by Sheffield (1941) who states that she always found the cytoplasmic inclusions (in Severe Etch) to develop later than the intranuclear ones, and these latter never formed until all *normal* nuclear division had ceased. The distribution of the cell inclusions is not uniform in plant tissues ; in tobacco Mosaic, for instance, they are most abundant in the leaf epidermal cells and hairs, while in potato virus " X " they seem to aggregate in the leaf palisade tissue (Salaman, 1938). Nor is this abundance related to the degree of severity of external symptoms, for Salaman (1938) found more in association with a symptomless (avirulent) strain of potato virus " X," and in one producing only a yellow mottle, than in the more virulent necrosis-producing strains ; an observation which was later confirmed by Bawden and Sheffield (1944). In any case both crystalline and amorphous " X " bodies are somewhat unstable, particularly the cytoplasmic crystals ; though not sufficiently so as to prevent fixation by normal technique. Bawden (1950) states that, under good growing conditions, the amorphous " X " bodies begin to develop within a week after the plant has been inoculated with the virus ; for a month or so they continue to increase in number and size, but after a further month they begin to disintegrate—often with the internal development of a crystal which enlarges until the original amorphous body disappears. Although crystals are known to form without the intervention of an amorphous stage, the cases of transition from amorphous form to crystal indicate that the two kinds of inclusions must at least have some common constituent.

The controversy as to the nature of cell inclusions received an impetus from the continued failure of workers to substantiate claims to have discovered the cause of virus diseases in the form of organisms such as bacteria, flagellates, amœbæ and Myxomycetes ; it is still far from being settled. Iwanowski's (1903) conclusions that the bodies represent either reaction products of the cell protoplasm or abnormal products of nuclear division are now known to be in error (when stated in this form at least) both as regards the crystalline and the amorphous forms. Both Iwanowski (1903) and Goldstein (1924) produced crystalline " needles " by adding dilute acid to cells containing crystalline plates, and Beele (1937) pointed out important resemblances between such needles and the paracrystalline precipitates obtained by Stanley (1935) from purified tobacco Mosaic virus maintained within a range of *p*H 4 to *p*H 3. There can be little doubt that the crystalline inclusions are very rich in virus, and Sheffield (1946) has demonstrated virus particles both in crystals and amorphous bodies by means of the electron microscope. Nevertheless, Bawden and Sheffield (1939) are of the opinion that the crystals are not wholly composed of virus, but rather of insoluble complexes formed by the union of virus with some constituent of the host cell ; a view which received strong support from Bawden and Pirie's (1937*a* and *b*) observations that purified tobacco Mosaic virus readily combines with some protamines and histones (*e.g.* Clupein), to form complexes whose behaviour in many ways resembles that of the crystalline cell-inclusions. A highly suggestive link between crystalline and amorphous inclusions is provided by potato virus "X." This virus forms liquid (para) crystalline solutions similar to those of tobacco Mosaic virus but, when precipitated by acids, salts, or clupein, the precipitate is not paracrystalline but amorphous (Bawden and Pirie, 1938); just as in the case of the cell inclusions with this virus. As regards the amorphous "X" bodies, the earlier work of Sheffield (1931, 1934) had suggested that they consisted of reaction products on which virus particles were adsorbed, but later studies have shown that the proportion of virus to reaction product is much higher than was imagined. Livingstone and Duggar (1934) found the concentration of virus to be higher in the protoplasm of the cell than in the cell-sap, while Sheffield (1939) proved that the individual "X" bodies consisted very largely of virus for, when extracted from the plant, they appeared to be about as infective as an equal weight of purified virus. The fact, however, that the "X" bodies often contain extraneous substances such as mitochondria and oil-drops, collected from the streaming protoplasm, indicates the probability that, as with crystalline inclusions, the "X" bodies are insoluble complexes of virus and cell proteins. Kleczkowski (1946) has demonstrated that tobacco Mosaic virus combines with, and is precipitated by, many cell proteins and material of opposite electrical charge but, on the other hand, Bawden (1950) suggests that this insoluble complex may only develop when a virus unites with cell products specific to that virus. Thus in the cases of tobacco Severe Etch, henbane Mosaic virus and potato virus "Y," the properties of the three viruses *in vitro* are very similar and they infect the same host-plants, yet Severe Etch produces copious inclusions in both nuclei and cytoplasm, henbane Mosaic virus inclusions are also abundant but are confined to the cytoplasm, while in the case of virus "Y" (where they are also confined to the cytoplasm) the inclusions are so rare and small in size that they escaped detection until recently. Bawden and Sheffield (1939) draw an interesting analogy between the formation of "X" bodies and the amorphous precipitates produced when strains of tobacco Mosaic virus are mixed with their antisera (see page 491) and note that the precipitate only forms if antibody and antiserum are present in correct proportions; the formation is inhibited, or the completed amorphous body is re-dissolved, in the presence of excess virus. Similarly, the cell inclusions are formed at an early stage of infection when the virus content may be assumed to be low, and tend to disappear later with increasing virus concentration. These authors, of course, do not suggest that, in fact, intracellular inclusions are formed in this way for there is no evidence that plants contain, or can produce, antibodies. They do suggest, however, that the formation of cell inclusions may in part act as a protective mechanism, for it is probable that a virus rendered insoluble in this way must exhibit greatly reduced biological activity. It may possibly be significant that all the substances (inhibitors) found capable of reducing virus infectivity are also able to combine with a virus to form an insoluble complex ; though it is agreed that the altered infectivity is not a simple relationship between inhibitor and virus, but includes also an effect on the host cell. The fibrous precipitates induced by the virus-inhibiting glycoprotein present in *Phytolacca* sp. (Kassanis and Kleczkowski, 1948) only form under certain rigid conditions and, as Bawden (1950) remarks, changes in the composition of the cell sap during metabolism such as variations in the type and concentration of electrolites or other metabolites, or *p*H changes, could determine whether a virus remains in solution or separates temporarily in some solid form ; while in the opinion of Kassanis and Sheffield (1941) the *type* of cell inclusion is largely controlled by environmental conditions, particularly the amount of light and heat available to the host plant. Whatever may be the ultimate outcome of these investigations into the nature of cell inclusions, we have obviously gone a long way to meet the view prevailing among students of animal viruses, that cell inclusions are aggregates of elementary bodies of approximately the same size as the estimated size of the virus particles, and are therefore to be regarded as visible aggregates of pure virus particles.

To assist in solving the problems presented by viruses, the pathologist has called upon chemist and physicist, physiologist and cytologist, so that it is not altogether surprising that the accumulation of data has increased faster than could be assimilated. Yet with all this addition to knowledge some of the fundamental questions still remain unanswered. We still do not know whether the viruses are (*a*) living organisms, (*b*) inanimate organic substances, perhaps enzymic in nature, or (*c*) a stage in the actual process of the evolution of life ; although the recent discovery that they are essentially nucleoproteins which, by aggregation, form paracrystals visible under the microscope, encourages the belief that even this problem may be solved. Apart from these aggregates, the almost unbelievable minuteness of virus particles precludes direct observation, and everything known of their behaviour in relation to disease is really deduction based upon circumstantial evidence, often difficult to interpret. The existence of a virus is inferred from the occurrence of an infectious disease in the absence of any visible germ. Its size is still often deduced by filtration experiments through filters of known pore-size, the coarsest of which is sufficiently fine to hold back any known organism ; yet it is also known that the ability to pass through a given size of pore depends upon many factors other than the size of particle. The reaction of a virus to heat and chemicals is largely an assumption based upon the success obtained in securing infection after treatment, notwithstanding the fact that infection depends upon factors which are still very imperfectly understood.

Still more difficult problems have to be faced in studying the interactions of these viruses and the plants in which they produce diseases. This is particularly true of potato virus diseases, and although much real progress has been made during recent years, not a little of what passes as authentic information appears to be based upon slender experimental evidence (often obtained under glasshouse conditions), or to be due to over-simplification of abstruse problems. The utmost which can be attempted in a book such as this, after eliminating anything not directly bearing upon potato degeneration, is to indicate the gradual development of ideas and to summarise the present position with regard to those facts generally accepted as fully established.

(2) Development of Methods of Identifying Viruses

(a) *Segregation by the Use of Different Methods of Transmission.*—Careful observation of infected plants was alone necessary to distinguish between different types of symptoms and therefore to recognise distinct diseases, but the identification of the different causal viruses was, and still is, a matter of the greatest difficulty. An analogy may help to make this clearer. A disease of potato is identified as " Blight " by the occurrence of certain characteristic symptoms in the affected plant. Before it can be accepted that the cause of Blight is the fungus *Phytophthora infestans* it is necessary to satisfy the following conditions known, after their author, as Koch's Canons or Postulates, *i.e.* :

(i) Under diverse conditions the organism must be constantly and abundantly associated with the disease.

(ii) The organism must be isolated from diseased tissue, grown in pure culture where possible, and its differential characters studied.

(iii) The characteristic disease must be produced by infection experiments with pure cultures of the organism.

(iv) The organism associated with the disease so induced must be identified as the one originally separated, and any abnormalities of the host should likewise correspond.

Some modification of these requirements is permissible in exceptional cases, *e.g.* in cases where the suspected causal organism can only be cultured in the living tissues of the host, or in the case of human diseases where experimental infection is usually carried out on the lower animals. The difficulties in satisfying these canons in the case of viruses, which are invisible in even the highest concentrations, are only now being surmounted by the recent discovery of methods of purification of viruses and the use of serological technique similar to that employed in diseases of animals. The first step in the isolation of different viruses was the recognition that, whilst all could be transmitted by graft, only the so-called " Mosaics " were transferable by inoculating a healthy plant with infective sap expressed from a diseased plant. This difference permitted the isolation of " Mosaic " from a plant infected with both Leaf Roll and Mosaic, whilst the absence of a sap-inoculable constituent would afford proof of the presence of Leaf Roll alone. It is now known that neither of these deductions was sound, since both sap-inoculable and others not so transmitted are included amongst the viruses capable of producing " Mosaic." Before this, however, K. M. Smith (1932) had laid the foundations for the isolation of viruses by his discovery that, of two " Mosaic " viruses present simultaneously in a plant, one only was transmitted by insects (*cf.* below).

(b) *Is a Symptomless Plant necessarily Virus-Free?*—An early advance in the isolation of different " Mosaic " viruses was made by Salaman and Le Pelley (1930) whilst raising virus-free stocks for multiplication. It was assumed that a plant would show more or less evident symptoms when infected with a virus and that in doubtful cases it was only necessary to graft on to symptomless plants of the two varieties President and Arran Victory, which reacted severely to infection, and were therefore accepted as a safe index of the presence of a virus. The method was regarded as satisfactory until these workers found that symptomless plants of the variety King Edward VII invariably induced severe symptoms like Crinkle when grafted on to the standard Arran Victory plants, but produced no symptoms when grafted on to President. That the President plants were really infected was proved by regrafting back on to Arran Victory, in which they induced the same severe symptoms as did the King Edward plants. *Absence of symptoms, therefore, could no longer be accepted as proof of freedom from virus infection.* Such infected but symptomless " carrier " plants had already been recorded, *e.g. Physalis Alkekengi* as a carrier of tobacco Mosaic (Nishamura, 1918). Also, similar naturally occurring carriers as the variety King Edward, referred to above, had been found amongst American potato varieties by Schultz (1925) and by Johnson (1925). The importance of Salaman and Le Pelley's observations lay rather in the simultaneous discovery of a new virus, carried naturally by a popular variety, and the fact that it was not revealed when grafted on to a standard index variety such as President. The number of viruses known to be capable of being carried without symptoms in one or other popular variety of potato is constantly receiving additions, and has resulted in a continuous search for index plants giving distinctive reactions with such carried viruses. Virus freedom can no longer be asserted in any instance with complete confidence, and a " virus-free " plant must now be defined as a symptomless plant in which all efforts used have failed to disclose the presence of any hidden " carried " virus.

(c) *The Symptom Picture depends on Variety of Potato as well as on Virus.*—Salaman and Le Pelley's experiments with the variety King Edward illustrated a fact, already known, that the reaction obtained with a virus differs considerably with the variety of potato infected, for the virus " carried " by this variety produced Mosaic in Arran Comrade, Great Scot and Majestic, and induced the much more severe symptoms of Crinkle in Arran Victory and Arran Chief. Conversely, the Crinkle symptoms induced in the Arran Victory could not be the same Crinkle as that commonly found in President, since this latter variety displayed no symptoms at all when infected with the virus from the variety King Edward. *Similar symptoms in different potato varieties could not, therefore, be accepted as proof that the causal virus was the same in each case.* This was recognised by Salaman and Le Pelley and they named the virus carried by King Edward " Para-Crinkle " to emphasise the similarity but non-identity of this virus with the cause of true Crinkle as seen in the variety President.

The reaction of a plant may be regarded as a balance struck between the plant and the invading virus. In the majority of cases this balance is expressed in the form of relatively stable symptoms which recur when the progeny also is grown on, but these may, on the other hand, be so severe as to kill the plant, *e.g.* Streak, and so automatically eliminate the virus as well. When the balance is almost wholly in favour of the plant the symptoms may be so slight or ephemeral that the plant becomes a more or less perfect " carrier " of the virus. It is probably because the individual plants of any one variety have much the same physiological reactions, and at the same time differ in important respects from individuals of another variety, that there is any justification at all for referring to " varietal " reactions to a virus rather than to " individual plant " reactions.

(d) *Virus Complexes.*—One outstanding question prior to 1930 was as to whether " Mosaic," " Crinkle," and possibly " Streak " represented advancing stages in degeneracy, due to the cumulative action of one virus, which reached its final stage in the prostrate type known as " Curly-Dwarf," or whether each disease was distinct and caused by a separate virus. If the latter were the case, there was a possibility that some of the " Mosaic " type of diseases might be due to combinations of two or more of these separate viruses. In 1931, however, this question was answered by K. M. Smith (1931*a*) successfully isolating two distinct viruses from a " Crinkle " and, by recombining them, producing the original Crinkle symptoms again. The controversy which has since arisen as to the interpretation of details of this work in no way minimises its importance as a relatively secure basis upon which future work could be built.

The methods used by Smith in this analysis and synthesis of Crinkle depended upon three important discoveries.

(1) That the disease contained two viruses of which only *one* was insect transmitted, whereas both could be transferred to healthy plants by needle inoculation of infective sap. The insect-borne virus he called " Y " and the one incapable of being so transmitted he named " X."

(2) The existence of " Indicator " plants and " Filter " plants. Of these two the indicator plants had the original function of " Index " plants in that they were believed to give a standard reaction to infection with a given virus. For this purpose tobacco and *Datura stramonium* plants (amongst others) replaced potatoes because of the great variability of the symptoms induced in the latter. " Filter " plants were remarkable in that they would accept one virus only when a mixture of viruses was inoculated by needle. Examples of filter plants which accepted virus " X," but remained immune from virus " Y," were *Datura stramonium* and *Solanum dulcamara*, whilst the garden Petunia was found to accept virus " Y " and resisted infection with most strains of virus " X."

(3) The discovery that the two viruses " X " and " Y " moved at different rates through the plant tissues when inoculated into tobacco seedlings, so that virus " Y " could be recovered in pure form from the youngest leaves before the virus " X " component of the mixture had reached these tissues from the point of inoculation.

In practice the analysis was effected by first extracting a pure sample of the virus " Y " from the complex in the potato plant. This was accomplished by feeding the aphid *Myzus persicæ* on the plant and then transferring the insects on to a healthy indicator plant. Virus " X " was extracted in a pure form by needle-inoculating the sap from a " Crinkle " infected plant into a filter plant such as *Datura stramonium*, which refused the " Y " and accepted the " X " ; this pure form of

" X " was then passed to an indicator plant by needle. The synthesis of the original complex was then accomplished by allowing the aphid to pick up the virus " Y " first and then to feed these now infective aphides on the indicator plant containing the pure " X," with the result that the original Crinkle symptoms developed in the indicator plant. This work was followed by Murphy and McKay (1932*b*) isolating a new virus, which they named virus " A," from symptomless plants of Irish Chieftain. Virus " A " differs from " X " in being transmitted by the aphid *Myzus persicæ*, and from " Y " in not being sap-transmissible by ordinary rubbing from potato to potato.

Murphy and McKay, in the same paper, pointed out the obvious limitations of separating viruses by analytical methods such as Smith employed, since it would be difficult in this way to distinguish between two viruses which agreed both in inoculability by sap and insect-transmission. Indeed, they put forward strong evidence that Smith was mistaken in attributing Crinkle to a mixture of viruses " X " and " Y," and showed that identical symptoms could be produced by the simple addition of virus " X " to Irish Chieftain carrying virus " A." Smith's results are explained as being due to the accidental presence of virus " Y " which, however, was not an essential constituent of Crinkle. The virus " Y " would be passed over by means of the aphid at the same time as the virus " A " ; and since the symptoms produced on tobacco by these two viruses are closely similar, they would be attributed by Smith to virus " Y " (virus " A " being as yet undiscovered). Cogent as this criticism is, it should be remembered that it applies equally to Murphy and McKay's own work, for synthesis depends either upon a preliminary analysis or the certainty that simple viruses are ready to hand for experiment. They are on stronger ground in objecting to the passage of potato viruses through other kinds of plants (indicator and filter plants), for there can be no guarantee that the virus is not modified by its sojourn in an alien plant, so that on retransfer back to potato there is no proof that the disease symptoms produced are such as naturally occur in potato diseases.

However, the investigation of potato viruses by a method involving only the use of potatoes had already been begun at Cambridge by Bawden (1936) as a logical development of

Salaman's original use of the two index varieties Arran Victory and President. Bawden made use of the increasing number of varieties believed to be virus-free, and to these he grafted and needle-inoculated all plants under test, discovering in this way certain differential reactions which enabled the known, and a number of new, viruses to be distinguished from each other. For instance, the virus of Para-Crinkle (which he now named virus "E") as well as virus "A" could be separated from viruses "X" and "Y" by the fact that the two former could not be needle-inoculated. Virus "A" was separated from virus "E" by grafting to Up-to-Date potatoes on which the former produced a necrosis (*i.e.* discoloration and death) in the upper part of the plant (and was therefore named Top Necrosis, or Acronecrosis) whilst the latter did not. Similarly, viruses "X" and "Y" were distinguished by the former producing Top Necrosis in the variety Epicure and only a vague mottle in President, whereas virus "Y" gave a necrosis of the plant which spread from below upward (Acropetal Necrosis) when either grafted or needled to Up-to-Date or President. Bawden's method is illustrated in Table XXIV, in which the four index varieties used are Up-to-Date, Epicure, President and Arran Victory, from which it will be noted that seven distinct viruses can be segregated.

As a working method of approach to the problems of segregating viruses this has much to recommend it, but its reliability depends of course upon the degree of certainty with which the reactions are reproduced in the four standard varieties. Now it is reasonably certain that all stocks of the variety Up-to-Date are carrying, without symptoms, either a Streak (identified by Bawden as virus "B") or virus "X," or both. Clearly then we may expect that the reaction of Up-to-Date to viruses will vary with its own virus content. Scott (1938), for instance, apparently used stocks of Up-to-Dates as index varieties, of which half only were carrying virus "B." When scions of Catriona known to be infected with virus "A" were grafted on to these Up-to-Dates, only half the latter showed the expected Top Necrosis. This is explained by Scott as being due to the fact that virus "B" induces Top Necrosis on Catriona, the presumption therefore being that such plants of Up-to-Date as contained this virus caused necrosis in the Catriona and so prevented the passage of the virus " A " contained in this variety, with the result that no reaction was produced on the index plant of Up-to-Date. The remedy seems to be to extend the list of index varieties and to restrict the method to the use of plants of proved virus-freedom.

Clinch, Loughnane and Murphy (1936) have shown Interveinal Mosaic to be a complex of the virus " X " and a new virus which they named " F." The steps taken to isolate this new virus illustrate both the complexity of the

TABLE XXIV

Bawden's Technique for Identifying Viruses

Virus.	Sap-inoculable without abrasive.	Up-to-Date.	Epicure.	President.	Arran Victory.
A	No	Top Necrosis	Apical Top Necrosis	...	...
B	No	...	Mosaic	Top Necrosis	Top Necrosis
C	No	Top Necrosis	Top Necrosis	Top Necrosis	...
D	Yes	Top Necrosis	Top Necrosis	Fol. Necrosis	Fol. Necrosis
E	No	...	...	...	Acute Crinkle
X	Yes	...	Top Necrosis	...	...
Y	Yes	Acropetal Necrosis	...	Acropetal Necrosis	...

N.B.—Fol. Necrosis = Foliar Necrosis, *i.e.* necrosis confined to leaves.

problems and the ingenuity required in solving them. Interveinal Mosaic was at first believed to be a simple disease due to virus " X," since this virus alone could be isolated ; and while the disease was readily passed from one potato to another by graft or sap inoculation, no success was obtained by the use of aphides as vectors. Irregularities in the reactions so obtained, however, suggested the possibility of the presence of another virus, and this was confirmed by Clinch and her colleagues when the aphid *Myzus persicæ* was allowed to feed on the sprouts of tubers containing virus " A " in addition to Interveinal Mosaic. Under these conditions the aphid picked up both virus " A " and a constituent of the Interveinal Mosaic. This constituent could not be virus " X " since it induced bright-yellow spotting of potato leaves and necrosis in the tubers of the variety President. The newly infected tubers of President had therefore none of the virus " X " from the Interveinal Mosaic, and the next problem was to remove the virus " A." This was done by taking advantage of the fact that virus " A " cannot be sap-inoculated to *Datura stramonium*, so that the new virus (now called " F ") was passed to *Datura* in pure form. All that remained was to transfer the virus " F " back to potato by graft and it could then be studied fully in regard to filtration, reactions to chemicals and heat, and the symptoms reproduced in a wide range of host plants. The circle was completed when it was found that the addition of pure " X " to the new virus gave typical symptoms of Interveinal Mosaic. These workers have also succeeded in isolating the virus responsible for Aucuba Mosaic of the potato and have named it virus " G." Its characters are closely similar to those of virus " F," but as yet no success has been achieved in transmitting this virus by means of insects.

(e) *Physical Characters as a Means of Identifying Viruses.*—The methods described above are within the reach of any experimenter equipped with suitable glasshouses from which extraneous insects can be excluded. They depend, however, on the symptom-picture presented by the infected plant rather than on the inherent characters of the viruses themselves; yet they are the only methods available in the case of viruses such as Leaf Roll which cannot be transmitted by sap inoculation. When the extracted sap can be shown to retain its infectivity, other methods of examining the properties of the virus become possible; though even here the most obvious one of form and structure is precluded, for direct observation is impossible and virus structure lies more within the province of protein chemistry than of biology. Nevertheless, with the isolation of individual or " unit " viruses attempts have been made to describe each in terms of its physical characters; such, for example, as the determination of the size of the infective particle by its ability to pass through special collodion filters of known pore-size, its reaction to dilution, heat, chemicals and longevity in expressed sap—all measured by its ability, after treatment, to infect healthy plants. Finally, a few of the most stable viruses have been prepared in what appears to be a pure form by the methods usually adopted in protein chemistry, and some advance has been made in the study of their chemical composition, their activity, specific gravity, precipitation and iso-electric points, and their optical properties have been, or are being, determined. A discussion on these physical characters is beyond the scope of this book. It must suffice to mention that some purified virus solutions (including several strains of potato virus " X " and, probably, virus " Y "), at high dilutions, are optically anisotropic and exhibit anisotropy of flow when gently agitated (*i.e.* the solution shows double refraction or birefringence) due to the formation of liquid or " para "-crystals from the virus particles ; at high concentrations the solutions are spontaneously birefringent owing to the fixed orientation of the liquid crystals. These can be precipitated either as para-crystals (tobacco Mosaic) or an amorphous mass (potato virus " X "). On the other hand, some virus solutions (*e.g.*, tomato Bushy-Stunt and tobacco Necrosis) are isotropic and form true crystals in the cubic system. Chemical analysis of viruses has shown them to be nucleo-proteins, containing an appreciable amount of phosphorus and carbohydrate in the form of nucleic acid, of high molecular weight (*i.e.* of the order of twenty million), and with a specific gravity around 1·3.

(f) *Immunology Tests for Viruses and Virus Strains.*—Very early in the study of what are now known to be virus diseases of man and animals it was discovered that the virulence of certain viruses could be experimentally reduced so that only mild symptoms developed in an inoculated animal. What was still more important was the discovery that infection with such an attenuated strain confers a form of immunity against subsequent attack by the naturally occurring more virulent strain of virus. This immunisation is due to the production within the affected tissues of toxic " antibodies " which unite with, and neutralise all forms of the virus, and " vaccines," as the attenuated strains are called, are now used in immunising against many diseases of man and animals. Plants, however, do not appear to possess the power to react to infection by producing antibodies, but nevertheless a form of immunising does occur in plants affected by attenuated strains of certain viruses. As regards potato viruses, one definitely known to exist in nature in strains of differing virulence is virus " X," of which it has been shown by Salaman (1933, 1938) at least six forms can be isolated. When inoculated into tobacco each of these " X " strains produces its own typical symptoms varying, according to the strain, from a fleeting mottle to severe necrosis. Salaman also proved that, although no antibodies were produced by the affected tobacco, an inoculated plant was incapable of being infected by a more virulent strain of the virus " X " ; it was, however, in no way protected from infection by other viruses such as " A " or " Y " or " G," etc. He suggests that this form of non-sterile immunity is perhaps due to nearly related forms of virus, forming an irreversible union with some specific protein molecule in the cell, with the result that all available supplies are taken up by the first invader ; the explanation is in fact one of " first come, first served." Distinct viruses, on the other hand, have need of different sources of energy and thus do not compete with each other. Apart from virus " X," the potato viruses have been regarded as relatively stable but, recently, Bawden and Kassanis (1947) have shown that several widely differing strains of virus " Y " exist in nature, and Botjes (1948) has reported the occurrence of an attenuated form of virus " A " in the variety Eigenheimer. The power of a virus to protect a plant from further infection by a related strain is now generally used as one stage in establishing the identity of an unknown virus. Thus, if the unknown virus is found to be capable of infecting a plant only when such a plant is healthy or infected with any virus *other* than virus " X," the assumption is that the unknown is either identical with virus " X " or so closely related to it that it may be regarded as a strain of this virus, however different its symptoms may be in an infected plant. In this way virus " B " (Clinch, 1942) and virus " D " (Bawden, 1934, 1936) have been identified as strains of virus " X."

Nevertheless, caution is required in interpreting " protective immunisation " in terms of the relationship between the two reacting viruses. Thus Bawden and Kassanis (1941) explained the fact that tobacco Severe Etch virus and Hyoscyamus virus 3 protected tobacco against infection with potato virus " Y " on the ground of a close relationship between the three viruses, but later (1945) they advanced a very different explanation. They pointed out that the reaction involved was quite different in kind from that in ordinary protective immunisation, since (*a*) the protection afforded was not mutual and (*b*) a mild form of Etch, which itself afforded complete protection against the severe form of Etch, was nevertheless unable completely to prevent the establishment of potato virus " Y," though it did appear to interfere with its multiplication. They bring forward evidence to show that a virus, on first entering a plant, is quickly adsorbed on, or combined with, some insoluble cell constituents and only occurs free in the sap after it has multiplied. The observed partial (mild Etch) or complete (severe Etch) protection afforded against potato virus "Y" was therefore explained as being due to the Etch virus so altering the metabolism of cells that some material or enzyme system essential for the multiplication of virus "Y" was partially or entirely inhibited. This explanation also served to clarify the still more surprising fact that Severe Etch could even cause the total disappearance of potato virus "Y" from the sap of leaves in which it has become fully established, the rate of disappearance being approximately the rate at which the virus would become "denatured" in *expressed* sap. Bawden and Kassanis draw two important conclusions from these facts: (*a*) they suggest that this wastage or denaturation in sap occurs normally in the living cell and that the virus content is only maintained by the continued production of fresh virus; they state that a high virus content in expressed sap is only found with viruses that denature slowly *in vitro*; (*b*) it is pointed out that the great differences between the virus content of sap from plants infected with tobacco Mosaic virus and potato virus "Y" may not indicate gross differences in multiplication, as usually believed, but may be due to the steady accumulation of one in the sap while the other is continually breaking down.

Although plants are apparently incapable of producing antibodies, many plant substances (mainly of a protein nature) can induce the formation of antibodies in the blood-serum of an animal (rabbits and guinea-pigs being most frequently used). These antibodies, however, are non-specific in that they will react when mixed with many substances in addition to the one which called them into being. In 1928, Helen Beale (*née* Purdy) discovered that, after eliminating these non-specific reactions, a specific antibody was produced in the blood-serum of a rabbit when inoculated with the sap from a Mosaic-infected tobacco plant. The serum containing this antibody (now known as an "antiserum") then reacted strongly when mixed with tobacco Mosaic virus extracted from either tobacco or any other plant, but did not react with any other virus occurring in tobacco ; thus this serological test could be used as a means of identifying (or distinguishing) an unknown virus and tobacco Mosaic. Since then, much work has been done to improve the technique and to indicate the limitations of the serological method of segregating viruses. For a comprehensive treatment of the underlying principles the student should consult other books (*e.g.* Bawden, 1950), but they may very briefly be summarised as follows :—

(1) Plant viruses (so far as they have been studied) induce the formation of antibodies in the blood-serum of an animal when injected either intravenously or intraperitoneally.

(2) Some plant viruses are " antigenic " in that the antibodies produced are specific and will react only with the virus causing their formation.

(3) Amongst the reactions resulting from a mixture of antibody and the antigenic virus is the formation of a copious precipitate, and this " precipitin " test is the simplest and most convenient to use in virus identification. Its formation depends upon there being an adequate concentration of both antibody and antigen in a solution containing electrolytes, and in the selection of experimental conditions suitable for the virus.

(4) The virus is probably the antigen itself, and may be conceived of as comprising an aggregate of molecules having specific surface groups (determinant groups) which combine with the antibodies. Antibodies appear to be serum globulins which have been modified so that they unite only with the determinant groups of the antigen inducing their formation ; hence the specificity of antigen/antibody reaction.

(5) Unrelated viruses are believed to have no determinant groups in common, and therefore there is no reaction with each other's antisera. When a reaction does occur with an antiserum produced by another virus, it does not necessarily indicate that the two viruses are *identical*, but only that they have one or more antigenic determinant groups in common and are therefore closely related ; such viruses are regarded as being different strains of the same virus rather than as distinct viruses. In addition to these common antigenic determinant groups they may each possess other groups peculiar or specific to themselves. Hence an antiserum produced by (say) strain number one of virus " X " will form a precipitate with strain number two, but there may be both

antibodies in the serum and antigenic groups in the second virus strain which remain unsatisfied or unabsorbed. The presence of the former can be demonstrated by adding a further sample of strain number one, when a new precipitate will form. The existence of the specific determinant groups in the second strain of the virus will similarly be shown by reversing the rôle of the two strains and using number two strain to produce the antiserum.

(6) In general, viruses which have similar serological reactions usually agree closely in physical characters and show mutual protective immunisation in a susceptible host plant. They, however, frequently exhibit very diverse symptoms in such a plant, *e.g.*, viruses " X," " B " and " D " are serologically similar, yet the potato variety Arran Victory shows the mildest of mottles when infected with most strains of virus " X " but is Top Necrotic to virus " B " and shows Foliar Necrosis with " D." Again, viruses " A " and " Y " may show serological relationship (Hansen, 1937), but their symptom-expression is quite different in potato varieties, *e.g.*, virus " A " gives Mild Mosaic and Top Necrosis in President and Up-to-Date respectively, whilst both varieties react with Acropetal Streak to infection with virus " Y." Nor is mutual immunisation between such related viruses invariable, for whilst virus " X " completely protects a plant against subsequent infection with " D," the converse is not equally true (Bawden, 1934); and viruses " A " and " Y " do not confer mutual protection when tested in the variety Up-to-Date (Hansen, 1937). In spite of these and other anomalies (some of which are now yielding to improved technique, *cf.* Bawden and Sheffield, 1944) the serological study of viruses presents a new outlook and marks a most important advance in the methods available for their identification.

In tracing the development of ideas concerning virus disease identification we have seen how at first reliance was placed on the effects produced by simply grafting diseased plants to others which, because they were symptomless, were regarded as healthy. This latter assumption being found to be far from the truth, it became necessary to extend the range of test plants and to use only such as gave no reaction when cross inoculations or grafts were made. The difference in the symptoms sometimes produced when different means of transmission were employed led to the discovery of virus complexes and the segregation of the unit viruses comprising them. Finally, these methods of direct observation on the host plant have been supplemented by physical and immunological studies of the viruses themselves. Indeed, in the view of some workers it is only by these latter studies that the real relationships between viruses can be determined and a start made on a rational form of classification.

(3) Characteristic Reactions of Potato Viruses

The viruses occurring in the potato may, for the present, usefully be grouped according to the methods by which they can be transmitted, it being remembered that all are graft transmissible.

Group I. *Not transmissible (or only with difficulty) from potato to potato by sap inoculation. No insect vector known*

Virus " B " (Bawden) = Up-to-Date Streak (Murphy), Solanum Virus 4 (K. M. Smith). This virus is carried, without symptoms, in most stocks of Up-to-Date, in which variety it was first identified as a " streak " (Schultz and Folsom, 1925; Murphy and McKay, 1926), and named " B " (Bawden, 1936). Bawden records it as occurring naturally also in Arran Banner, Arran Consul, American Wonder, Bliss Triumph, Burbank, Duke of York, Earliest of All, Eclipse, Great Scot, Green Mountain and Majestic, in all of which the virus appears to be " carried " without symptoms. It is sap inoculable from potato to *Datura stramonium* and tobacco. Graft transfers to different potato varieties produced reactions varying from Top Necrosis (*cf.* page 538) to " mosaics " of varying intensity, or there was no visible reaction at all. Virus " B " was at one time thought to be non-inoculable by sap from potato to potato, but Clinch and Loughnane (1933) recorded a successful transfer in this way to the variety Arran Crest and, later, Clinch (1942) found that it was readily transmitted by sap to all varieties except those reacting with Top Necrosis when grafted. No insect vectors are known but, according to Clinch *et al.* (1938) and Loughnane and Murphy (1938), the virus may spread in the field by foliage contact. Virus " B " is rendered inactive (*a*) at a dilution of 1 in 1000, (*b*) after four weeks' storage as expressed sap, and (*c*) after immersion for ten minutes at a temperature of 70° C. (Bawden, 1936).

The ætiology of virus " B " has been the subject of much controversy. Bawden (1936) distinguished the virus from virus " X " on two grounds ; virus " X," but not virus " B," became systemic when inoculated to President and Arran Victory and, secondly, virus " X " gave Top Necrosis in Epicure but not in President and Arran Victory—while a mixture of the two viruses produced Top Necrosis in all three varieties. It seemed improbable that virus " B " existed in nature except in association with virus " X," as in Up-to-Date, but Scott's (1938) discovery of a source of virus " B " free from " X " has provided material for critical studies on the relationship of the two viruses. Bawden and Sheffield (1944) found that grafts with this newly isolated virus " B " gave Top Necrosis in President and Arran Victory while sap inoculation produced only black necrotic lesions and no systemic disease ; with Epicure and King Edward, however, both grafts and sap inoculation gave mottled and distorted upper foliage together with some necrotic spotting and fall of lower leaves. As in the case of virus " X," the U.S.D.A. seedling 41956 proved to be immune from virus " B " whether by graft or sap inoculation. This conflicted with Dykstra's (1935, 1939) and with Dennis' (1939*a*) claim that the seedling was susceptible to virus " B " and, indeed, both authors believed thay had isolated the virus from a mixture of " X " and " B " by using the seedling as a filter plant to remove the virus " X " constituent. Clinch (1942), however, demonstrated that recovery of the virus from the seedling did not, in fact, imply susceptibility, for both viruses " B " and " X " were readily passed through seedling 41956 by graft without establishing themselves or multiplying in the tissues—the seedling merely served as a conduit for the viruses. Clinch's main object was to clarify the status of the " Streak " virus known from Murphy and McKay's (1926) work to be an almost universal associate of virus " X " in Up-to-Date, and which had been separated by Bawden (1936) as a distinct virus " B." Clinch concluded that this streak virus or virus " B " was in fact merely a strain of virus " X," with which it was identical in serological reactions and in other respects except as regards the ability to produce Top Necrosis in varieties such as Epicure and King Edward to which virus " X," as generally understood, is lethal. With this view Bawden and Sheffield (1944) fully agree and accept the logical conclusion that such a simple test, based on host reactions is not a valid test of relationships between viruses. Further, they record the existence of another virus, suspected by Scott as a strain of " X " although it failed to produce Top Necrosis in any potato variety. This virus reacted with antiserum prepared against " X " and " B " and protected tobacco against subsequent infection with virus " X " ; these agreements with virus " X " were accepted by Bawden and Sheffield as conclusive and the virus was named " X^a." Finally, Matthews (1947), while confirming virus " B " as a strain of " X," reports that a serological comparison between Up-to-Date " streak " supplied by Clinch, and virus " B " supplied by Bawden, revealed certain differences ; he concludes that virus " B " is no more a single entity than is virus " X."

Virus " C " (Bawden) = Di Vernon Streak (Salaman), Solanum Virus 5 (K. M. Smith). This virus, like virus " B," is capable of producing Top Necrosis when grafted to certain varieties (*cf.* page 538). It was first recorded as occurring naturally in the variety Di Vernon by Salaman (1930*a*) and, later, in Monocraat (Bawden, 1936), but in both varieties it was accompanied by virus " X " and, in the former, also by virus " Y." Dykstra (1935) considered that he had obtained the virus in pure form by grafting the mixture " C "+" X " to the U.S.D.A. seedling 41956 which he had shown to be immune from infection with virus " X." Clinch (1942), however, proved that this seedling allows the *passage* of virus " X " through its tissues, and there is therefore no evidence that the virus " C " recovered from the seedling was free from this virus. Cockerham (1943) has recorded the virus in pure form in field plants of the varieties Edgecote Purple, Arran Rose, Cardinal, International Kidney, Liddesdale Lads, Kepplestone Kidney and Maud Meg. All these varieties react with Top Necrosis when grafted with a source of virus " X " or " A," so that the absence of both these viruses in field plants could be assumed (page 588) ; similarly the absence of virus " B " was proved by the failure of Arran Victory to react with Top Necrosis when grafted with scions of these plants. Cockerham agreed with Bawden (1936) and Dykstra (1939) that the virus was not sap-inoculable in the ordinary way but he had no difficulty when carborundum powder was added as an abrasive to the sap. He regarded virus " C " as closely related to virus " Y " because of the similarity of symptoms these two viruses produced on tobacco, tomato and *Hyoscyamus*, but nevertheless considered them to be distinct since (*a*) virus " C " produced only local lesions when sap-inoculated into Epicure, Majestic, British Queen, Up-to-Date and President, whereas with virus " Y " sap-inoculation resulted in Leaf-Drop Streak ; (*b*) the aphid *Myzus persicæ* repeatedly failed to transmit virus " C " under conditions in which successful transmissions occurred with virus " Y." Bawden and Sheffield (1944) agreed with most of Cockerham's views but put forward strong evidence that virus " C " is so closely related to virus " Y " that it is more accurately to be regarded as a strain only of that virus. In support of this view they point to (*a*) the fact that virus " C " reacts to antiserum prepared for virus " Y," though with a lower precipitation end-point ; (*b*) virus " C " becomes systemic in tobacco and, under such conditions, affords complete protection against subsequent infection with virus " Y " ; (*c*) *Datura stramonium* is immune from infection with either virus ; (*d*) cell inclusions, while equally rare with both viruses, are similar in type and differ markedly—particularly in being smaller—from cell inclusions induced by virus " X " ; (*e*) virus " C " behaves like virus " Y " in being inactivated in tobacco sap by exposure for ten minutes to a temperature of 57° C., or for a week at room temperatures. Bawden and Sheffield regard these similarities as fundamentally more important than the observed differences between the two viruses, *i.e.* (*a*) varieties which react with Leaf-Drop Streak when infected with virus " Y " either by graft or sap-inoculation, react with Top Necrosis when grafted with virus " C," and show only local lesions without systemic infection when sap-inoculated with the latter virus ; (*b*) the insect vector of virus " Y " is unable to transmit virus " C." Hutton and Bald's (1945) work suggests that the difference between Top Necrosis and Leaf-Drop Streak may, indeed, not be fundamental since, with certain seedlings, virus " Y " may produce Top Necrosis. Also, Hutton (1946), in supporting the view that virus " C " is a strain only of virus " Y," states that the two viruses produced similar reactions in duplicate sets of certain seedling crosses.

Bawden and Kassanis (1947), while reiterating that virus " C " only, and not virus " Y," produces Top Necrosis, report that virus " C " is capable of inducing a wider range of symptoms in different varieties than can be obtained with any other strain of virus " Y." They confirm the inability of *Myzus persicæ* to transmit virus " C," an inability which was shared by every aphid tested, including *Myzus ornatus*, *Macrosiphum solanifolii*, *Aphis rhamni*, *Aphis fabæ*, *Aulocorthum* (*Myzus*) *circumflexum*, *Canariella pastinaceæ* and *Macrosiphoniella sanhorni*; all these insects transmitted virus " Y " from tobacco to tobacco, but, under the same conditions, none was able to transmit virus " C." Nevertheless, Cockerham (1943) records three cases of field transmission of virus " C " under conditions of high aphid infestation. Virus " C " has been recorded in many European varieties (Salaman, 1930*a*; Quanjer, 1931; Bawden, 1936; Cockerham, 1943), in South American (Andean) varieties by Dennis (1939), in a single old Australian variety (Bald and Pugsley, 1941), but not in any North American variety (Dykstra, 1939)—a fact which, as Cockerham (1943) points out, may be related to Dykstra's observation that all the American varieties tested succumbed with Top Necrosis when infected with virus " C " from European sources.

Virus " E " (Bawden) = Para-Crinkle (Salaman and Le Pelley), Solanum Virus 7 (K. M. Smith). This virus, which was discovered by Salaman and Le Pelley (1930), is apparently " carried " without symptoms in all stocks of the variety King Edward. These writers noted that on grafting the variety with healthy scions of Arran Victory, not only did widely different symptoms develop in the scions but varying periods of time were required before the symptoms became manifest. Salaman (1932) interpreted these differences as suggesting that the disease (Paracrinkle) is really a complex of two or more viruses which occasionally become disrupted. Bawden *et al.* (1950), however, regard the variation in symptom intensity, and in the time required for symptom expression, as due to incomplete systemic invasion, much as has been recorded in the case of virus " Y " (page 508). No insect vector of the virus is known, and all attempts to transmit it by sap inoculation failed until Bawden *et al.* (1950) succeeded with the aid of an abrasive (carborundum or celite). In their view, the necessity for the use of an abrasive, as in the case also of virus "A," arises from the fact that the virus concentration in the cell is too low for successful infection. This explanation is scarcely a complete one since no abrasive is required in transferrng the disease to tomato. It would appear therefore that tomato is not only more susceptible than potato to virus "E," but that susceptibility is linked in some way with the dosage (*i.e.* the number of infective units in the inoculum). Susceptibility is also connected with the photosynthetic activity of the inoculated plant (Bawden and Roberts, 1948), and Bawden *et al.* made use of this fact, and greatly increased the number of successful sap-inoculations of virus "E" to potato, by a preliminary darkening of the recipient plant for some three or four days before inoculation.

The fact established by Salaman and Le Pelley (1930) that the potato variety President, when *grafted* to King Edward, carries the virus of paracrinkle without symptoms was only of academic interest since grafting is not a natural means of virus transmission, but Bawden *et al.* (1950) found that tomatoes infected by *sap inoculation* also act as perfect "carriers," and this at once opens up the possibility that other plants, in nature, might also become infected by contact with the variety King Edward without arousing any suspicion caused by the development of symptoms. This possibility is doubly important in view of the fact that Bawden *et al.* (1950) found that, when susceptibility was increased by pre-darkening, a proportion of the Arran Victory plants which became infected showed no symptoms until their tuber-progeny, after breaking their dormancy, were planted and produced new foliage.

When infected and clarified sap from King Edward and Arran Victory plants was examined under the electron microscope, Bawden *et al.* found it to contain rod-like particles of varying length but with a constant width of about 10 mμ. Strong evidence was obtained that these rods were particles of virus "E," notwithstanding the fact that quite similar rods are the produce of normal cell activity in potato leaves. The two types of rods (virus and normal cell constituent) could be differentiated by their reaction to heat, for the virus particles disintegrated when exposed for ten minutes to a temperature of 60° C., while the "normal-rods" proved to be very resistant to heat and temperatures exceeding 90° C. had no effect.

Using a common technique for the isolation of viruses, these workers found that the presumed paracrinkle-virus particles, in sap from infected tomato leaves, were precipitated by one-third saturation with ammonium sulphate and redissolved in water apparently unchanged; few of the rods in sap from uninfected potato plants were precipitated at this salt concentration.

Group II. *Sap-inoculable but not ordinarily transmissible by insects*

Virus " F " or Tuber-Blotch Virus (Clinch, Loughnane and Murphy) = Pseudo-Net Necrosis Virus (Quanjer), Solanum Virus 8 (K. M. Smith). The virus was first recognised as a separate entity by Quanjer (1931) but was fully studied by Clinch, Loughnane and Murphy in 1936. It has been found in nature only in the varieties Up-to-Date and Monocraat, but this fact may not measure its importance in potato culture. Artificial infection with a number of varieties produces only a few small yellow spots confined to the lower leaves and described as " veiled aucuba " symptoms, so that it is probably either overlooked in the field or confused with the more obvious symptoms of virus " G," causing Aucuba Mosaic. Virus " F " is an important cause of tuber necroses. It is easily transmissible by needling infective sap into potato and a number of other host plants, and is rendered inactive at a dilution of only 1 : 100, or by storage for two or three days at 15·5° C., or by ten minutes' exposure to a temperature of 63° C. to 65° C. In pure form it cannot be transmitted by means of insects, but for some reason, as yet obscure, it is picked up and transmitted by the aphid *Myzus persicæ* from plants which are already infected with virus " A." Virus " F " was originally isolated by Clinch, Loughnane and Murphy (1936) from a plant of the variety President affected with Interveinal Mosaic; two sister-tubers being selected in 1928 to provide stock material of the virus. A descendant of one of these tubers was found in 1932 to contain a " streak " element (Koch and Johnson, 1935) which was later shown by Clinch (1941) to be a virulent strain of the original virus " F." This strain, to which she refers as " Virulent Tuber Blotch," is assumed to be a mutant of virus " F " which arose spontaneously within the plant at some date between 1928 and 1932. The descendants of one of the original tubers all displayed the mutated form, whereas none of the descendants of the other tuber behaved abnormally. The distinctive character of the virulent strain is its ability to induce a rapid and destructive Top Necrosis (following streaking of the lower leaves) in certain varieties in which also severe necrosis of the tuber, involving the vascular tissue and destruction of the "eyes," occurs. The varieties affected in this way include Arran Cairn, Arran Consul, Arran Crest, Arran Peak, Arran Pilot, Arran Signet, Bliss Triumph, Catriona, Di Vernon, Dunbar Cavalier, Dunbar Yeoman, Epicure, Gladstone, Irish Chieftain, King Edward VII, Majestic, Ulster Monarch and Up-to-Date. Sap-inoculation of intolerant varieties was possible by adding an abrasive to the sap, and resulted in the appearance of local lesions after some nine days, followed later by systemic necrosis; sometimes it was necessary to cut off the tops of the inoculated plant in order to induce the latter symptom.

Virus "G" (Clinch, Loughnane and Murphy) = Potato Aucuba Mosaic (Murphy and Quanjer), Solanum Virus 9 (K. M. Smith). The virus has been most extensively studied by Clinch, Loughnane and Murphy (1936), by whom it was named virus "G." It appears to be closely related to virus "F" and, like the latter virus, produces necrosis of the pith and cortex in tubers of certain varieties (*cf.* page 450). Indeed, the fact that virus "G" and a strain of virus "F" are mutually protective (Clinch, 1941), *i.e.* a plant infected with either virus is completely protected against subsequent infection by the other, suggests the possibility that virus "G," also, is merely a strain of virus "F." Virus "G" is known to occur naturally in many varieties, particularly "first earlies." It is easily sap-inoculable to potato and other host plants and is inactivated at a dilution of from 1 : 200 to 1 : 500, or when stored in darkness for four days at a temperature of 13° C., or when exposed for ten minutes at a temperature of 65° C. No insect vectors are known, and there is no evidence of spread under field conditions.

Group III. *Sap-inoculable and non-insect transmissible as for Group II, but serologically distinct*

Virus "X" (K. M. Smith) = Simple Mosaic Virus (Murphy), Solanum Virus 1 (K. M. Smith). This is the most widespread of potato viruses; occurring in nature with symptoms varying from an almost imperceptible mottle, or "typical" Mosaic, to a lethal Top Necrosis. Virus "X" also forms a unit in "Severe" Mosaic diseases such as Crinkle (page 459) and Rugose Mosaic (page 464). In U.S.A. virus "X" is more or less "carried" without symptoms in most commercial varieties, and is commonly referred to as the "healthy" potato virus, or as "Latent" Mosaic, though Larson (1943, 1944) has described a form which induces a severe necrotic disease. Apart from this strain, the American "Latent 'X'" is usually segregated into "Mottle" or "Ring-Spot" forms according to the reaction in tobacco (Johnson, 1925; Koch, 1933), but Clinch (1944*a*) has pointed out that the plant reaction is influenced by the environment, and that a form which, in Ireland, gave a mild ringspot in tobacco was regarded as a "Mottle" by Koch and Johnson (1935) in U.S.A. Salaman (1938) first studied the strains of the virus occurring in the British Isles; isolating three direct from field potatoes ("X^H," "X^N" and "X^D"); and three, *i.e.* "X^G," "X^L" and "X^S," which occurred in combination in potato, were separated by selective inoculations through several generations of tobacco. The latter method, however, does not entirely exclude the possibility of some modification occurring during the long sojourn of the virus in tobacco. These strains were shown by Bawden (1936) to induce Top Necrosis (page 538) in the varieties Arran Crest, Epicure and King Edward, while giving only a mottle in Arran Victory and President. The one exception was "X^D" which gave Top Necrosis in the first three varieties and a characteristic necrosis of the foliage with the two latter varieties; a difference which led him to regard "X^D" as probably a distinct virus. Hence the ability of a virus to produce Top Necrosis in Arran Crest, Epicure and King Edward, while giving a mottle in Arran Victory and President became accepted as specifically diagnostic for all strains of virus "X." However, with the general agreement that virus "B" is, in fact, merely a strain of virus "X" (*i.e.* virus "X^B") and not a distinct entity (*cf.* page 495), it has become evident that such a simple test, based on host reactions, is not a valid test of virus relationships (Bawden and Sheffield, 1944). The criteria now insisted upon are that, on comparison with a known strain of "X," the virus under examination (*a*) should show similar—though not necessarily identical—serological reactions (page 492) and, (*b*) infection with either virus should afford complete protection against subsequent infection, by sap-inoculation, with the other (page 489). All strains are readily sap-inoculable to potato and other host plants, and are rendered inactive at a dilution of about 1 in 10,000; or on exposure for ten minutes at a temperature of about 66° C. They remain infective at room temperatures for a period of from two to three months, and are not affected by exposure for twenty-five days to a temperature of 37·5° C. (Kassanis, 1949); in which latter respect virus "X" differs from Leaf Roll, which Kassanis has shown can be "removed" under these conditions from infected tubers.

In testing for the presence of virus "X" it should be noted that the virus content of immature tubers is too low to give a precipitin reaction with antiserum, but extracts from growing sprouts have almost as high a virus content as the foliage (Bawden *et al.*, 1948). Possibly this difference in virus concentration may account for the fact that while transmission readily occurs by the rubbing of tuber-sprouts in storage (McIntosh, 1944) or in sacks (Bawden *et al.*, 1948), all workers are agreed (with the exception of Mai, 1947) that transmission does not occur by means of the cutting knife (Denny, 1946; Lihnell, 1947; Bawden *et al.*, 1948). No insect vector is known, but Loughnane and Murphy (1938) demonstrated the spread of virus "X" in the field by mere foliage contact. There is general agreement that field transmission in this—apparently the only—way, occurs only slowly, and in one field trial Smith (1943) obtained no transmission of virus "X," from tobacco to tobacco, under conditions in which there was abundant spread of virus "Y." Nevertheless, there can be no doubt that most, if not all, natural spread of virus "X" is by contact between diseased and healthy plants. Thus, in the Irish seed-growing districts of Donegal, Clinch *et al.* (1938) found that four stocks of Champion and five of Arran Banner, initially virus-free, showed from 40 to 66 per cent. "X"-infection in Champion and 38 to 94 per cent. in Arran Banner, after being grown in the field from five to seven years. Roberts (1948) concluded after three years' trials with five strains of virus "X" (including "X^B") and seven varieties of potato, that spread occurred, not only as a result of direct foliage contact, but also underground by contact of roots, or by some means as yet unknown—although her trials at least exonerated the fungus *Rhizoctonia solani* as a possible agent. She was led to investigate the possibility of subterranean transmission by the common experience of finding virus " X " in the tuber progeny of plants which, in the growing season, had given no evidence of being infected. Later, she found that protection of foliage against infection did not prevent infection of the tubers, and that under such conditions tomato and *Datura stramonium* became infected when planted in soil containing pulped infected material. According to Roberts the more virulent strains of virus " X " reach a high degree of concentration in the plant and spread to healthy plants more readily and rapidly than the less virulent forms ; even so, in only one experiment did more than 10 per cent. of spread occur. This work not only emphasises the importance of adequate rotations in seed-growing districts in order to eliminate the risk of infection from " groundkeepers " or " self-setts " (Bawden *et al.*, 1948), but also the need for thorough cultivation to eradicate weeds and other plants from potato fields ; Clinch (1944) has experimentally infected *Solanum nigrum*, *Lamium hybridum*, *Veronica agrestis*, as well as beetroot and mangold, though only in *Lamium hybridum* did the disease become systemic, while Salaman (1938) also reports Horse Beans as reacting to virus " X " with local lesions. On the other hand, Clinch (1944) found that even close contact failed to cause transmission of the virus to potato varieties (*e.g.* Arran Crest and Epicure) which, in glasshouse grafting experiments, react to virus " X " with a Top Necrosis. This " Field Immunity " has been shown by Cadman (1942) to be inherited as a Mendelian dominant, and no insuperable difficulties appear to stand in the way of breeding varieties displaying field immunity (*cf.* page 548). Added importance must be attached to breeding work since evidence is accumulating to show that mutants of virus " X " may arise more frequently than was once believed. Salaman (1938) noted what might have been a " mutation " from a severe form of " X " to a mild one, though he did not rule out the possibility of selection from a mixture. Clinch (1944), however, has presented strong evidence that an extremely virulent form, which arose spontaneously in the field, was converted into an avirulent form with great regularity in the fourth season after inoculation.

Virus " D " (Bawden) = Foliar Necrosis Virus (Bawden) = President Streak (Murphy), Solanum Virus 6 (K. M. Smith). The virus was recorded by Murphy and McKay (1926) as causing Streak in the variety President, but apart from this there is no evidence of potatoes being infected in nature. It was fully described by Bawden (1934), who regards it as probably a stable form of virus " X " (" X^D ") but deserving of separate consideration because of differences from that virus in its reaction on some potato varieties and in certain physical properties. Virus " D " is easily sap-inoculable and is inactive at a dilution at 1 : 5000 when extracted from young rapidly growing tobacco leaves, or at 1 : 750 when taken from mature potato foliage. It is likewise rendered inactive by ten minutes' exposure to a temperature of 67° C. Its activity in storage varies greatly with the temperature ; at 25° C. it ceases to be active after six or seven days, at 10° C. after twelve days, and at 1° C. it is only rendered inactive after some six weeks' storage. No insect vector is known.

Group IV. *Insect transmissible but not transmitted by sap-inoculation*

Potato Leaf Roll = Phlœm-Necrosis (Quanjer), Solanum Virus 14 (K. M. Smith).—The virus of Leaf Roll is the only one amongst potato viruses known to be transmitted effectively by insects yet incapable of being transmitted by needling infective sap. This latter fact, as in other cases already noted, has prevented any study of the virus apart from its living host plant. These interactions have been described in the previous Chapter, to which it is only necessary to add that the temperature at which the virus is inactivated is not known with any degree of precision. Blodgett (1923) concluded from his tests that the thermal death-point of the Leaf Roll virus is certainly higher than that of the tuber, but this view is contested by Kassanis (1949). The latter worker found that, under moist atmospheric conditions, potato tubers remained viable after considerable periods of exposure to temperatures of 37° C. to 40° C. Leaf Roll infected tubers held at a temperature of 37·5° C. (99·5° F.) for at least twenty-five days produced plants free from the virus ; whereas at shorter periods of from ten to twenty days the reaction was uncertain, some tubers having the virus inactivated while others produced plants showing the full symptoms of the disease. Leaf Roll is one of the best examples of a "persistent" virus (*cf.* page 561).

Group V. *Both sap-inoculable and insect transmitted*

Virus "A" (Murphy and McKay), Solanum Virus 3 (K. M. Smith). The virus was isolated from apparently normal plants of Irish Chieftain by Murphy and McKay in 1932 and has since been found to occur naturally in Golden Wonder, Immune Ashleaf and Catriona, most stocks of these varieties carrying the virus sometimes with little or no symptoms. Virus "A" has been regarded as one of the most stable of potato viruses, but recently Botjes (1948) has recorded the marked attenuation of the virus in the variety Eigenheimer, kept in isolation from 1923 to 1947. It is included among the "non-persistent" viruses (page 561) by Watson and Roberts (1939) and is transmitted—apparently with some difficulty—by the aphid *Myzus persicæ* (Loughnane, 1933) and according to Bawden (1950), by *Macrosiphum euphorbiæ*, *Aulacorthum circumflexum*, and *Aphis rhamni*. K. M. Smith (1937) also lists the latter insect as a vector of virus "A." The virus is sap-transmissible by ordinary rubbing from potato to tobacco, but curiously enough it can only be transmitted by sap to potato if an abrasive such as carborundum is added to the sap. As to its physical properties, the virus appears to be inactivated at the very low dilution of from 1 : 50 to 1 : 100, or after storage at room temperatures for twenty-four hours, or exposure for ten minutes at a temperature of 50° C.

The position of virus "A" in relation to virus "Y" has been the subject of some controversy. Murphy and Loughnane (1936) expressed the opinion that, in any natural system of classification, viruses "A" and "Y" must be placed in the same broad Group—a suggestion which does not imply identity. Indeed, they instance several important differences; in particular the fact that prior infection of *Solanum nodiflorum* with virus "A" affords no protection against infection with virus "Y," and they state that this is equally true of potatoes in nature, for Irish Chieftain "carrying" virus "A" becomes naturally infected with virus "Y." Hansen (1937) considered the relationship to be a very close one since he found the two viruses to give similar serological reactions. Bawden and Sheffield (1944), however, were unable to confirm this relationship but, on the other hand, they agreed with Murphy and Loughnane that neither virus affords protection against infection with the other. In practice the two viruses may be distinguished in the following ways: (1) sap-inoculation to *Solanum nodiflorum* gives either no symptoms (virus "A") or a veinal Mosaic (virus "Y"); (2) grafts on Epicure give a bright Mosaic with either Apical Top Necrosis (virus "A") or necrotic spotting of lower leaves (virus "Y"); (3) grafts on Up-to-Date give either Top Necrosis (virus "A") or Acropetal Necrosis, *i.e.* Leaf-Drop Streak (virus "Y"). Köhler and Panksens (1944) and Köhler (1948) suggest the use of *Solanum demissum* as a test-plant for virus "A," this virus producing blackish, circular, necrotic spots on sap-inoculated leaves. They dismiss, as unimportant, the fact that strains of tobacco Mosaic produce similar symptoms, but unfortunately this is also true of virulent forms of potato virus "X" at "midsummer" temperatures under glass. To avoid confusion with virus "X," therefore, Köhler suggests that the inoculated leaf should be detached, placed on damp filter-paper in a petri-dish, and exposed for the five days required for symptom development in a well-lighted room, but away from direct sunlight.

Virus "Y" (K. M. Smith) = Streak Virus (Orton) = Leaf-Drop Streak (Murphy), Solanum Virus 2 (K. M. Smith). This virus was first recognised as a separate entity by Orton (1920), and since then it has been studied under various names by Murphy (Leaf-Drop Streak, 1921), Atanasoff (Stipple Streak, 1922), K. M. Smith (Potato Virus "Y," 1931), Quanjer (Acropetal Necrosis Virus, 1931), Hamilton (Hyoscyamus Virus II, 1932). It is probable also that Valleau and Johnson's (1930) Vein-banding Virus is the same virus. This is a typical example of a non-persistent virus (page 561), and the chief insect vector to potato in the field is *Myzus persicæ*. The delicate inter-relationship existing between the plant, the virus, and the insect vector is well illustrated by recent work by Bawden and Kassanis (1947). These authors found that whereas, of the aphides tested, *Myzus persicæ* alone was able to transmit virus "Y" from tobacco to potato, many species of aphides readily transmitted the virus from tobacco to tobacco; these including *Myzus persicæ; Myzus ornatus;*

Macrosiphum solanifolii; Aphis rhamni; Aphis fabæ; Aulacorthum (Myzus) circumflexum; Aulacorthum (Macrosiphum) solani; Canariella pastinaceæ, and *Macrosiphoniella sanborni*. It is easily transmitted by sap-inoculation to potato and other host plants, but *Datura stramonium* is immune. According to Reddick (1936) virus "Y" is transmitted in a small percentage of cases through the true seed; Stelzner (1942) confirms the presence of the virus in the potato embryo but says that it is usually inactivated during the process of ripening and storage. It is inactivated at dilutions in the neighbourhood of 1 : 1000, or on storage at room temperatures for from twenty-four to thirty-six hours; or after ten minutes exposure to a temperature of 52° C.

Virus "Y" is said to be the sole cause of Streak in potato fields (Murphy, 1938), and has been found to occur naturally in many varieties of potato and, according to Bawden and Kassanis (1947), in a number of strains of differing degrees of virulence as judged by the symptoms produced on the same host plant (*cf.* page 463). Hansen (1941) records several cases of partial infection of a plant giving rise to a mixed crop of healthy and diseased tubers, and states that the virus may even be localised in certain areas of the one tuber. In such tubers one or more shoots may show Rugose Mosaic, while the remaining shoots remain healthy until they are gradually invaded by the slow-moving virus. Hansen believes that in dormant tubers the virus is not only quiescent but is present in only low concentrations, as is shown by serological tests. Bawden and Kassanis (1947) also explain similar cases of temporary freedom from symptoms of single shoots as due to delayed infection, and they consider that necrosis only develops in a tissue when infected at an early stage of initiation; they were not able to detect the presence of virus "Y" in tissues before symptoms actually developed. Apart from the characteristic symptoms produced in certain potato varieties (*cf.* Leaf-Drop Streak, page 462) virus "Y" can be distinguished from all potato viruses, except virus "A," by the reaction in tobacco, *i.e.* a clearing of the veins followed by an outlining of the veins in green, deeper in colour than the rest of the lamina (vein-banding); virus "A" produces similar, but much milder, symptoms on tobacco, while other viruses give an interlocking mottle or "mosaic," with or without chlorotic or necrotic spotting. The production of non-systemic, necrotic spots, is often a useful guide to diagnosis and their frequency may afford some measure of virus concentration. Hence Dennis (1938) suggested the use of *Lycium barbarum* as a test plant for virus " Y " since it reacts with characteristic necrotic spots ; its usefulness, however, is limited by the fact that similar, though fainter, spots are produced by viruses " X " and " B." From sap-inoculation experiments with virus " Y " into 100 species of plants, Ross (1948) found four which reacted with necrotic spots, i.e. *Chenopodium urbicum*, *Physalis floridana*, *Lycium halimifolium* (Mill) and *Lycium chinense* (Mill) ; the last two, however, may = *L. barbarum*. According to Ross, the fact that *Physalis floridana* may be infected with a mild strain of virus " X " does not limit its use as a test plant for virus " Y," since the number of lesions is not affected by the presence of " X " and the symptoms produced by the latter virus are only faint.

CHAPTER XXVIII

SOME ASPECTS OF THE RELATION BETWEEN VIRUS AND PLANT

FULL consideration will be given later to the practical importance of the relations between the insect vector and virus but, intricate as these are, there remains ample evidence to show that the plant is the final arbiter as to whether transmission is, or is not, successful. It will be clear from the preceding pages that the relation between the virus and the infected plant is an intimate one, and indeed the problems involved are too complex for detailed consideration here. Some aspects, however, have a direct bearing on the question of degeneration in potatoes and these must receive some attention.

(1) INFECTION.—No conclusive evidence has been produced that a virus can arise *de novo* in a plant by the modification of some cell constituent (but *cf.* Bawden *et al.*, page 499), so we must assume that all infected plants have either themselves contracted infection from some outside source or are descendants of plants infected in this way. Infection, therefore, presupposes *entry* or inoculation from outside the plant followed by *multiplication* of the virus particles.

(a) *Entry or Inoculation of the Virus.*—Most of the earlier inoculations with viruses involved deliberate crushing and bruising of the foliage, but evidence soon accumulated to show that increased efficiency was obtained by methods which aimed at reducing tissue-damage to a minimum. The question therefore arose as to whether viruses could penetrate through unbroken cell-walls. Holmes (1931) and Samuel (1931) found that, in the case of tobacco Mosaic virus, a mere bruising of the leaf-hairs (trichomes) produced by stroking the tobacco leaf with a finger or glass spatula smeared with infective sap, considerably increased the likelihood of successful infection. Even this minute injury to cells was regarded as unnecessary by workers who believed they had obtained infection by merely spraying suspensions of viruses over unbruised leaf surfaces (Duggar and Johnson, 1933; Smith and Bald, 1935; and Smith, 1935); the last named work being of particular interest to us since the virus used by Smith was potato virus "X." However, Caldwell (1931, 1932), Sheffield (1936) and J. Johnson (1936, 1937) all failed to secure infection except when bruises, however slight, were inflicted. Similarly, Price (1938) tested a number of different hosts with a tobacco Necrosis virus, and Kalmus and Kassanis (1945) used a number of different viruses (including potato viruses "X" and "Y") on *Nicotiana glutinosa*, with the same failure unless the leaves were first bruised. Price also showed that a tobacco Necrosis virus, confined to root tissues, could not be transmitted to healthy roots in the absence of slight wounds. Duggar and Johnson (1933) explained their successful inoculations through unbroken leaf surfaces as the result of penetration by the virus *via* the stomata, but this still leaves unexplained the method of penetration into the cells lining the sub-stomatal chamber. Boyle and McKinney (1938), indeed, deny that there is any relationship between the number of stomata and infection, and they had about equal success in inoculations through the upper and lower surfaces of tobacco leaves, although the latter had quite twenty times the number of stomata as the upper surfaces.

Whether stomatal inoculation is possible or not, there can be no doubt of the increased likelihood of infection through slightly bruised tissue and a number of substances have been tested for this purpose; *e.g. sand* (Fajardo, 1930; Samuel, and Bald, 1933), *charcoal* of both animal and vegetable origin (Stanley, 1935*a*; Bald, 1937), *carborundum* (Rawlins and Tompkins, 1934, 1936; Bawden, 1936; Black, 1938; and Costa, 1944). Kalmus and Kassanis (1945) made comparative tests with these substances and obtained the best results with one form of carborundum (400 mesh), one form of animal charcoal, and *celite* (this latter being a diatomaceous silica and least likely to produce excessive wounding). These workers point out that the effect of using an abrasive is not confined to viruses difficult to transmit by sap-inoculation, but the advantage gained is shown in the case of potato viruses "X" and "Y"; and even with tobacco Mosaic virus, which is one of the most readily transmitted viruses known. Doubt as to the possibility of infection occurring in the absence of minute wounds is strengthened by some of their results involving the use of the "argentaffin" test, in which the presence of reducing substances is demonstrated by the blackening of ammoniacal silver hydroxide under the influence of light. Kalmus and Kassanis found that while unwounded leaves of potato and other plants give no reaction when placed in the reagent, when the leaf is first rubbed with the finger the surface becomes stippled with black spots, mainly at the sites of the broken leaf-hairs ; when an abrasive is used, the epidermal cells also are bruised and the leaf surface is uniformly blackened. So much could be anticipated but what was surprising was the fact that, although the injured cells continued to be permeable to the silver salt, within three hours the semi-permeability of the protoplasm had been restored sufficiently to prevent the passage of the relatively large virus protein particles.

(b) *Establishment and Multiplication of Virus.*—Before infection can follow on inoculation, the virus must establish itself in some way favourable for multiplication. This, it is usually assumed, involves the attachment of the virus particle to some specific cell constituent probably of a protein nature, which can act in this way only to one virus or to a group so closely related as to be regarded as merely different strains of one virus (*cf.* page 489). Distinct viruses require different establishment sites and hence can usually multiply within the cell without mutual interference, but competition for available sites may arise between virus strains. To discuss fully what is understood by "multiplication" would involve questions regarding the "nature" of viruses which are beyond the scope of this book. Nevertheless, multiplication almost certainly does not take place by "binary fission" as in the case of bacteria, but rather by some form of protein synthesis. One might expect this to result in an over-all increase in the protein content of the plant, and this is what Stanley (1937) claimed to occur in tobacco infected with tobacco Mosaic virus and tomato Aucuba Mosaic virus, though in other diseases (including potato virus "X") there was an actual reduction. Other workers have shown that although, in tobacco Mosaic, there is an increase in extractable protein and nitrogen there is no increase in total amounts of either (Martin *et al.*, 1938 ; Holden and Tracey, 1948). Bawden and Pirie (1946) state that on the average about one-third of the total nitrogen present in Mosaic-infected tobacco is in the form of active virus, and this may even increase to about 60 per cent. in plants deficient in nitrogen but abundantly supplied with phosphorus (Holden and Tracey, 1948). Bawden (1950) concludes that the presence of so large a proportion of the total nitrogen in the form of a virus, without any corresponding increase in inert forms of protein, suggests that the virus is largely produced at the expense of normal proteins. This view is supported by the statement of Martin *et al.* (1938) that during the first few days of infection the increase in virus is accompanied by a parallel decrease in the normal protein. Takahashi (1941, 1947) also found that detached infected leaves, which were kept in darkness, showed an increase in virus content while the normal proteins were autolysing. On the other hand, Spencer (1941) believes that a virus cannot utilise normal proteins for its synthesis and that it can only multiply when other supplies of nitrogen are available. We must conclude, however, on the balance of evidence at present available, that virus multiplication is to be envisaged as occurring in much the same way as in the normal increase in cell protein, though the mechanism is quite unknown. Certainly, it is unnecessary to assume that the product of multiplication is in any way a lineal descendant of the original virus particle.

2. SUSCEPTIBILITY.—This term may be defined as the likelihood of inoculation being followed by infection. Clearly, susceptibility describes the result of an interaction between the virus and the plant and must be influenced by any factor capable of modifying either the one or the other; among the more obvious of such factors are the following:—

(a) *The Method of Inoculation.*—All known plant viruses can be transmitted to healthy plants by grafts even when other methods fail. During the process of tissue-union it is likely that physiological activity is accelerated and, with abnormally rapid interchange of metabolic products, there is a mass inoculation of virus particles which "swamps" even relatively resistant cells. Viruses normally producing only local lesions by sap-inoculation of the leaf may become systemic, while the protection afforded by one strain of a virus against infection by another may wholly or partly break down. Again, it would seem that some viruses must be inoculated directly into particular tissues such as the phlœm (*e.g.* potato Leaf Roll), others, not insect transmitted, may be successfully inoculated *via* minute wounds into the ordinary parenchyma cells (*e.g.* potato virus " X "), while still others are transmitted by both methods with varying degrees of success (*e.g.* potato viruses " Y " and " A "). Since wounds appear to be indispensable to successful sap-inoculations, we must assume that the greater susceptibility usually shown by young plants or organs, or by plants grown under poor illumination, is partially, at any rate, due to the greater fragility of tissues under such conditions.

(b) Susceptibility also depends on the *concentration of virus particles* in the inoculum for, when this is too low, there is apparently no multiplication of the virus in the invaded cells and the plant remains uninfected. This minimum concentration (or " dilution end point ") is not an intrinsic character of a virus, for it varies with the method of inoculation and with the host plant (Kalmus and Kassanis, 1945). As regards the method of inoculation, these workers found that the effect of using an abrasive may be to raise the dilution end point of the virus by a hundred-fold (*i.e.* the minimum infective dose is only 1/100th of the concentration required without an abrasive). Obviously the virus concentration is not altered by an abrasive, so that the effect must be to reduce the resistance of the host in some way ; it may be merely by increasing the number of minute wounds, and hence of possible entry points for the virus, but the effect is at least as likely to be due to the fact that epidermal cells are more susceptible to infection than are the hair-bases which, without an abrasive, are the cells most likely to be injured by rubbing. Kalmus and Kassanis (1945) noted that the upper, hairy, leaves of *Nicotiana glutinosa* usually give relatively few lesions as compared with the lower leaves but, when an abrasive is used, the *increase* in the number of lesions is from five to ten times greater on the upper than on the lower leaves. Even individual epidermal cells may differ in their susceptibility according to Sheffield (1936), for when she inoculated individual cells separately by means of a micro-pipette she obtained only one-tenth of the expected successful infections. The minimum infective dose also varies with the host plant. Thus potato virus " Y " is readily transmitted from tobacco to tobacco by infective sap diluted to 1/10,000, whereas a dilution greater than 1/500 is unable to infect President potato. Again, potato virus " A " is transmitted freely, without abrasive, from potato to tobacco but an abrasive is necessary before a potato leaf can be infected from the same sap (Bawden, 1936). This seems to imply not only a low concentration of the virus in potato as compared with tobacco, as Bawden (1950) suggests, but also that the minimum concentration of virus required for infection is greater in potato than in tobacco. The virus concentration may vary considerably in different varieties of potato (Bawden and Kassanis, 1946) and this fact may influence the likelihood of the variety serving as a source of virus for an insect vector (*cf.* page 563). Similarly, the varying susceptibility to infection by potato virus " Y " shown by different varieties, when colonised by equal numbers of infective *Myzus persicæ* may, in Bawden and Kassanis' experiments, be a reflection of differences in the minimum infective dose required for infection. Using the percentage infection of tobacco plants as a standard, Bawden and Kassanis found the variety Ulster Monarch to be almost as susceptible as tobacco, with the following varieties in decreasing order of susceptibility :—May Queen, King Edward, Arran Pilot, Arran Consul, Kerr's Pink, Gladstone, Sharpe's Express, Redskin, Arran Banner, Majestic, and, by far the most resistant of all, the American variety Katahdin.

(c) The *nature of the cell contents* and factors influencing their production affect susceptibility, and the products of photosynthesis, in particular, have been shown markedly to reduce the susceptibility of a plant to infection by such viruses as have been tested. This may explain the *increased* susceptibility to four different viruses noted by Bawden and Roberts (1947) when various host-plants were grown continuously in reduced light ; the susceptibility as measured by the number of lesions being increased from five- to ten-fold, while the virus concentration increased twenty-fold in inoculated leaves and up to ten-fold in leaves systemically infected. In later work (Bawden and Roberts, 1948), they demonstrated that this effect of poor illumination was confined to treatment immediately *before* inoculation, for exposure to low light conditions immediately after inoculation either had no effect, or even reduced susceptibility. They conclude that the products of photosynthesis affected only the establishment—and not the multiplication—of the virus. It is not known whether these products confer resistance by reacting specifically with virus particles to render them non-infective, or act mechanically by increasing cell-turgor or by interfering with the attachment of particles at multiplication sites. It was already known from Bawden and Pirie's (1945) work that tobacco and French bean plants showed great differences in susceptibility to infection by a tobacco Necrosis virus at different seasons of the year, and it seems probable that the predominating factor was the effect of variable light intensity upon carbohydrate production. Thus, plants inoculated between the months of November and February were extremely susceptible. Inoculated leaves became completely necrotic without the aid of an abrasive and the tissues, which contained only a small amount of normal proteins, yielded from 100 to 200 mg. of virus per litre of extracted sap. In spring and autumn an abrasive was necessary in order to induce the development of a large number of lesions, considerably more normal proteins were present in the cells, and it was rare to obtain more than 10 mg. of virus per litre; while in the summer months (June to September) few lesions developed even when an abrasive was used, and it was never possible to make satisfactory preparations of virus. Unfortunately, Bawden and Pirie did not carry out parallel determinations of proteins in healthy plants so that, although a low protein synthesis might be expected in winter-grown plants as a concomitant of low photosynthetic activity, it is not possible to say to what extent the protein was kept at an abnormally low level by its use as a pabulum for virus multiplication. It is, however, clear that the mere presence of an abundance of normal protein does not guarantee the multiplication of a virus already established. In the above experiments the only variable factor considered was light, other factors being assumed to be relatively constant. If, however, light intensity is high and constant, the limiting factor in carbohydrate production in a normal plant may be the external concentration of CO_2 (at any rate up to the level at which the gas acts as a narcotic). Kalmus and Kassanis (1944) made use of this fact by treating detached leaves of French bean with atmospheres containing from 30-60 per cent. CO_2. They found that the effect of two hours' exposure to the gas *immediately* before or after inoculation was to reduce the susceptibility to infection by tobacco Necrosis viruses; susceptibility being measured by the number of lesions produced. When the treatment was delayed for more than four hours after inoculation, however, the gas had no effect upon susceptibility and the authors conclude that, as in the case of the direct action of light, the effect of the gas was upon virus establishment at the multiplication sites. It would appear that the CO_2 in Kalmus and Kassanis' experiments acted as a stimulant of photosynthesis and not as a narcotic, for cyanide salts (Woods, 1940, 1943), other narcotics (Rischkov and Gromiko, 1941), and even malachite green (Takahashi, 1948) have been shown to prevent the multiplication—though apparently not the establishment—of viruses. This effect of narcotics is said by Woods to be due to a direct (but reversible) inhibition of the respiratory system of the plant on which virus multiplication is stated to depend. However we may assess the evidence for the effects of physiological processes on susceptibility, there can be no doubt that the plant must be in a " receptive " state if infection is to follow inoculation, but there is, as yet, little precise knowledge of what constitutes a " receptive " state. Certainly, different organs on the same plant are subject to continuous, and differential, changes in this respect, and the conditions predisposing to infection by one virus may be unsuitable for another. Thus, Bawden (1950) states that if opposite halves of each leaf of a well-grown *Nicotiana glutinosa* plant are rubbed with tobacco Mosaic and tomato Bushy Stunt viruses, the former will cause lesions on all leaves though mostly on the middle and lowest ones, whereas the Bushy Stunt virus will produce no lesions on the lowest leaves, a few on the middle ones and most of all on the upper.

According to Kleczkowski (1946) the power to combine with, and precipitate, a virus is apparently possessed by any cell constituent having an opposite electric charge, such as might occur over a wide range of *p*H if the virus and cell substance possessed very different isoelectric points. Some, but not all, of these virus precipitants also reduce the infectivity of the virus, *i.e.* they act as " inhibitors." No inhibiting substance appears to have been demonstrated as yet in potato, but many have been isolated from other plants and have been shown to inhibit a virus either in the plant or when the virus *in vitro* is mixed with expressed sap, *e.g.* tobacco Mosaic virus is rendered largely non-infective by the sap of *Phytolacca* sp. (Duggar and Armstrong, 1925), sugar-beet (Hoggan, 1933), or even the sap from micro-organisms such as the mould *Aspergillus niger* (Johnson and Hoggan, 1937). Some, at least, of the inhibiting substances are forms of proteins, *e.g.* trypsin (Stanley, 1934); ribonuclease (Loring, 1942); globin and clupein (Kleczkowski, 1946) and a glycoprotein from *Phytolacca esculenta* (Kassanis and Kleczkowski, 1948), while at least one, isolated from yeast, is a polysaccharide (Takahashi, 1942, 1946). Bawden (1950) puts forward the view that inhibition results from the production of non-infective complexes between the cell constituent and the virus, in which the groups essential for infectivity become " blocked." He suggests, further, that the apparent differences in complexity between different viruses may to a large extent reflect the fact that their basic particles adhere with different degrees of tenacity to other constituents of host-cells, rather than that their basic particles differ widely. This last opinion adds point to Walker's (1926) comparison of the viruses of cucumber Mosaic and the Mosaic of ground-cherry (*Physalis pubescens*) in respect of longevity *in vitro*, effects of heat, alcohol or antiseptics. Walker found that when cucumber Mosaic virus was transferred to ground-cherry, and then examined in ground-cherry sap, it lost its labile characters and behaved like ground-cherry Mosaic virus; conversely, ground-cherry Mosaic virus, in cucumber sap, acquired the labile characteristics of cucumber Mosaic virus and no longer showed resistance to standing, heat, alcohol or antiseptics. These characters, in fact, were due, not to intrinsic attributes of the viruses, but to interaction with some sap constituent. How far these modifying or inhibiting substances are normal cell constituents is not known, but they should not be ignored in studying the reactions of viruses *in vitro*; the possibility must not be overlooked, for instance, that their presence may afford a partial explanation of " resistance " to infection by certain viruses. It is true that many inhibitors appear to be non-specific in their action, but that is not invariably the case. Thus, Bawden and Pirie (1945) found that French beans apparently possessed an inhibitor of tobacco Necrosis virus not present in tobacco plants, yet Sadasivan (1940) demonstrated that sap expressed from healthy tobacco leaves reduced the infectivity of potato virus " X " and tomato Aucuba Mosaic virus.

What appears at first sight to be a similar phenomenon is the reaction of one virus with another. Sadasivan (1940), found that if, instead of healthy sap, he mixed the sap from a " Y "-infected plant with potato virus " X " the reduction in infectivity of the virus " X " was of the same order as with healthy sap, but that infectivity was reduced to a much greater extent if the " Y "-infected sap were replaced by sap from a plant containing another *strain* of virus " X " In other words, the reaction between related viruses was much greater than between unrelated ones. It may be thought that this result might have been anticipated from the known effects of " protective immunisation " (page 489). Protective immunisation, however, is usually explained as due to the pre-emption of all available multiplication sites by the virus first inoculated, whereas Sadasivan showed that, *in vitro* at all events, the reduction in infectivity was due to the direct action of one virus on another, in which metabolic products in the sap played no part. Sadasivan's results may, however, to some extent explain the reactions of tobacco Etch viruses on the unrelated potato virus " Y." Bawden and Kassanis (1941, 1945) have shown that while potato virus " Y " is quite unable to interfere with the entry or further development of the Etch viruses, the Mild Etch virus affords partial (and the Severe Etch virus complete) protection against infection of a plant by virus " Y." Hence the protection is not mutual and, indeed, so far from virus " Y " affording protection against Severe Etch virus, it is dominated so completely by the Etch virus that, even when already established in a plant, potato virus " Y " is eventually suppressed and inactivated by the newly inoculated virus. If Sadasivan's (1940) conclusions apply in these cases, the suppression of one virus by another in no way affects the susceptibility of the host-cell, and the same is probably true of cases of combined infection by two unrelated viruses which result in the production of symptoms expressing only the separate effects of each virus, *e.g.* potato plants infected with virus " Y " plus Leaf Roll. When, however, combined infection by two unrelated viruses produces different, and more severe, symptoms than can be accounted for by a summation of the separate effects of the two viruses, there is obviously an added effect upon the plant cell itself. This added effect should not be regarded as evidence of increased susceptibility, however, but rather as an increased *sensitivity* ;

for what has been intensified is the symptom expression and not the likelihood of infection. Examples of this increased sensitivity are common, *e.g.* the necrotic Streak disease of tomato following combined infection with tobacco Mosaic virus and potato virus " X " ; or the severe Crinkle disease of potato due to potato viruses " X " plus " A," each of which, alone, produces the mildest of mottles in most varieties of potato.

(d) *Effect of Nutrition on Susceptibility.* Most virus workers would agree that the likelihood of infection, and of the development of full symptoms (*i.e.* susceptibility and sensitivity) is increased if inoculations are made into actively growing plants. From this it is a small step to assume that successful infection is directly related to the rates of application of various manurial elements, *e.g.* that varying the nutritional level will profoundly affect the susceptibility of the plant to infection. No doubt, in a general sense this is true enough, but efforts to segregate the effects of the different factors involved in " nutrition " have met with only qualified success. First, it must be remembered that nutrition in any real sense involves the utilisation of the products of photosynthesis as well as the intake of mineral salts. Indeed, this is probably the underlying cause of the gradient in susceptibility found by Holmes (1929) in leaves of varying age on the same plant ; an observation which has been repeatedly confirmed. Samuel and Bald (1933) pointed out the necessity for rigid standardisation of conditions of growth in any comparative work on virus susceptibility. They showed that poorly-grown, small, hard plants gave far fewer lesions than did larger and better plants inoculated with the same sap, and that the susceptibility of the small plants, as measured by the number of lesions, greatly increased after the application of ammonium phosphate. These workers demonstrated that in order to compare the susceptibility of a plant to two viruses, sufficiently uniform physiological conditions could only be obtained if the two viruses were inoculated into opposite halves of the same leaf ; a technique which is now universally applied. Secondly it must be borne in mind that the optimum conditions for establishment are not necessarily equally suitable for the multiplication of the virus. Bawden (1950) has pointed out that by counting the number of lesions one can hope to measure the establishment—but not the rate of multiplication of the virus—for the latter has no fixed quantitative relation to establishment (*cf.* below); further, since one effect of raising the nutritive level is to increase the size of the leaves, any response to a change in nutrition will appear very much larger if the count of lesions per *leaf* is taken as a standard instead of the number per *unit area* of surface, and he quotes an addition of phosphorus which, on the leaf standard, gave an increase of 500 per cent. as opposed to the 50 per cent. increase in number of lesions when calculated per 100 sq. cm. of leaf surface. Again, no real appreciation of the rate of virus multiplication is possible without determining the virus-content in the infected tissues and, in order to eliminate the effect of differences in the number of " entry " points, the determination should be made in systemically infected tissues rather than in local lesions. Here, also, Bawden gives a warning that very different conclusions will be drawn if the amount of virus per ml. of sap or per unit weight of leaf is considered rather than the total virus of the whole plant.

Spencer (1935, 1935*a*) attempted to assess the effect on susceptibility of applications of nitrogen, phosphorus and potassium in the case of tobacco, *Nicotiana glutinosa* and French bean. Relying on counts of local lesions he concluded that there is no close correlation between growth-rate and susceptibility, but that a quantitative relationship does exist between susceptibility and the amounts of nitrogen, phosphorus and potassium applied. With nitrogen he found increasing susceptibility even when the amount applied was so excessive as to decrease growth, whereas phosphorus only increased susceptibility so long as growth also was encouraged. Potassium, on the other hand, increased susceptibility when applied in small doses but decreased it when large amounts were applied, although in neither case was there any apparent effect on growth. Bawden and Kassanis (1950), however, found with the same technique that potash had little effect either on susceptibility to tobacco Mosaic virus or on the rate of growth of tobacco plants in soil. Applications of nitrogen or phosphorus increased susceptibility and their effects were correlated with the growth response of the plants. Phosphorus was the more important element affecting susceptibility and, in the absence of adequate phosphorus supplies, increasing the nitrogen actually reduced the number of lesions. The effect of nutrition on virus multiplication, also, has only been tested in the case of tobacco Mosaic virus. Rischkov and Smirnova (1939) found that the virus concentration in nitrogen-deficient tomato plants equalled that in plants adequately supplied with the element, and Holden and Tracey (1948) state that the virus content may increase to 60 per cent. of the total protein in plants deficient in nitrogen so long as they are well supplied with phosphorus. On the other hand, Spencer (1939) found that virus concentration was directly correlated with nitrogen supply, and stated that, within thirty-five days after inoculation, the virus concentration in the sap from plants abundantly supplied with nitrogen was 80 times that from the sap of nitrogen-deficient plants. Bawden and Kassanis (1950) have found no such correlation with any of the three elements except in so far as they individually, or collectively, affected the growth response of the plants. They note, for example, that in summer, when tobacco plants respond rapidly to nitrogen, an application of nitrogen increases virus production more than it does in winter when a corresponding amount of nitrogen may inhibit plant growth.

(3) Distribution of a Virus within the Plant.—(a) *Systemic and Local Infections.*—The fact that, usually, viruses spread to most parts of the plant from the point of inoculation (*i.e.* that the infection is systemic) is a characteristic of virus diseases which was first emphasised by Allard (1914); it tends to align such diseases with the effects of mineral deficiencies rather than with maladies due to fungi, or even bacteria. Nevertheless, it has long been known that a virus is frequently—and perhaps always—unevenly distributed throughout the plant tissues; it has, for instance, only rarely been demonstrated in the seed-embryo, and has never been satisfactorily proved to occur in the embryo of the potato (but *cf.* pages 450 and 453). Viruses have been shown to occur in other parts of the sexual organs of plants but how common this may be is not known; roots are apparently frequently affected although in such low concentrations as to make isolation difficult. According to Sheffield (1936*a*), viruses are unable to penetrate into the stomatal guard-cells. Samuel (1931) showed that when the tobacco Mosaic virus was transferred to tomato, some regions of the stem remained free

from virus although these lay between infected zones. As early as 1886, Mayer assumed that the green areas of tobacco leaves infected with Mosaic were free from virus, but Beijerinck (1898) demonstrated this to be an error since, when an affected plant was severely cut back, the newly developed foliage again showed the full mottled symptoms ; he considered, however, that the mottling itself was an indication of uneven distribution. Apart from Samuel's observation there are other examples of discontinuity in virus distribution. Thus Smith and Bald (1935) and Smith (1937*a*, *b* and *c*) described what is now known to be a group of viruses in apparently healthy tobacco plants which, although normally confined strictly to the root system, proved to be capable of infecting aerial organs when these were artificially inoculated. Some viruses, in certain host-plants, appear to be able only to infect a small area immediately around the point of inoculation. These areas consist usually of dead, necrotic cells, *e.g.* tomato Aucuba Mosaic in *Nicotiana glutinosa* (Sheffield, 1936*b*), but this is not always the case, for one of Smith and Bald's tobacco Necrosis viruses (*cf.* above), although carried without symptoms by *Primula obconica* when artificially inoculated, is almost entirely confined to small areas of tissue around the inoculation point (Bawden and Kassanis, 1947). More frequently these tobacco Necrosis viruses produce local necrotic lesions, but there is sufficient movement out of the lesions to cause infection and death of the inoculated leaf though not of other leaves on the plant ; even systemic infection with these viruses may occur in a few plants when inoculated under glass but it is only recently that natural systemic infections have been discovered, *e.g.* in tulip (Kassanis, 1949) and French bean (Bawden and van der Want, 1949). It must therefore not be assumed that necrosis-producing viruses are absent from the non-necrotic areas, for that is usually not the case, as is sufficiently proved by the occurrence of an over-all mottle. In potato there is a good deal of evidence of uneven virus distribution whether necrosis occurs or not. Thus Schultz and Folsom (1920, 1923) demonstrated this to be true of both foliage and tubers in plants affected with " Mosaic " ; and Clinch (1944), working with a virulent form of potato virus " X," found that not all the " eyes " of an infected tuber contained the virus, an observation which should induce caution in applying the "tuber-unit" system in Potato Certification Schemes (*cf.* page 180). She, however, did not find any instance of an infected tuber in which all "eyes" gave rise to healthy haulms. On the other hand, it is only in plants in which the foliage is infected relatively early in the growing season that the virus succeeds in invading all the tubers, so that the proportion of tubers escaping infection from the current-season infected foliage can be used as a rough guide to the time at which the foliage contracted infection. Even in fully infected tubers, Bawden *et al.* (1948) have shown that virus "X" is very unevenly distributed. Thus in immature tubers the virus could only be demonstrated in tissues near the "eyes," and it only doubtfully occurred in the pith parenchyma of older tubers. The concentration of virus near the "eyes," although much higher than elsewhere in the tuber, was far below that of the developing sprouts where, in fact, the concentration was as high as in the foliage; the practical value of this observation lies in the ability to test the health, or otherwise, of tubers in the sprouting stage, without waiting for the development of leaves before carrying out the necessary inoculations to tobacco or other test plant. It is thus possible to ensure that only healthy tubers are planted in the case of valuable nuclear stocks.

(b) *Local Lesions and their use in Quantitative Work.*—A technique for the quantitative estimation of a virus, based on the number of necrotic lesions produced on an inoculated leaf, was suggested by Holmes (1928, 1929). He found that, within certain limits, the number of lesions produced when tobacco Mosaic was inoculated to *Nicotiana glutinosa* was proportional to the concentration of the inoculum, and could therefore be used as a measure of the concentration (or more correctly, the infectivity) of any given sample of infective sap. Further work by Samuel (1931), Samuel and Bald (1933), and Bald (1937) showed that the number of lesions also depended upon (i) the method of inoculation, (ii) the particular leaf and its position on the stem, (iii) on plant nutrition and other factors affecting the rate of growth. There was, however, little difference in the number developing on opposite sides of the mid-rib when inoculum was applied to the whole lamina, so that by rigid standardisation of method in order to eliminate the above-mentioned sources of variance, it has become a routine method of comparing the activity of one virus with others. The "standard" virus inoculum is inoculated into one-half of each leaf (using alternately left and right halves of a leaf) and the remaining halves are used for the inoculation of the virus under test; by a judicious randomising of half-leaves it is also possible to compare several virus preparations, in a single experiment, with the standard. Yet another advance was made when Youden and Beale (1934) suggested that, by arranging inoculations of all the leaves of a number of plants in such a way that each virus preparation appeared the same number of times on each plant and at each leaf position (*i.e.* so as to give a "Latin Square"), the results would be amenable to statistical evaluation and the need to refer all results to a standard virus preparation would be avoided. This method does not, of course, diminish the need for rigid standardisation of plants and growing conditions but, properly carried out, it has proved a valuable aid in virus work. There are, however, many pitfalls in interpreting the results of such comparisons, some of which may be very briefly mentioned. Any two viruses, or dilutions of the same virus, will differ physically in many ways (*e.g.* in the concentration of particles, hydrogen-ion or salt concentration, or the possible presence of an inhibiting substance) which will affect the efficiency of the virus in producing infections. Best (1935) showed by plotting the logarithms of the number of lesions against the dilutions that it was only in the middle range of dilutions that a linear relationship existed between them; at very high or very low concentrations a change in the concentration produced far less change in the number of lesions than would be expected. This was confirmed by Price and Spencer (1943), who found comparisons to be most sensitive when the more concentrated inoculum produced from 15 to 35 lesions per half-leaf; comparisons should therefore be made between preparations at optimum dilutions determined by separate, preliminary tests. For further details the reader should consult Bawden (1950), or Smith (1951).

Holmes (1931) made yet another important advance by demonstrating that the local lesion technique was applicable in many cases of systemic infections where either no visible lesions were produced or, at best, were not sufficiently sharply outlined to be counted. By using a modification of Sach's

Iodine Test (page 441) for starch accumulation, in which the detached leaf is darkened for only some twelve hours, Holmes found that even these vague spots became sharply delimited from the rest of the leaf tissue. In leaves detached in the evening and immediately stained, the spots showed far less concentration of starch than other parts of the leaf, whereas if the affected plant were kept in darkness for several hours before treatment of a leaf, the localised spots showed up as blue-black areas against the unstained remainder of the leaf. The method has been used successfully with non-necrotic strains of potato virus " X " and with potato virus " Y."

(4) MOVEMENT OF VIRUSES THROUGH PLANT TISSUES.—(a) *The Path Taken.*—As early as 1898 Beijerinck drew attention to the fact that the first sign of the spread of tobacco Mosaic in a plant was the appearance of symptoms in the leaf directly above the one inoculated, and concluded that the phlœm provided the means of transporting the virus. Assuming that movement was real (*i.e.* that virus particles were transported, and not " created " in healthy cells by a form of autocatalysis stimulated from an adjacent infected cell) it can scarcely be denied that movement of viruses is of two kinds. Since infection of superficial cells is frequently followed by systemic invasion of the whole plant, there must be a form of diffusion from one parenchyma cell to another, yet that alone will not account for the very short time-lag before symptoms appear in organs remote from the point of inoculation. Thomas (1947), for instance, estimates that the diffusion of even an electrolyte such as a 10 per cent. solution of NaCl would require almost a year to transport one mg. over a distance of one metre ; while in the case of viruses, which appear to consist of large protein molecules, there is direct experimental evidence that simple diffusion through the protoplasmic membrane must be excluded (*cf.* Kalmus and Kassanis (1945) under (1) INFECTION). Naturally, therefore, many workers have expressed the opinion that movement from cell to cell was *via* the protoplasmic cell-connections or plasmodesmata (Quanjer, 1931 ; Drake *et al.*, 1934 ; Livingstone, 1935 ; Martin and McKinney, 1938) ; but the first experimental evidence was provided by Sheffield (1936*a*), who also explained the apparent absence of virus from stomatal guard-cells as due to the absence of connections between these cells and the

adjacent epidermal cells. How slow such movement must be is shown by Uppal's (1934) estimate that tobacco Mosaic virus travelled from the upper to the lower epidermis of a leaf of *Nicotiana sylvestris* at the rate of 8 μ. per hour and that the movement was not influenced by either food or water movements; this is a rate which is not inconsistent with diffusion over a concentration gradient resulting from virus multiplication at the point of inoculation. Caldwell (1931, 1934) believed that even long-distance movement was of this kind. He found that tobacco Mosaic virus, inoculated into tomato stems, was unable to traverse a ring of tissue in which all living cells had been killed by steam or chloroform, although the continued turgidity of the leaves showed that the xylem was functioning properly; when wood vessels were injected with virus it was unable to escape unless the vessel-walls were damaged. In Caldwell's view the phlœm, also, had no special significance in virus movement since the movement was not influenced by the direction or rate of food translocation but was, in fact, constant and equal in all directions. Grainger (1933) and Matsumoto and Somazawa (1933), however, found that tobacco Mosaic virus invaded all tissues, including the xylem, but the former agreed with Caldwell that virus movement was not influenced by either food translocation or transpiration. Three questions emerge from this controversy, *i.e.* does virus movement occur in either xylem or phlœm (or both) and, if so, is the movement a purely passive one along the food or transpiration streams?

There is overwhelming evidence of the importance of the vascular tissue in the transport of viruses over long distances. Storey (1928) showed that the movement of the virus of the Streak disease of maize and sugar-cane was greatly retarded by severing the leaf mid-rib, and suggested that movement at all was then only possible *via* the minute, anastomosing veins. Holmes (1930, 1931, 1932), using the starch-iodine technique with tobacco Mosaic, reported that, after a period of multiplication at the inoculation site, the virus moved very slowly through the parenchyma until a vein was reached; there was then a sudden change to a rapid movement which quickly carried the virus into the stem and root apices. He found that an uninoculated leaf first showed infection near a vein and that cutting the leaf mid-rib greatly retarded movement, whereas severing the interveinal tissue had little effect. It has already been mentioned that Grainger (1933) and Matsumoto and Somazawa (1933) concluded that the xylem as well as the phlœm was invaded by the virus of tobacco Mosaic; similarly, Bennett and Esau (1936) stated that the virus of beet Curly-Top invaded all tissues, including the xylem vessels. Since, however, the virus also passed into the intercellular spaces and exuded as droplets on the leaf surface due, the workers said, to the bursting of the over-turgid phlœm elements, the same cause might also explain the flooding of the xylem. But that virus invasion of the xylem is not always accidental is suggested, in the case of Pierce's disease of vine and alfalfa, by Houston's *et al.* (1946) statement that infection is dependent on the leaf-hopper vector succeeding in reaching the xylem with its stylet. Nevertheless, whatever may be the rôle of the xylem in certain cases, there can be no doubt that the weight of the evidence points to the phlœm as the main conduit for a virus over long distances; the only conflict of opinion being as to the mechanism of transport.

(b) *The Relation between Virus and Food Translocation.*—Many workers in this field have demonstrated that viruses move much more freely and rapidly in a downward than in an upward direction, which not only indicates the phlœm as the medium of transport but suggests that the virus particles are passively carried in the food stream rather than that they possess power of independent movement. Quanjer (1913) interpreted the necrotic effects upon the phlœm as an indication that potato Leaf Roll virus was transported in this tissue and later (1920) extended this statement, with perhaps less justification, to the transport of potato "Mosaic" virus. No one, however, has suggested that potato virus "Y" travels in the collenchyma of the stem because necrosis is most evident in this tissue, and McKinney and Hills (1941) give a very different interpretation of the fact that tobacco Mosaic, in *Capsicum frutescens*, induces necrosis of the xylem well in advance of the virus; this necrosis, they say, is directly caused by the translocation of the products of deranged metabolism which, in turn, is induced by small amounts of virus in remote zones. More convincing evidence that potato Leaf Roll is transported in the phlœm is provided by the fact that the virus is apparently only transmitted to a healthy plant when it is directly introduced into the phlœm either by graft or by means of a phlœm-feeding aphid ; the same being true also of the virus of sugar-beet Curly-Top though in this case the insect vector is a leaf-hopper. Clinch (1942, 1944) found evidence of a very rapid downward movement and very slow upward movement of potato virus " X," and attributed the former to translocation in the phlœm because interference with food movement equally retarded virus movement. The upward movement she believed was dependent upon multiplication of the virus in the parenchyma, and clinched her argument by interposing a 12 cm. length of the immune seedling U.S.D.A. 41956 between an " X "-infected stock and a healthy scion ; the inability of the virus to multiply in the immune seedling effectively prevented any upward movement, whereas when the top scion was infected and the stock was healthy the interpolated seedling had no effect on the downward movement of the virus. Perhaps the most conclusive evidence of virus movement in the phlœm is that contained in a series of papers by Bennett (1927, 1934, 1937, 1939, 1940) from which only examples may be quoted. When either of two raspberry Mosaic viruses was inoculated to a single cane, symptoms were produced on the leaves and the virus passed downward to the roots ; there was no infection, however, of the remaining canes in the current year unless they were cut back to stimulate new demands on the food supply, whereupon the new foliage on these canes developed symptoms. Again, by grafting *Nicotiana glauca* plants on the apex and on basal suckers he found that whereas the virus passed from the top to the bottom scion in seven days it took months to pass from the bottom to the top scion ; when, however, he reversed the direction of the food-stream by defoliating the plants or placing them in the dark, the virus passed from the bottom to the top scions in a few days. Virus moved out of normal leaves within four hours after inoculation, but for etiolated leaves kept in the dark the time required was twenty-one days, unless they were illuminated, in which case the passage outwards was accomplished within twenty-four to forty-eight hours. Cochran (1947) also found that 75 per cent. of healthy plants connected, by dodder, to plants infected with different viruses contracted infection when the dodder was heavily pruned and the healthy plants kept under poor illumination, but none was infected when unshaded and the dodder left unpruned. Samuel (1931), using the starch-iodine technique, confirmed Holmes' (1930) statement that the virus of tobacco Mosaic moves slowly through parenchyma until the phlœm is reached, whereupon movement is suddenly accelerated and is very quickly detectable in the veins of newly developed leaves. Later, Samuel (1934) advanced our knowledge of the direction and mechanics of virus movement by an interesting experiment with tobacco Mosaic virus inoculated into tomato. One terminal leaflet on each plant was inoculated and, at intervals, the plants were cut into pieces, incubated to ensure the multiplication of any virus present and then tested for its occurrence. No virus passed out of the inoculated leaflet during the first three or four days but, thereafter, it was demonstrated in the roots within twelve hours and within twenty-four hours had reached the stem apex. That movement took place in the phlœm was strongly suggested by the fact that developing fruit-trusses often became infected simultaneously with the roots, while neighbouring leaves remained uninfected for days or even weeks; an interpretation which was later supported by Bennett (1940) in reporting an acceleration in the movement of tobacco Mosaic virus, in tobacco, in the direction of the developing seeds. Perhaps an even more important observation by Samuel was the occurrence of pieces of stem, often several centimetres long, quite free from virus although virus-infected pieces occurred both above and below. Clearly virus movement was by actual transference of separate particles and not by a process of multiplication, or as a continuous stream of particles; an observation later confirmed by a number of workers (Kunkel, 1939; Capoor, 1949; Matsumoto, 1941), while Clinch (1942, 1944) reached much the same conclusion with potato virus "X" by interposing a piece of the immune Seedling 41956 between healthy and infected parts of potato (*cf.* above). Bawden (1950) has pointed out that there is no reason to suppose that large scale movements of virus occur in plants; all that is necessary is the transference of enough particles to ensure multiplication at the new site. In some cases this is certainly what occurs, *e.g.* in the infection of tubers from the haulm, for although there is a continuous flow of food to these tubers the virus "X"-content of immature tubers may be less than one-thousandth that of the leaves. There is therefore no need to attribute to viruses a power of movement not found in other plant proteins (fruit proteins, for example, do not pass into the leaves, nor leaf-proteins into the roots), the difference lying in the fact that the translocated virus multiplies in its new site and so becomes detectable.

(c) *The Rate of Virus Movement.*—If it be accepted that the path of movement is the phlœm, it does not, of course, follow that the rate of movement is necessarily that of the metabolites. Nevertheless, it may be expected that a measurement of the rate of transport of a "foreign body" such as a virus will give valuable information on the translocation of elaborated food. Unfortunately, our knowledge of virus movement is still fragmentary and not wholly trustworthy for, as might indeed be expected, this movement is dependent upon many factors as yet incompletely understood. Briefly, the method used is to introduce the virus into the plant and then to determine the distance traversed, in a given time, by severing portions of the plant at varying distances from the point of inoculation; finally testing each portion for the presence of virus. The main sources of error are obvious. (*a*) After inoculation of a virus there is usually an interregnum before active transportation begins; if the introduction of the virus is by means of grafts there is an unknown, and variable, time-lag before there is sufficient union of tissues to permit the virus to pass, while if juice-inoculation is the method employed, the virus must apparently multiply in order to build up a "concentration head" to allow of the slow cell to cell diffusion before the phlœm is reached. Neither of these delays occurs when the virus is introduced directly into the phlœm by means of a phlœm-feeding insect vector, but it is not irrelevant to remind ourselves that (i) if the virus selected is one which apparently *must* be delivered into the phlœm (*e.g.* potato Leaf Roll or beet Curly-Top), the timing of the experiment will depend on the caprice of the vector or its ability to reach the phlœm, and this may vary, according to Roberts (1940), from fifteen minutes to at least twenty-four hours; (ii) that the use of a virus such as potato virus "Y" will introduce even more uncertainty than with juice-inoculation since the cells inoculated may be at any level between the epidermis and the phlœm. (*b*) Movement of a virus in the phlœm is presumed to be at a constant rate although (i) it takes place in a medium which contains different kinds of solutes, each moving in a direction and at a rate controlled by its own " concentration head " (Mason and Maskell, 1928-1934; Mason and Phillis, 1936); solutes moreover in which mobility may be affected by any factor such as a narcotic (Deleano, 1912) or lack of oxygen (Mason and Phillis, 1936*a*). (ii) A movement which results in occasional lengths of up to 49 cm. (Capoor, 1949) of phlœm containing apparently no virus particles at all (*cf.* Samuel, above) cannot be used to postulate constancy of flow without some supporting evidence. (*c*) The methods of testing for the presence of virus in regions remote from the infection sites vary, as Capoor (1949) has pointed out, in their sensitivity in revealing low concentrations of virus, so that the rate of movement may be very much under-estimated. These methods include detaching potato tubers at intervals and " growing on " after storage; rooting axillary shoots of potato and then " growing on " the resulting tubers; rooting layers, or severed portions of tomato or tobacco; severing inoculated leaves at varying intervals of time and awaiting the development of symptoms in the plant, *e.g.* sugar-cane and maize; inoculating sap from severed portions into test-plants either immediately or after incubation.

These difficulties have not deterred workers from attempting some estimate of the rate of virus movement in plants, as the two following tables show.

Table XXV summarises the various estimates of the " time-lag " within the inoculated leaf before the virus enters the stem; this will include the time required for the initial multiplication of the virus and for its diffusion to the phlœm, as well as a small fraction of time representing movement within the phlœm of the leaf. Three facts seem to emerge from these results: (1) Böning apparently demonstrated that the rate of multiplication, and/or diffusion, differs in the same virus when inoculated to different host plants, while Capoor showed a similar variation when different viruses were introduced to the same host; (2) Samuel considered that the rate of movement depended upon the growth-rate of the host; a conclusion which is supported by the work of Kunkel and Capoor; (3) All the results suggest that a period of from two to five days is required for initial multiplication and slow diffusion of a virus from the inoculation site before the rapid movement throughout the plant begins.

In considering the results summarised in Table XXVI, the early work of Murphy and McKay (1926), McCubbin and Smith (1927, 1930), and of Böning (1928) are outstanding as indicating an extremely low rate of virus movement, and contrasting sharply with the high rates recorded by Bennett (1934) for the movement of beet Curly-Top virus. As regards

TABLE XXV

Rate of Movement of a Virus from a Sap-inoculated Leaf

Author.	Virus.	Host-Plant.	How Confirmed.	Rate of Movement.
Allard (1914)	Tobacco Mosaic	Tobacco	Inoculated to healthy plant	3-4 days
Böning (1928)	Tobacco Mosaic	Tobacco	Inoculated to healthy plant	2 days
Böning (1928)	Tobacco Mosaic	Tomato	Inoculated to healthy plant	3 days
Samuel (1934)	Tobacco Mosaic	Tomato (90 cm.)	Inoculated to healthy plant	3-4 days
Kunkel (1939)	Tobacco Mosaic	Tomato (34 cm.)	Inoculated to healthy plant	44 hours
Capoor (1949)	Tobacco Mosaic	Tomato (65 cm.)	Inoculated to healthy plant	5 days
Capoor (1949)	Tomato Aucuba	Tomato	Inoculated to healthy plant	3·5-4 days
Capoor (1949)	Potato "X"	Tomato	Inoculated to healthy plant	3 days
Capoor (1939)	Potato "Y"	Tomato	Inoculated to healthy plant	2-3 days

the grafting of potato Leaf Roll, Murphy and McKay succeeded in their main object of ascertaining that fifteen days was the maximum time-lag between infection of the foliage and infection of the tubers. The quoted rate of 0·12 cm./hr. has been arrived at by later commentators who divided the length of potato stem traversed (37·5 cm.) by the mean of the time taken; the figure is, of course meaningless since it neglects the time required for the tissues of scion and stock to "knit" together. The graft-union is initiated by the formation of undifferentiated callus tissue in which a somewhat tortuous path for watery salts is achieved by the lignification of some of the elongated parenchyma cells. According to Dufrenoy and Shapavolov (1934) other parenchyma cells proliferate and become entwined, but until protoplasmic connections are established between these cells there can be no movement of either virus or any other colloid particles. However, the regeneration of these plasmodesmata has been

TABLE XXVI

Rate of Movement of a Virus in the Phlœm

Author.	Virus.	Host.	Inoculation.	Method Used for Testing for Virus.	Rate (cm./hr.).
Murphy and McKay (1926)	Potato Leaf-Roll	Potato	Graft	Tubers grown from plant and from axillary shoots	0·12
McCubbin and Smith (1927)	Tomato Mosaic	Tomato	Sap-Inject.	Axillary shoots rooted	0·084-0·127
McCubbin and Smith (1930)	Tomato Mosaic	Tomato	Sap-Inject.	Axillary shoots rooted	1·2
Böning (1928)	Tobacco Mosaic	Tomato	Inoc. in wound	Sap from portions inoculated to healthy plants	(*a*) 0·125 (*b*) 0·208-0·1
Kunkel (1939)	Tobacco Mosaic	Tomato (34 cm.)	Leaf-inoc.	Sap from portions inoculated to *Nicotiana glutinosa*	17·78
Capoor (1949)	Tobacco Mosaic	Tomato (65 cm.)	Leaf-inoc.	Sap from portions inoculated after incub. to *N. glutinosa*	7·16
Capoor (1949)	Tomato Aucuba	Tomato (65 cm.)	Leaf-inoc.	Sap from portions inoculated after incub. to *N. glutinosa*	7·83
Capoor (1949)	Potato "X"	Tomato (65 cm.)	Leaf-inoc.	Sap from portions inoculated after incub. to tobacco	8·0
Severin (1924)	Beet C. Top	Beet	Insect	Leaf severed at known time and distance	35·56
Bennett (1934)	Beet C. Top	Beet cotyledon	Insect	Cots: severed at known distance; plants grown on	76·2
Bennett (1934)	Beet C. Top	Beet Leaf	Insect	Leaf severed at known time and distance; plants grown on	152·4
Bennett (1934)	Beet C. Top	Tobacco	Insect	Stem sections rooted	1·27
Storey (1926)	Zea Virus 2	Sugar-Cane (30° C.)	Insect	Leaf severed at known distance; plant grown on	13·3
Storey (1928)	Zea Virus 2	Maize (50° C.)	Insect	Leaf severed at known distance; plant grown on	10-20

shown to occur in graft-hybrids and there is no reason to doubt that they are developed in all callus tissues. Finally, union is achieved between the phlœm of scion and stock by the development of vascular procambial strands within the callus; it is probably not until this occurs that viruses such as potato Leaf Roll or beet Curly-Top can pass from the diseased to the healthy stem. Bennett (1943) has been able to separate two viruses (tobacco Ringspot and cucumber Mosaic) from beet Curly-Top by taking advantage of the fact that the first two diffused through the parenchyma of the graft-callus whereas the Curly-Top virus was apparently immobilised in the scion until a phlœm bridge had been formed ; he even separated tobacco Ringspot virus from cucumber Mosaic virus because the former diffused more rapidly than the latter. In an experiment involving the use of "double grafts," Clinch (1942) showed that the time taken by potato virus "X" in traversing a 12 cm. length of stem of the immune potato seedling 41956 to reach a healthy, susceptible stock, was not appreciably longer than was required for the virus to pass directly from the diseased scion when no immune stem was interpolated.

From the recorded results of McCubbin and Smith (1927, 1930) and Böning (1928), it would seem that neither injection of infective sap, nor the use of mashed inoculum into the stem, is a sufficiently exact method of introducing virus into the phlœm, for their duplicate experiments indicated a ten-fold and a two-fold *increase*, respectively, in the rate of virus movement as compared with the rate recorded in the initial experiments ; there is no doubt, though, that many complex factors are involved. Thus, Böning (1928) found that the virus of tobacco Mosaic moved, in similar plants, with equal facility in a downward or upward direction according to whether the inoculum was placed in the top or base of the stem, the inference being that two equal and opposite translocation gradients, or currents, co-exist in the phlœm. There is little doubt that environmental factors play their part and there may be substance in the claim by McCubbin and Smith (1930) that the slower rates of virus movement recorded in their first experiments reflected a retardation due to low temperatures, though it is unlikely, for instance, that the temperature of 103·5° F. at which Severin worked was appreciably lower than the "air temperature" at which Bennett (1934) recorded much higher rates of virus movement. The physiological activity of the host plant certainly influences the rate of virus movement, and Bennett (1937) states that while seedling plants may be systemically infected by the Curly-Top virus within two to four days, this may be delayed for four weeks in the case of mature plants ; a difference which does not seem to be accounted for by the difference in size, as Bennett believes. The very different rate of movement he obtained (1934) when Curly-Top virus was introduced into a cotyledon and an actively developing leaf may also reflect the differences in the physiological activity of the two organs, though other factors such as the feeding habits of the insect vector may have contributed. Certainly factors other than host activity are required to explain the different rates of virus movement obtained by Kunkel and Capoor. The latter author considers the movement to be intermittent, fast in the zones later found to be free from virus and slow in the zones of virus concentration; the recorded rate is therefore a minimal one, and the true rate of movement may well approximate to that obtained by Kunkel. In any case it seems clear that the movement is not a purely passive one, regulated only by the rate of movement of solutes in the translocation current; a passive movement would certainly not explain Bennett's (1934) recording of at least a hundred-fold difference in the rate at which beet Curly-Top virus moved in beet and tobacco respectively. An interesting feature of all these determinations is the evidence they provide of a rate of particle-movement in the phlœm far in excess of that possible by simple diffusion. Dixon (*cf.* Dixon and Mason, 1923) measured the rate of accumulation of carbohydrates in a potato tuber and, from the cross-sectional area of the phlœm, calculated that conduction of carbohydrates in the phlœm would require a rate of movement as high as 50 cm./hr.; this, he believed, could only be achieved under the tensile forces developed in the xylem in which, alone, mass movements of liquid were possible. It now appears that virus particles do, in fact, attain a much higher rate of movement in the phlœm than that postulated by Dixon, though no light whatever has been thrown on the mechanism of this movement.

(5) Effects of Viruses on Plant Efficiency.—The loss in yield which follows virus infection, and which is usually proportionately greater with increasing severity of external symptoms, is ample proof of a reduced efficiency, though the factors bringing this about are by no means clear. The reduced "over-all" size of affected plants is, of course, partly responsible for reduced yields, for one cannot expect a normal output from a small plant with abnormally small leaves and a reduced root

system. But this statement over-simplifies the problem, for a plant " carrying " a virus without symptoms appears to crop as well as a normal plant (Whitehead, 1937), although a heavily mosaicked plant of the same size may give a considerably lower yield. Again, the loss due to Leaf Roll is influenced by the variety of potato and cannot be forecast by the degree of stunting or the number of rolled leaves on the plant (Whitehead, 1930*b*). It is clear, therefore, that we must turn to the internal effects for further information on the causes of reduced efficiency.

Internal Effects on Plant Tissues.—The most drastic internal effect is that involving first the browning and then the death of groups of cells, *i.e. Necrosis*, though in fact this is less serious in reducing efficiency than a systemic mottle, unless the necrosis destroys the conducting tissue or is so severe as to cause the death of the whole plant.

(i) *Necroses*

The sequence of events in the production of necroses is usually the same whatever the virus concerned or the tissues involved may be. First the affected cell-wall thickens and the primary walls (middle lamellæ) between the cells partially separate so that small intercellular spaces arise. The thickened cell walls become lignified, suberised or cutinised, and the cell contents degenerate into a brown gummy mass rich in pectins, which may or may not persist; sometimes the intercellular spaces also are filled with the brown degeneration products. There are apparently specific differences in the tissues affected by necrosis and in the rate and direction of its spread, which are characteristic of the inter-action between a particular host-plant and a particular virus; the same plant will react necrotically in different ways, or not at all, to different viruses, while the same virus may cause necrosis in one host and not in another. Since these differences in necrotic reaction have some diagnostic value, the chief characteristics are given below:—

Leaf Roll.—Necrosis is confined to the phlœm, originating in either the internal or external phlœm but, whereas in the latter case the necrosis does not extend beyond the primary elements, in the former it spreads throughout the secondary phlœm and may cause the collapse of most of the sieve-tubes.

Even in severe cases, however, it is rare for all the phlœm groups to be affected, and there is no explanation as to why, in an anastomising tissue such as the phlœm, some groups show no signs of being infected. It is characteristic of phlœm-necrosis that the thickened cell-walls become lignified.

Acropetal Necrosis (Leaf-Drop Streak).—Necrosis first develops in the leaf parenchyma surrounding the veins; the affected cell-walls giving the characteristic reactions for suberin and cutin, but not for lignin. From the lamina the necrosis spreads into the petiole where it is usually very severe, and may convert the whole of the ground tissue (cortex) into a corky mass. The vascular tissue remains unaffected, so that connection with the stem is maintained even when the collapse of the normally turgid ground tissue causes the leaf to hang limply (Fig. 87). In the stem, necroses rarely affect the apex and only develop relatively late in the inter-nodal zones, but they are severe and extensive in the nodes just below affected leaves; the axillary buds are not killed. The stem necroses are confined to the cortex and mainly to the collenchyma in which tissue they spread laterally to produce arcs of brown necrosed cells as seen in transverse section; the cell-walls of which are swollen and suberised. The main spread of necrosis, however, is upward so that brown vertical streaks are produced, visible to the naked eye through the green epidermis. No symptoms have been confirmed in affected tubers.

Top-Necrosis.—Due to viruses " X " (including the aberrant form " B "), " A " and " C." The necrosis arises usually, but by no means invariably, in the internal phlœm of the stem. From thence it spreads in all directions, but mostly through the perimedullary zone towards the wood, the swelling of the parenchyma cells and the large intercellular spaces produced completely obliterating many of the sieve-tubes and companion cells. The wood parenchyma is particularly affected and many cells either collapse or are filled with gummy degeneration products; tyloses may block the lumen of some wood vessels. When the outer phlœm is attacked the spread is also towards the wood. Near the apex of the stem the necrosis extends beyond the vascular bundles and into the cortex with the result that the death of all the apical tissues follow. In young, actively growing plants the necrosis now spreads downward until, in extreme cases, the whole plant is involved (Fig. 82). When old plants become infected, however, the necrosis is largely confined to the upper, actively growing regions ; the basipetal spread being hindered or stopped by the formation of cork cambiums around the necrotic areas, this being particularly evident under relatively high temperatures. The leaves on affected plants show severe pathological changes, disclosed externally as black spots which penetrate the thickness of the leaf. These appear to begin in the phlœm elements of the smallest vascular bundles or veins and spread into the leaf parenchyma cells which lose their contents, become suberised and collapse. The effect on the petiole tissues is extremely severe, all the phlœm elements are involved and the whole vascular tissue becomes degenerate so that the leaf shrivels and dies. The axillary buds also become affected, for necroses arise in the young vascular bundles and ultimately the bud is killed. Tubers from Top-Necrotic plants are of two kinds, some being normal and others with pathological effects visible to the naked eye, in the cut tuber, as dark, discolored areas in the parenchyma. The necrosis in the tuber develops much as in the stem, and spreads from the phlœm groups to the storage parenchyma, the contents of which disappear and the walls are suberised. The necrotic areas are surrounded, often incompletely, by moderately well developed phellogens which cut off layers of cork cells. Starch grains, though abundant in unaffected parts of the tuber, are absent from otherwise normal cells abutting on the cork cambiums. The tuber-necrosis spreads to the " eyes " and kills them (Fig. 81). It will be noted that necrotic tissues in all organs, including the phlœm, react to suberin reagents (*cf.* Bawden, 1932). Top-Necrosis does not normally occur under field conditions, for varieties which react in this way do so only as a result of grafting. Nevertheless, an occasional typical case is to be seen in field crops for which at present there is no adequate explanation.

Foliar Necrosis.—Due to virus " D," shows characteristic differences from all the foregoing. It differs from Top-Necrosis in the direction of spread—being acropetal—and in the freedom of the main and axillary growing points from destructive necroses. It differs from Acropetal Necrosis by the essentially interveinal character of the lesions and the absence of elongated streaks on veins, petioles and stems. It differs from both in the absence of any internal lesions in the stem and by the rapidity with which two distinct phases follow each other in the first year of infection. From eight to ten days after infection, the leaf develops circular black spots which penetrate through the leaf with little or no lateral spread, and ultimately tend to fall out so as to give a " shot-hole " effect to the leaf. A week or so later greyish necroses develop on the underside of leaves occupying an intermediate position on the stem; they are soft and damp to the touch and give the leaf a wilted appearance. Each necrosis starts in the parenchyma next to small vascular bundles, the cells swell and the walls become suberised or cutinised. The spread is outwards to the epidermis and along the length of the leaf, affecting both spongy tissue and palisade cells. All the vascular tissues are affected and the necrosis spreads thence into the petioles; the leaves wilting and falling off. In the stem the spread is acropetal, causing a wilt and fall of the leaves in succession from below upward. At relatively high temperatures all leaves except the youngest may fall so that a " palm-tree " effect is produced, but at lower temperatures, especially in older plants, the wilting and falling are confined to the intermediate leaves which first showed systemic necroses. The apical and axillary buds are never killed. These primary symptoms are then at once followed by secondary symptoms which consist of black lesions resembling the localised lesions of the primary stage, together with a pronounced and rather blotchy interveinal mosaic. With the secondary stage of the disease the wilting and falling of leaves is arrested and any new growth shows only the mottle and scattered black necroses. Tubers from plants showing Foliar Necrosis are small but are apparently healthy and sprout normally; the resulting plant, however, will probably show a blotchy mottle and occasional scattered, black, interveinal necroses which may increase in severity and cause leaf deformity. Diseased plants are much smaller than healthy ones and mature earlier, but there is no wilting and leaf-fall as in the first year of infection (Bawden, 1934). Varieties which react with a Top-Necrosis when graft-infected with virus " X," show a similar reaction when graft-infected with virus " D."

(ii) *Non-Necrotic Effects on Plant Tissues*

Effects on Leaf Histology.—In " Mosaic " infected plants the chlorotic (light-green or yellow) areas of the leaf are usually thinner than the dark-green areas; the ratio in potato " Mosaic " being respectively 90 μ. and 120 μ. according to Melchers (1913). This was confirmed in several forms of potato mosaics by Clinch (1932), who found that the difference in thickness increased with the severity of the external symptoms. Thus there was little difference in the thickness of light and dark-green areas in Mild Mosaic (virus " X "); a greater difference in the case of Interveinal Mosaic due to the combined action of viruses " X " and " F," and a maximum difference in Crinkle (virus " X " plus virus " A ") where the ratio was as 113 μ. in the yellowish areas to 137 μ. or 148 μ. in the shiny, dark-green areas. There was also a definite retardation of growth in the chlorotic tissues, for the length of the palisade cells was only 45 μ. as compared with the normal length of from 52 μ. to 56 μ.; also the cells of the mesophyll or " spongy tissue " were smaller, more compact, and with smaller intercellular spaces. Yet the viruses producing the Crinkle disease at the same time stimulate growth in the dark-green areas for, although the total leaf-thickness was the same as in normal leaves, the palisade cells were longer (57 μ. to 72 μ.) than normal; we must therefore face the fact that the same virus complex may both decrease and increase growth in adjacent tissues. Iwanowski (1896) had long before pointed out that, in tobacco Mosaic, the affected palisade tissue formed a double layer of cuboid-shaped cells instead of the single layer of rather longer cells found in healthy leaves. These facts were confirmed by Dickson (1922) who hazarded the opinion that, whereas a mild infection (represented by the dark-green areas) stimulated growth and cell division—and so produced hypertrophied tissues—the heavier infections inhibited growth and resulted in the hypoplasia of the thinner, chlorotic, areas. Possibly, abnormally stimulated growth may be as usual a reaction to virus infection as is retarded growth. For instance, in Fiji disease of sugar-cane the virus causes leafy galls to form as a result of the proliferation of the phlœm sieve-tubes (Kunkel, 1924), while abnormal growth and cell division of the phlœm parenchyma appears to be responsible in tomato

" Big-Bud " for the swollen truss pedicels characteristic of the disease (Samuel *et al.*, 1933). In the case of potato Leaf Roll, the increased thickness of the leaf as compared with the normal was shown by Murphy (1923*b*) to be due, not to hypertrophied growth, but to distension of the spongy tissue by the accumulation of osmotically active carbohydrates ; the effect being that this tissue occupied 60 per cent. of the total leaf-thickness instead of the normal 50 per cent. In Leaf Roll leaves there is an increase also in the size of the palisade cells according to Clinch (1932), though it is not clear whether this is due to distension or to abnormal growth. Murphy (1923), however, says that occasionally the palisade cells are shorter than normal, and may even more than counter-balance the effects of distension of the spongy tissue, so that the infected leaf is thinner than a healthy one. What seems to have been established by many workers (*e.g.* Woods, 1899 ; Iwanowski, 1903 ; Dickson, 1922 ; Cook, 1925 ; Smith, F. F., 1926 ; and Goldstein, 1926) is that chlorotic areas in mosaic-infected leaves show a lack of differentiation, and reduced growth, which must adversely affect the efficiency of these organs. According to Goldstein (1926), the extent to which this occurs depends upon the age of the cells when invaded, rather than upon the intensity of attack as was supposed by Dickson (1922). She believes that the development of the cell is arrested at the time of virus invasion, so that the chlorotic areas are regarded as the result of an early attack upon immature tissues whereas the less severe effects seen in the dark-green areas indicate a certain maturity of the cells when invaded ; a view which is not easy to harmonise with the mottled appearance of very young leaves developing from infected tubers. Indeed, Cook (1930) states that the difference in thickness of chlorotic and green areas can usually be detected in the buds of mosaic-infected plants. This author (1947) considers that a virus inhibits the growth and differentiation of the meristematic cells of young leaf tissues, but that if the infection occurs after the tissues are fully differentiated these remain normal and unaffected ; he believes that the extension of chlorotic areas is due to cell division and growth of these areas and not to the invasion of adjacent healthy cells by the virus.

Effects of Viruses on Cell Contents.—Not only is the assimilatory tissue reduced, as described above, but the chloroplasts are fewer, smaller, and paler in colour than normal (Iwanowski, 1903; Melchers, 1913; Smith, K. M., 1924; Smith, J. Henderson, 1930). There can be no doubt of the serious effect this must have on the food-manufacturing efficiency of the leaf, for it is said that about 90 per cent. of the total dry matter content of a plant is produced by the photosynthetic activity of the chloroplasts. Normally, a chloroplast is a complex body consisting of 50 per cent. protein and a very large amount (30 per cent.) of lipoid. Apart from the carbohydrates it manufactures, it contains the green colouring matter, chlorophyll, various enzymes including catalase and oxidising enzymes as well as the hydrolising enzyme chlorophyllase, and ribonucleic acid (Mencke, 1938) which is particularly interesting in view of its occurrence in viruses. " Chlorophyll " is an omnibus term for the colouring matter which consists of two green pigments (chlorophyll *a* and *b*) and two yellow ones (xanthophyll and carotene), the ratio of green to yellow pigments being (weight for weight) 10 to 1. The main photosynthetic activity seems to be concentrated in the two green pigments while the function of the yellow ones is still a matter for speculation; they may act as energy transformers or as oxidising catalysts. Lubimenko (1928) claims that the stability of chlorophyll is attained by the reciprocative action of two enzymes, one an oxidase which in medium amount is optimum for chlorophyll development but which, in excess, destroys the pigments; coupled with this is a reducing enzyme which regulates the action of the oxidase. However this may be, there can be no doubt of the importance of the enzyme system within chloroplasts; photosynthesis is not a mere light/chlorophyll relation for, as Willstätter and Stoll (1926) argue, the rate of photosynthesis is governed by an enzymic factor as well as by the amount of chlorophyll.

From this outline of the constitution and function of chloroplasts it will be seen that carbohydrate production can be hindered by a virus affecting either the plastids themselves, the chlorophyll, or the controlling enzymic system. A reduction in the size and number of chloroplasts in virus-infected cells has already been mentioned, but how this is brought about is the subject of controversy which centres around the question as to whether the virus actively destroys the plastids or is restricted to retarding or inhibiting their formation. Actual disintegration of plastids has been described, among others, by Dickson (1922), Hoggan (1927), Esau (1933, 1934) and Bawden (1934); the last-named author stating that disintegration of plastids may be the first obvious sign of infection by potato virus " D." On the other hand, Cook (1930), in a study of Mosaic in many kinds of host-plants, found evidence of inhibition of plastid formation but none of a destructive action on plastids already formed; observations which Sheffield (1931) independently confirmed. Clinch (1932), however, believes that, while the formation of plastids is certainly inhibited by a virus, this cannot be the sole explanation of the continued chemical and physical changes which occur in plastids already formed, or of the abnormalities in their starch content, or the observed fatty degeneration of the plastids; while in one disease (potato Aucuba Mosaic, due to virus " G ") she describes a destructive action on mature plastids. It is true, as Cook and Sheffield point out, that mottling rarely develops in an inoculated mature leaf, but this fact is susceptible of other explanations. Thus, Smith (1935) showed that a chlorosis can be induced in mature tomato leaves if inoculated with a concentrated virus inoculum, and Bawden (1950) has pointed out that the virus concentration is usually low in mature leaves, and this alone would suggest that the destructive action of the virus would be reduced. In any case the controversy rather obscures the fact that the pallor partly arises from the destruction of chlorophyll in mature plastids. This pallor, according to Elmer (1925), is due not only to a reduction in the amount of chlorophyll and the yellow pigment xanthophyll, but to a doubling in the amount of the other yellow pigment carotene. Clinch (1932) described a destructive action on all the pigments in the most chlorotic areas of leaves affected with potato Aucuba Mosaic (virus " G "). The most complete study of the effect of viruses on " chlorophyll," so far, is that of Peterson and McKinney (1938), in which they used three strains of tobacco Mosaic virus giving various forms of chlorosis, and a potato Mosaic virus which was probably virus " Y." In all four cases the constituents of " chlorophyll " were reduced proportionately in the chlorotic areas, so that in their view chlorosis is the result of a simple unmasking of the normal colour, without any stimulation of the development of the yellow pigments. What may be even more important is their observation that the normal ratio between " chlorophyll " and the enzyme chlorophyllase is upset. The most chlorotic leaves contained the greatest amount of the enzyme and, similarly, the yellowish areas in any mottled leaf had more chlorophyllase and less " chlorophyll " than the green areas. An excess of enzymes in mosaicked leaves has long been known to occur, for as long ago as 1899 Woods and Heintzel (1900) independently attributed tobacco Mosaic disease to the direct action of oxidases on chlorophyll. Among later workers, Rouzinoff (1930) has described the occurrence of excess oxidases and peroxidases in potato Leaf Roll, and Wynd (1942) in reporting on enzyme activity in Mosaic-infected tobacco leaves states that increased activity was shown by oxygenase, catalase and invertase, but that peroxidase was little affected. He further makes the, as yet, unconfirmed claim that these profound disturbances occur in an inoculated leaf many days before the leaf-juice becomes infectious and that, in consequence, they are to be attributed to abnormal cell metabolism and not directly to virus metabolism. Enzymes as a *cause* of virus diseases have long been discredited, but work such as that of Peterson and McKinney serves to establish enzymic activity as among the more important of the *effects* of virus infection. It would seem, therefore, that the destructive effects of a virus on chloroplasts may be due to an increase in enzymic activity rather than to the direct action of the virus ; the possibility also of the virus utilising some constituent of the plastid in multiplication—such as ribonucleic acid—must not be overlooked.

Many workers on " Mosaics " have followed Woods (1900) in commenting on the reduced amount of carbohydrates present in chlorotic areas of affected leaves, and this has invariably been assumed to reflect the lower photosynthetic efficiency. No doubt this is true, but it is by no means true to accept the abnormal accumulation of carbohydrates in potato Leaf Roll, or most of the " Yellows " type of virus diseases, as evidence of *increased* efficiency. There is, indeed, evidence to the contrary, for reduced photosynthesis was recorded for potato Leaf Roll by Barton-Wright and McBain (1932), and for sugar-beet Yellows by Roland (1939) ; the accumulation of carbohydrates being probably accounted for by the hindrance to translocation caused by necrosis of the phlœm. A similar interference with the movement of carbohydrates from cells is also found in the chlorotic areas of leaves affected with one or other of many " Mosaics " in which phlœm necrosis has not been described, *e.g.* tobacco Mosaic and potato viruses " X " and " Y." In such cases, although there is less starch during daylight in chlorotic areas as compared with the greener tissues, the position is reversed at night, as can easily be shown by a " Sach's Iodine " test in the early morning (see " Local Lesions," page 525). Just what is the cause of this hindrance to translocation is not known, though Wynd (1943) attributes it to a reduced permeability of the protoplasm.

(6) The Role of the Potato Breeder in Combating Viruses

Stated simply, the aim of the breeder is to neutralise the serious effects that many viruses have on the potato crop ; to achieve this he has the following alternatives open to him :—

(i) To breed for complete *Tolerance*, *i.e.* the perfect " Carrier." Such a variety, while readily accepting a virus, retains a high cropping power and, being infected, is in consequence immunised against further infection with a more virulent strain of the virus. The disadvantages of breeding for tolerance are, however, great and decisive. It would involve ensuring tolerance in all varieties for all known viruses since (*a*) tolerance to one virus affords no protection against an unrelated virus and (*b*) an intolerant variety would be exposed to a much greater risk of infection by the presence of a tolerant variety serving as a reservoir of disease. Further, this tolerance would need to cover any combination of viruses, for a plant may be quite tolerant of each of two viruses when infected with either, but intolerant of either in the presence of the other, *e.g.* the variety President shows the mildest of mottles when infected with either virus " X " or virus " A " separately, but with the two viruses present the reaction is severe, and typical, Crinkle.

(ii) *Resistance to Infection.*—Complete immunity from infection by a virus has only been confirmed, in potato, in one case, *i.e.* in respect of the U.S.D.A. Seedling No. 41956, which is immune from virus " X " (Schultz, 1934 ; Dykstra, 1935, 1939 ; Dennis, 1939). This immunity according to Clinch (1944), while permitting free transit to the virus, prevents it from multiplying, and hence from establishing itself in the plant tissues. Stevenson *et al.* (1939) have shown that this immunity is heritable and is controlled by two dominant and complementary genes inherited in an auto-tetraploid manner. Resistance of a very high order, amounting perhaps to immunity, has been reported for virus " X " in several " wild " species of *Solanum* (*S. Rybinii*, *S. andigenum* and *S. curtilobum*), for these species have not, as yet, been successfully infected even by grafts (Cockerham, 1943). A variety of *S. Rybinii* is also unique in exhibiting almost total immunity from infection with virus " Y " (Anon, 1949), while a very high degree of resistance to infection with the virus of Leaf Roll was demonstrated in the wild diploid species *Solanum edinense*, some thirty years ago (Salaman, 1921).

Resistance to infection with Leaf Roll has been shown to exist in varying degree, in many commercial varieties of potato (page 445). It is heritable and quantitative (Cockerham, 1945 ; Anon, 1949) and therefore no sharp distinction can be drawn between resistant and susceptible varieties in the field. There is evidence that several unit factors are involved, each determining some expression of resistance. At present these factors are dispersed among many commercial varieties but, by breeding and selection among the resistant sorts, it should be possible to concentrate some of the factors and so produce varieties displaying much higher resistance in the field than many of our present popular varieties. It would seem that such a concentration of factors may explain the almost complete immunity from infection shown by the variety Skerry Champion, and the scarcely less resistant variety Shamrock (*cf.* under Leaf Roll, page 447). In U.S.A. Stevenson *et al.* (1943) have shown that a number of progenies, mostly related to the variety Katahdin (Seedling 42667), exhibit a high degree of resistance to Leaf Roll as compared with the very susceptible varieties Green Mountain and Chippewa. The variety Katahdin is also said (Bawden and Kassanis, 1947) to show resistance to infection with virus " Y," although when infected the effects are severe. They suggest that breeding for resistance to this virus, combined with intolerance when infected, should be worth while. That such a form of resistance to virus " Y " is heritable has been demonstrated in U.S.A. by Schultz *et al.* (1947) for they find that a greater number of resistant seedlings result from the crossing of resistant parents than are obtained from susceptible varieties. This appears to be an example of resistance to infection such as has been described for Leaf Roll for, according to these authors, the extent to which field resistance is exhibited depends on the aphid (*Myzus persicæ*) dosage, and high resistance in the field is not necessarily repeated in " cages " in which there may be heavy aphid infestation.

(iii) *Hypersensitivity.*—It would seem paradoxical to expect any control of a virus by breeding for extreme susceptibility, but in many respects this method has given the most encouraging practical results. It is important to remember that, by the term " hypersensitivity," is meant (as in the case of cereal rusts) a susceptibility of so extreme a form that the tissue surrounding the point of inoculation is immediately killed, so that a barrier is interposed which effectively prevents the virus becoming systemic, *i.e.* affecting the plant as a whole. When, however, the virus is introduced to such a plant by graft, the virus invasion overwhelms the susceptible plant and produces a necrosis which kills the young tissues (growing point and young leaves whether of the main stem or lateral shoots) and, spreading downwards, is lethal eventually to all the green parts of the plant, and sometimes also to some of the tubers ; it is this form of reaction, as a result of grafting with a virus, which is known as Top-Necrosis (page 538). The control achieved by " hypersensitivity " in the field is usually explained by the localisation of the virus to minute spots around the points of infection (whether due to an insect vector or to mere contact bruising of foliage) so that the plant as a whole escapes any ill-effects. This condition has been described, not too happily, by Clinch *et al.* (1938), as " Field-Immunity," for while the term aptly indicates the practical importance of the reaction to the grower, it obscures recognition of the underlying hypersensitivity of the plant and leads to misconception of the breeding problem. The first indications of such a new approach to virus control date from Holmes' (1938) and Ternovsky's (1938) demonstration in U.S.A. and Russia, respectively, that the ability of *Nicotiana glutinosa* to localise the virus of tobacco Mosaic in necrotic spots, is heritable and controlled by a single dominant gene, and that by repeated back-crossing it was possible to transfer this power to the species *N. tabacum* to which commercial tobacco varieties belong. In Scotland Cockerham (1937, 1939) found that a number of varieties of potato which reacted with a Top-Necrosis when grafted with virus " X " (as well as others which did not), gave a quite similar Top Necrosis when grafted with one or other of viruses " A," " B " and " C," and that such varieties rarely, or never, showed infection with such a virus in the field, *i.e.* they are " field-immune " from a virus to which, on grafting, they react with a Top Necrosis. Cadman (1942), in Scotland, demonstrated that this hyper-sensitivity is heritable and is controlled in the case of each virus by a single, separate, and dominant gene, which is inherited in autotetraploid manner and is usually found in the simplex condition. These genes are symbolised respectively as **Nx**, **Na**, **Nb** and **Nc**; and have been found to occur in the following proportions in commercial varieties: **Nx** in 38 of 219 varieties; **Na** in 97 of 190; **Nb** in 71 of 154, and **Nc** in 75 of 154 varieties (Cockerham, 1943); it is this low frequency of **Nx** in present commercial varieties which is reflected in the preponderance of a non-lethal Mosaic due to virus " X " in so very many of our crops. Very active breeding work at the Scottish Plant Breeding Station has resulted first in the production of the variety Craigs Defiance, field-immune from viruses " X," " A," " B " and " C " (Black, 1939), and then of others of which perhaps the most interesting is Craigs Snow White, which is not only field-immune from these four viruses but also immune from strains " A " and " C " of potato Blight (Black and Haigh, 1949); this Report also states that the following varieties are now known to be field-immune from virus " A ": Arran Pilot, Di Vernon, Edzell Blue, May Queen, Puritan and Witchhill. Cockerham (1945) has stressed the fact that the factor (**Nx**) for hypersensitivity is not effective against some aberrant strains of virus " X," and indeed such strains have been recovered in the field from varieties regarded as field-immune from virus " X "; nevertheless, they appear to occur very rarely, and in an analysis of some 160 sources of the virus in Scotland (Anon, 1948*b*), no strain was found which did not produce Top-Necrosis in any field-immune variety. The significance of these aberrant strains is that their existence may indicate a tendency for a field-immune plant to exercise a selection in favour of such a " non-necrotic " mutant of a virus which, by its spread, may nullify all the efforts of the plant breeder. Fortunately, there is evidence that these aberrant strains are also genetically controlled by genes related to **Nx** (Cockerham, 1945). It may be that some aberrant strain of virus " A," also, might account for the observation of Schultz *et al.* (1940) that potato varieties susceptible to virus " A " tend to group themselves into (*a*) those readily infected in the field ; (*b*) those rarely infected, and (*c*) those never found infected in the field.

The problems in breeding against virus " Y are particularly interesting and difficult. No commercial variety shows hypersensitivity (of the type with which we are concerned) when infected with virus " Y," although many varieties are known to be field-immune from the strain of the virus known as virus " C " (*cf.* Table XXXIII, page 684). However, Cockerham (1945) has pointed out that varieties carrying the **Nc** gene responsible for hypersensitivity to virus " C " manifest strikingly similar necrotic symptoms during the early stages of infection with either virus " C " or virus " Y " but, whereas infection with virus " C " rapidly passes into a lethal stage, infection with virus " Y " leads only to a non-lethal Streak followed by a severe Mosaic disease. Varieties carrying the recessive allele (**nc**) usually respond to both viruses with similar *a*-necrotic " mosaics," and Cockerham suggests that this correlation shows that the gene **Nc** determines, not only hypersensitivity to virus " C," but also the non-lethal Streak reaction to virus " Y." True hypersensitivity to virus " Y " has been demonstrated in three " wild " species of *Solanum*, and Cockerham and M'Ghee (1946) have concluded from their work with a number of forms (*S. simplicifolium*, a variety (EPC 4) of *S. demissum*, and their seedling progenies) that this hypersensitivity in all probability has the value of field-immunity from virus " Y." They believe that by a replication of the gene determining field-immunity in potato varieties from virus " C," *e.g.* by selective breeding within the range of cultivated varieties, it will be possible to produce commercial varieties which are field-immune from virus " Y." Independent Australian work seems to have brought similar conclusions.

Hutton (1945) pointed out that tolerance to virus " Y " is dominant, and that hypersensitivity is controlled by a recessive allele or alleles. Hypersensitive seedlings (selfings and crosses) fall into three classes: those giving (*a*) local lesions only; (*b*) Top-Necrosis; (*c*) a lethal necrotic collapse; of which the first two are the most valuable to the breeder. In the following year Hutton (1946) stated his agreement with the view that virus " C " is merely a strain of virus " Y " since, in his work, the course followed by the symptoms in these seedlings was very similar for the two viruses. Hutton and Bald (1945) describe the production of hypersensitive seedlings in this Australian work, by the use of the American variety Katahdin as one parent in crosses with the varieties " Snowflake " and " Brown's River." They found that selfing or crossing the hypersensitive hybrids gave at least 30 per cent. of progeny with promising necrotic reactions to virus " Y," and that by crossing hypersensitive hybrids with potato varieties (normally showing Rugose Mosaic on infection with virus " Y ") they obtained 5 per cent. of progeny which gave a valuable necrotic reaction with this virus. Hence we may look forward with a cautious optimism to the breeding of a variety of potato, field-immune from virus " Y," in the not too distant future.

CHAPTER XXIX

THE SPREAD OF VIRUS DISEASES UNDER FIELD CONDITIONS

(1) THE RISKS INVOLVED IN THE SPREAD OF DIFFERENT VIRUSES.—The importance of the different viruses to the potato grower clearly depends both upon the effect produced on the plant and the liability of healthy stocks contracting the disease from infected sources. Viruses " B," " C " and " E," belonging to group I (page 494 *et seq.*), for instance, are believed to be rarely or never capable of being transmitted to healthy plants except by grafting; they are not therefore a practical source of danger when grown in proximity to other varieties. Nor is there any evidence that such infected plants suffer more severely when another virus is superimposed than would be the case if viruses " B," " C " or " E " were absent, although a complication is added, in nature, since these viruses are commonly (and perhaps almost invariably in the case of " B " and " C ") associated with virus " X." Groups II and III viruses (pages 500, 501), *i.e.* " F," " G," " X " and " D," are readily sap-transmissible and may conceivably be transferred to healthy plants in the field by mere contact of foliage. Certainly this is true of viruses " X " and " F," as has been shown by Loughnane and Murphy (1938) while, in the case of virus " X," Roberts (1948, 1950) has given evidence of an underground method of transmission by contact or some other, as yet unknown, agency. No doubt the relative importance of these two means of transmission will vary with the climatic and soil conditions, but all available evidence suggests that the spread of virus " X," under field conditions, only takes place slowly; thus Clinch *et al.* (1938) showed that stocks of the varieties Champion and Arran Banner, possibly infected with virus " X " to the extent of 33 per cent. and 50 per cent. respectively, had in some cases doubled these percentages after from five to seven years in the field, while in others the increase was trivial. In any case virus " X " is already so widely distributed in most commercial varieties that the methods and rate of spread are of importance only in seed-stocks, in which every effort

should be made to eliminate the virus. It is the occurrence of the aphid-transmitted viruses in groups IV (Leaf Roll) and V (" A " and " Y ") which are of predominant importance to the grower, since not only are these viruses limited in their distribution solely by the range of flight of the insect vector, but by their combination with the less mobile viruses of the others groups, *e.g.* virus " X," they produce the most serious degeneration diseases. The problems of degeneration in potato stocks, therefore, very largely centre around the conditions underlying the spread of the viruses in groups IV and V (pages 505, 506).

(2) THE INSECT VECTOR IN RELATION TO VIRUS TRANSMISSION.—Some consideration has been given in the preceding Chapter to the relation between the virus and the plant host it infects. In this section we are concerned with the equally important and remarkable differences in the reactions of insects to viruses.

(a) *Specificity of Relationship*

It is generally accepted that aerial insects are the main if not the sole agency by which viruses can be transferred from one plant to another, when such plants are not in contact. It is true that in a very few cases of plant virus diseases (*e.g.* Wheat Rosette, McKinney, 1925 ; potato virus " X," Roberts, 1950) there is strong evidence of transmission *via* the soil, but the vector, if any, is unknown. Quanjer *et al.* (1916), Murphy (1921) and Whitehead (1923) all believed they had evidence of transmission of potato Leaf Roll through the soil, but the agency was not determined. Later, Elze (1927) claimed to have secured such transmission by means of leather-jackets (*Tipula paludosa*, MGN), but this still awaits confirmation.

Of the aerial insects reported as being responsible for virus transmission, only a very few are insects with biting mouth-parts. Most of these are associated with the transmission of the American potato virus diseases known as " Spindle Tuber " and " Unmottled Curly Dwarf " ; they include several species of grasshoppers and beetles (Goss, 1931), whilst the flea-beetle (*Psylliodes affinis*) is stated by Elze (1927) to be capable of transmitting potato Leaf Roll and a number of " Mosaics." Caution may be necessary in accepting some of these conclusions, but there can be no doubt of the ability of biting insects to transmit viruses in certain cases. Thus Markham and Smith (1949) have shown that turnip Yellow Mosaic virus is transmitted by the flea-beetle (*Phyllotreta undulata* Kuts), the mustard beetle (*Phædon cochleariæ* Fab), a grasshopper (*Chorthippus bicolor* (Charp)), and an earwig (*Forficula auricularia* L), while none of the tested insects having piercing and sucking mouth-parts proved capable of acting as a vector. Apart from these cases, all known insect vectors of plant viruses are equipped with sucking mouth-parts. Thrips are responsible for transmitting several plant viruses, *e.g.* tomato Spotted Wilt, but as regards potato viruses the only evidence, not amounting to proof, is the work of K. M. Smith (1937*c*), showing that thrips may be associated with the spread of virus "X" under field conditions. The plant-bug (*Lygus pratensis*) is believed by Elze (1927) to be a vector of Leaf Roll and of many of the potato-mosaics. Aphides, however, are by far the most important group of insects responsible for the transmission of potato viruses as well as of those of many other crops.

Storey (1931) and K. M. Smith (1933) have drawn attention to the "group specificity" shown between different types of symptoms and particular groups of insect vectors. Thus "Mosaics" are mainly transmitted by aphides; "Yellows" by jassids (leaf-hoppers); diseases characterised by leafy outgrowths and vein thickenings are associated with Aleyrodidæ (white-fly), whilst those showing as more or less complete circles of necrotic tissue on affected leaves appear to be largely transmitted by thrips. A still narrower degree of specificity can be traced in some cases between certain diseases and a particular genus or even species of insect vector. Thus Table XXVII shows that aphides are responsible, so far as is known, for the spread of all insect-transmitted potato viruses in Britain, and that a peculiar affinity would seem to exist between these viruses and the genus *Myzus* with this character most marked in the peach aphid *Myzus persicæ*.

Some results obtained by K. M. Smith (1929) when feeding the aphid *Myzus persicæ* on potatoes containing the two viruses of Leaf Roll and "Y" suggest a selective action by the aphid even in this case where both viruses are normally transmitted by this insect. Only Leaf Roll was passed over to the healthy potatoes in this experiment, although both viruses were clearly picked up by the insect, since virus " Y " was successfully transmitted to tobacco. This supposition appears to be confirmed by the work of Salaman and Wortley (1939) with potatoes showing symptoms of Leaf Roll and carrying virus " Y " without symptoms. Conversely, we have the statement of Clinch, Loughnane and Murphy (1936) that,

TABLE XXVII

Insects confirmed as Vectors of Potato Viruses

Myzus persicæ Sulz.	Virus " A " (Loughnane, 1933) Virus " F " in presence of virus " A " (Clinch, Loughnane and Murphy, 1936) Virus " Y " (K. M. Smith, 1931) Virus of Leaf Roll (Botjes, 1920; Murphy, 1923)
Myzus pseudosolani Theob.	Virus of Leaf Roll (Elze, 1927; Murphy and McKay, 1929)
Myzus circumflexus Buckt.	Virus of Leaf Roll (Whitehead, 1930; K. M. Smith, 1931) Virus " Y " (Watson and Roberts, 1939)
Macrosiphum solanifolii Ashm.	Virus of Leaf Roll (Schultz and Folsom, 1921; Murphy and McKay (rarely), 1929; Whitehead (once), 1931) Virus " potato Mosaics" (Schultz and Folsom, 1923) Virus " Y " (Watson and Roberts, 1939)
Aphis rhamni Boyer	Virus of Leaf Roll (Elze, 1927) Virus " A " (K. M. Smith, 1937) Virus " Y " (B. Kassanis, 1942)

whereas virus " F " is normally not transmitted by insects, it is readily transferred by *Myzus persicæ* from potatoes also affected with virus " A."

Finally, Storey (1932) has discovered the extremely interesting fact that even *individuals* of the leaf-hopper (*Cicadulina mobila* Naude) differ in their power to transmit Mosaic of maize, so that he divides the species into " active " and " inactive " strains. The immediate cause of this difference appears to lie in some property of the insect gut-wall, which in the case of the " active " individuals permits the passage of the virus from the gut into the body fluid, and thus presumably allows access to the salivary glands from which the virus is injected into the maize leaf. On the other hand, the virus imbibed by the " inactive " insect does not pass into the body fluid and transmission to maize is thereby prevented. When, however, the gut-wall of these latter insects is artificially punctured, so that the virus and body fluid can intermingle, the individual becomes an "active" vector of the virus. This difference in gut-walls is genetical in origin; the inheritance is Mendelian with "activity" dominant over "inactivity," and with a sex-linkage in which the male is heterozygous. According to Black (1941*a*) a similar division into "active" and "inactive" strains is found in the clover leaf-hopper (*Aceratagallia sanguinolenta*) which acts as a vector of the American potato virus disease known as Yellow Dwarf (page 467). An added interest in this case is afforded by the fact that this species of leaf-hopper is only capable of transmitting the "New York" strain of the virus; the "New Jersey" strain being transmitted only by the allied leaf-hopper *Agallia constricta* (Black, 1941*b*). No such differentiation into strains has been recorded in aphides; there are, however, so many puzzling cases of irregularity in transmission by even *Myzus persicæ*, as well as of the existence of areas in which certain viruses do not spread rapidly, notwithstanding an abundance of the vector, that the possibility of the existence of "active" and "inactive" forms of this vector cannot entirely be ignored.

(b) *Mechanism of Transmission*

The existence of "active" and "inactive" strains is only one example of the intimacy of the relationship between vector and virus which appears to be required for successful transmission and which, in practice, restricts the dissemination of any insect-transmitted virus to the action of a very few forms amongst the many kinds of insects feeding on the host plant. It is fortunate also that direct transference from one insect to another does not seem to occur and that, with two exceptions, virus infection is not inherited in the insect. These cases are found in (i) Dwarf disease (Stunt) of rice in which, according to Fukushi (1933, 1934, 1935), the virulent condition is inherited through the maternal parent to the third generation; and (ii) in the clover club-leaf virus disease in which, according to Black (1948, 1950), the leaf-hopper vector (*Agalliopsis novella*) has continued to deposit infectious progeny for more than five years, through 21 generations of insects, without having recourse to a fresh source of the virus; the dilution of the original virus, assuming *no* multiplication in the insects, would, he says, at a conservative estimate exceed $1 : 2{\cdot}8 \times 10^{26}$. The inheritance described by Storey is, of course, one of potential "activity" and not of actual virulence.

In some cases the interrelationship between virus and insect vector is a very subtle one. Peach Yellows, for instance, was long regarded as not transmissible by insects, but has now been shown by Kunkel (1933) to be transmitted by a leaf-hopper (*Macropsis trimaculata* Fitch) which only produces one brood of young annually, and this brood is only capable of acting as a vector during one month in the year. The same worker (Kunkel, 1937, 1938) also finds that the insect vector (*Cicadula sexnotata*) of Aster Yellows loses its power to transmit whilst exposed to high temperatures, but regains this power with the return of normal conditions. These, and other instances given below, show the need for caution in accepting experimental failures with insects as proof that a virus is not insect-transmitted under certain conditions in nature, although in such well-established cases as potato virus "X" the possibility that a vector will be discovered seems remote.

(i) *Structure of Mouth-Parts.*—There is no evidence that insect transmission occurs in any way other than by means of the mouth-parts during feeding, although in a few cases a virus has been isolated from the fæces. It also seems clear that mere contamination of the mouth-parts does not explain many of the known facts in transmission in which the virus is apparently first ingested and then returned to plant tissues, presumably in the saliva of the vector. A brief non-technical description of the feeding mechanism in those insects most implicated in virus transmission is therefore essential in order to understand the difficulties of interpreting what appears to be conflicting evidence on virus transmission. Apart from the thrips, which belong to the somewhat primitive Order Thysanoptera, practically all known vectors of plant viruses are members of the Order Hemiptera, *e.g.* leaf-hoppers, white-flies and aphides (green-flies). In the Hemiptera the facts regarding feeding and ingestion which concern us may be summarised as follows: (1) The mouth-parts are both piercing and suctorial, and include a stylet formed from two extremely fine bristles arising on the left and right side of the insect mouth respectively. Each bristle, in cross section, is shaped like a capital "E" (*i.e.* with two longitudinal grooves) so that by the close attachment of the two bristles is formed a median tube containing entirely separate upper and lower canals. Of these canals the upper or forward one is a conduit for the plant sap imbibed as food, whilst the lower canal, which is to the rear during feeding, is connected with the large salivary glands and permits of the passage of saliva into the plant tissues. On each side of the stylet is a separate free bristle possibly serving to strengthen or guide the stylet during its insertion into the plant. (2) There is no direct connection between the stylet canals, so that any virus imbibed can only contaminate the saliva after passage through the gut-walls into the " blood " or body fluid which bathes the salivary glands—the possibility that ingested food (with virus) might be regurgitated being normally prevented by " non-return " valves within the gut. (3) Penetration of plant tissues is effected by the saw-like movement of the stylet and is lubricated by saliva. (4) Salivation is due to the action of the " salivary pump " and is therefore intermittent. According to Storey (1939*a*), saliva passes into the plant tissues during the backward movements which alternate between the forward thrusts of the stylet. The feeding mechanism of thrips, though less highly developed, is essentially similar to that described for the Hemiptera. The only plant virus disease, transmitted by biting insects, which has been at all fully studied is turnip Yellow Mosaic (Markham and Smith, 1949). The insects involved (*cf.* page 554), *i.e.* a flea-beetle, mustard beetle, a grasshopper and an earwig, have mouth-parts as described on page 201. Markham and Smith consider that the power to transmit this virus is dependent on the method of feeding of the insects. They point out that many beetles lack salivary glands, but habitually regurgitate fluid from the crop; there being no œsophageal valve. Similarly, grasshoppers also regurgitate although they do possess well-developed, though sometimes weakly functioning, salivary glands. That regurgitation of previously ingested food is necessary for transmission of this virus is suggested by the fact that caterpillars, which are biting larvæ possessing salivary glands, do not regurgitate and do not transmit the virus; if, however, they are forced to regurgitate after feeding on an infected plant, active virus can be found in the regurgitated fluid.

(ii) *Some Factors determining Infection.*—Even systemic viruses are not uniformly distributed throughout the plant, so that transmission possibly occurs only by means of insects which habitually feed on those tissues in which the virus is most concentrated. Potato Leaf Roll is a typical phlœm disease, and Dykstra and Whitaker (1938) found that the phlœm-feeding insects *Myzus persicæ*, *Myzus solani* and *Myzus circumflexus* were all efficient vectors, whereas *Macrosiphum solanifolii*, which usually failed as a vector but occasionally transmitted in a high percentage of cases, was only observed to feed on phlœm tissues in about 50 per cent. of the experiments. It is a remarkable fact that although there is no reason to doubt that any sucking insect which feeds on infected tissue must pick up any viruses present, some viruses so acquired are not transferred to another plant whatever insect is feeding, and most insects are ineffective whatever virus is involved. Storey (1933), for instance, found the virus of the insect-transmitted maize Streak within the intestine of *Peregrinus maidis* after feeding on infected tissue, but this insect failed to transmit even when the gut was punctured to allow the virus and body fluid to intermingle. Similarly, the insect-transmitted virus of sugar-beet Curly Top was extracted from the gut of several species of aphides, thrips and leaf-hoppers, but of these only one leaf-hopper (*Eutettix tenellus*) acted as a vector (Bennett and Wallace, 1938). It is possible that the ineffectiveness of most insects is due to some toxic effect on the virus from the saliva or other secretion of the insect, but this is certainly not a complete explanation, for Bennett and Wallace (1938) showed that the virus of Curly Top remained virulent in the gut of non-vectors for at least a fortnight after ingestion, and, according to Hoggan (1931), insects which are unable to transfer common tobacco Mosaic from one tobacco plant to another can successfully transmit the same virus from tomato to tobacco. Failure to transmit certain viruses is no doubt due to some inherent property of the virus itself, although its nature is still obscure. There does not appear, for instance, to be any clear relation between the degree of infectiousness of a disease and insect transmission, although Watson (1936) has pointed out the surprising fact that some insect-transmitted viruses are amongst those most difficult to transfer by sap inoculation. Finally, as has been pointed out in the previous Chapter, the plant itself should not be overlooked as an important factor determining whether an inoculation of a given virus results in infection. Thus Bawden and Roberts (1948) have shown that the rate of photo-synthesis definitely influences the predisposition of some plants to infection with a virus; susceptibility being consistently increased by darkening plants for varying periods before they were inoculated. They suggest that the successful establishment of infection occurs in two stages, the first of which is affected by the accumulation of photosynthetic products. Whether these products confer resistance by increasing cell turgor or by reacting specifically with virus particles is unknown, but the authors state that sap from plants exposed to light possesses no greater virus-inhibiting power than sap from plants kept in the dark. Again, for instance, although wounds seem to be necessary to secure the entrance of a virus into a plant, it seems equally necessary that the damage inflicted should be reduced to a minimum for successful infection to occur; this fact in itself is probably sufficient to exclude practically all biting insects from acting as vectors, and possibly many of the sucking insects also. In several viruses it has been shown that transmission may be effected by single vector insects, and that the symptoms then produced in no way differ from those induced when many infective individuals are allowed to feed on the healthy plant. Nevertheless, it frequently happens in such cases that an individual will fail to transmit on some occasions whilst succeeding on others, one possible explanation being that failure is due to the insect not having acquired the minimum dose of virus necessary for successful infection of the plant. This raises the interesting question as to whether a number of such insects, each carrying a sub-minimal dose, would successfully infect a plant by the cumulative effect of all these small inoculations. Evidence is increasing to show that this "mass action" does not, in fact, occur, but that the inoculation from each insect is independent of the effects produced by the other feeding vectors. This hypothesis of independence was put forward by Watson (1936) and Storey (1938) to explain the results each obtained by the use of single vectors, in some experiments, as against large numbers used in others. It implies that a greater number of successful transmissions may be expected from colonising plants with a large number of insects merely because there is thus a greater chance that an infective individual has been included than would be the case with a few or only one potential vector; the chances of successful infection, therefore, by a group of insects depend solely on the likelihood that one individual in the group would have been equally successful if feeding alone. An illustration is provided by the observations of G. W. Simpson (1935) that whilst single specimens of *Myzus persicæ* and *M. circumflexus* frequently transmitted potato Leaf Roll, it was necessary to use at least one hundred (and often far more) of either species to secure transmission of potato "Mosaic." The "independence" hypothesis would explain this as indicating that less than one hundred insects never contained one individual carrying an infective dose, though an unknown, large, number might inject sub-minimal doses into the experimental plants without their cumulative effect producing infection.

(iii) *Non-Persistent and Persistent Viruses.*—One discovery of great scientific and practical importance in the tripartite relationship between vector, virus and plant is that most if not all insect-transmitted viruses fall into one of two groups (*cf.* Table XXVIII). In the first of these the vector is able to transmit the virus successfully to a healthy plant within a few minutes after feeding on infected tissue, but the virus is then either quickly depleted, or rendered inactive, within the body of the vector, *i.e.* the virus is non-persistent. On the other hand, in the second Group transmission by the vector only becomes possible after the expiration of a (longer or shorter) waiting or "latent" period after feeding on the infective tissue, but in this case the virus remains active within the body of the vector for a considerable time, and possibly throughout its whole life; it is said to be a persistent virus. Storey (1939*b*) has pointed out that all leaf-hopper vectors, thrips and probably white-flies which have been adequately studied show transmission typical of the second Group, whilst aphides usually transmit viruses belonging to the first Group. This is interesting as suggesting an obligate relationship with the insect vector as the determining factor, but does not explain the cases in which the same vector may be responsible for the transmission of viruses in each Group; *M. persicæ*, for instance, is a vector both of potato virus "Y" in the first Group and of potato Leaf Roll belonging to the second, and Osborn (1935, 1937) has shown that *Macrosiphum pisi* as well as

Macrosiphum gei can transmit both pea virus No. 2 and No. 1, belonging to the first and second Groups respectively.

Of course, any alignment of opposed characteristics of viruses such as is shown in Table XXVIII is an over-simplification, for a number of viruses do not wholly conform; they may have one or more properties regarded as typical of Group 1, and others equally typical of Group 2. For instance,

TABLE XXVIII

Characters of Non-Persistent and Persistent Viruses

Group I (Non-persistent).	Group II (Persistent).
1. Readily transmitted by sap-inoculation.	1. Sap-transmitted with difficulty or not at all.
2. Thermal death-point and time of survival *in vitro* lie within relatively small ranges.	2. Properties *in vitro* vary considerably.
3. All transmitted by one family of vectors (Aphididæ).	3. A great variety of vectors.
4. Vectors infective after a few minutes' feeding on source.	4. Vectors infective only after several hours' feeding on source.
5. Vectors transmit at once, with no "latent" (non-infective) interval.	5. After removal from source, vectors are non-infective for a measurable interval.
6. Pre-infection starvation increases vector efficiency.	6. Pre-infection starvation has no effect on vector efficiency.
7. Vector efficiency decreases with increased feeding-time on source.	7. Vector efficiency increases with increased feeding-time on source.
8. Virus survival in the "fasting" vector is short (measured in hours).	8. Virus survival not affected by starving the vector and is measured in days.
9. Survival is shortest in feeding vector (whether on infected or healthy plant).	9. Survival (*i.e.* infective period) increases with increased time on source of infection.

the virus of strawberry Mild Crinkle is most efficiently transmitted after vectors have fed for twenty-four hours on the source of infection yet it only persists within the vector for about three hours (Prentice, 1946). Dandelion Yellow Mosaic is only effectively picked up by the vector after at least three hours' feeding but is rendered inactive within the next hour; while the recently described turnip Yellow Mosaic virus, which is transmitted by biting insects, persists in the vector for a week but has given no evidence of a preliminary non-infective interval, and the power to transmit appears to depend on the regurgitation of the ingested virus fluid (Markham and Smith, 1949). The search therefore continues for some reliable, fundamental character, the presence or absence of which can be used in the grouping of all known viruses. Storey (1939*b*) attached equal importance to the development (latent) period and to persistency within the vector. He therefore defined viruses as (i) those in which transmission was negative on the first plant of a series and positive on the remainder, and (ii) those giving positive transmission on the first plant only. Several workers, however, have shown that, by selecting suitably short feeding times, it is possible to transmit viruses belonging to Storey's category (ii) to a number of healthy plants in succession. Watson (1946) discounts the value of "persistence" as a criterion and points to the lack of precision in the use of the term; thus the persistence of sugar-beet Mosaic virus (usually classed as non-persistent) may over-lap that of sugar-beet Yellows virus though the latter is regarded as a persistent virus. Temperature may affect "persistence," for Kleczkowski and Watson (1944) showed that the virus of sugar-beet Yellows was more sensitive to changes in temperature than any non-persistent virus, and Kassanis (1941) found that the rate of loss in a non-persistent virus (tobacco Severe Etch) was much slower when the vectors were held at a low temperature. Again, the persistence of the virus of sugar-beet Curly-Top is increased with increasing time spent on the source of infection (Freitag, 1936; Bennett and Wallace, 1938), and the same is true of sugar-beet Yellows virus (Watson, 1940, 1946), and even of sugar-beet Mosaic virus if the vectors are not previously starved (Watson, 1946). This dependence of persistency upon feeding time implies a quantitative relationship between persistence and the virus content of the vector, and Watson (1946) points out that plant hosts vary in the amount of virus which vectors can obtain from them. Aphides, for instance, become more highly infective when fed on tobacco infected with potato virus "Y" than if fed on some varieties of "Y"-infected potatoes, and some persistent viruses may exist in hosts which provide such a poor source of virus that vectors would remain infective for scarcely any longer time than they would if fed on a non-persistent virus. Watson also questions the fundamental nature of a latent or non-infective interval. In persistent viruses the latent period is usually measured from the termination of a *short* feeding time on the source of infection, whereas optimum infectivity of the vectors may not be reached for a much longer period and may, indeed, require a feeding time exceeding the whole duration of the "latent" period; in other words, the vectors are at first at minimum infectivity level and may, for that reason, be unable to infect the first plants of a series. Something very like this happens with certain, supposedly typical, non-persistent viruses also. Thus in sugar-beet Mosaic virus (Watson, 1946), the overall picture conforms with Group I in that vectors attain their highest infectivity (*i.e.* can infect the greatest number of plants) after only two to three minutes' feeding on the source of infection, and infectivity declines by 60 per cent. during the first hour; but if feeding on the source is *continued* for several hours the infectivity again increases sometimes to the original maximum, while without preliminary fasting of the vectors their infectivity is low for the first two to three hours' feeding on source and then increases in the same way as with vectors given a preliminary fasting. She explains these results as due to a gradual increase in the *number* of vectors exhibiting infectivity as the feeding time on the source is increased; many of these vectors being unable to infect the first healthy plants to which they are transferred, *i.e.* a "latent" period is claimed even for a "non-persistent" virus. This may also be true of the non-persistent strawberry Mild Crinkle virus (virus I), for Prentice (1946) states that while occasional transmission occurs after only one hour's feeding on the infected plant, it is much more effective when twenty-four hours' feeding is given. Watson (1946) therefore considers that neither "persistence" nor the existence of a "latent," non-infective, interval is a reliable criterion of fundamental differences between viruses, and proposes to substitute the reaction of the vector to preliminary fasting before feeding on the source of infection. It is true that the many viruses which *are* affected by a preliminary fasting of the vector do show a remarkable uniformity in other respects and appear to form a "natural" group, but that is far from being the case in those viruses not so affected. Attention to the effects of starving the vectors is of immense importance in giving precision to experimental work; the effects appear to be effects on the virus itself, for they are very different with two viruses such as sugar-beet Mosaic virus and sugar-beet Yellows virus when the same vectors are used on the same host-plants. Nevertheless, until much more is known of the mechanism involved in this reaction to starvation, there are good practical reasons for retaining persistence in the vector as a criterion for separating viruses; it may at least give some indication of the length of time a vector of a disease will remain infective (*i.e.* a source of danger to a crop) without a further feeding on an already infected plant.

There are clearly some fundamental differences, either in the nature of the viruses, or in the mechanism of transmission in the two Groups which, though still obscure, must be given brief consideration here. The fact that viruses of the first Group may be transmitted by a vector after feeding for only a few minutes on infected tissue, followed by an equally short time on the healthy plant, seems to preclude any biological relationship between vector and virus. This supposition of a purely mechanical transfer of virus, probably by contamination of the insect mouth-parts, was suggested by Doolittle and Walker (1928) for cucumber Mosaic, and has been adopted by a number of workers with other viruses (Hoggan, 1933; Storey, 1935; Osborn, 1937; Kunkel, 1938; and Bennett and Wallace, 1938). It is supported by the fact that the viruses concerned are usually transferred with ease by needle inoculation of infective sap, but become inactive within a few hours whether in the vector or in sap expressed from the infected plant. Nevertheless, there are strong reasons for rejecting this explanation, at least in the case of some of the Group I viruses which have been studied. If the insect's stylet is nothing more than an animated needle it is difficult to understand why potato virus "X" and tobacco Mosaic, amongst the most easily inoculable of all viruses, should not be insect-transmitted or, accepting Hoggan's (1931) statements mentioned on page 559, why the latter virus can only be transmitted by insects from tomato to tobacco and not from one tobacco plant to another. Indeed, specificity of vectors seems without meaning in any case of mechanical transfer of a virus, yet many included in Group I do show such a specificity in their insect vectors. Even the shortness of time required for transmission is not so conclusively against a biological relationship between insect and vector as might be supposed, for Swezy (1930) has shown that a stain can reach the salivary glands of the leaf-hopper *Eutettix tenellus* within an hour after the insect has begun to absorb it and suggests that it may occur in an even shorter period of time, the implication being that passage of a virus through the internal organs, in however short a time this is accomplished, gives the necessary opportunity also for biological reactions to occur. The most important evidence, however, against the mechanical transmission theory is provided by the work of Watson (1936, 1938) on Hyoscyamus virus III, potato virus " Y " and two strains of cucumber Mosaic, in which she used *Myzus persicæ* and *Myzus circumflexus* as vectors. Employing single insects, she found its efficiency as a vector was greatly increased by preliminary starvation, the best results being obtained with insects which had first been starved for at least one hour, were then allowed to feed on the source of infection for only two minutes, and were finally transferred to healthy plants on which again they were only allowed a few minutes' feeding. Insects which were starved of food either before or immediately after these experiments remained virulent for twelve hours, whereas if they were allowed to feed continuously either immediately before or after imbibing the virus they ceased to be infective within one hour. Moreover, she found that increasing the time allowed for feeding on the source of infection greatly reduced the efficiency of the insects, so that after one hour on the infected plant there was no difference in efficiency between those previously starved and unstarved insects. It is clear from these results that this decrease in efficiency was due solely to the act of feeding, and that, in nature, circumstances would rarely occur in which a vector would remain in an infective condition for more than a short time. Mrs Watson explains this apparent anomaly, that the more time the insect has in which to imbibe the virus the less likelihood there is of its transmitting efficiently, by assuming the production of an inhibitory substance of the nature of an enzyme within the vector during the process of feeding. Hence, preliminary fasting brings the inhibitory factor to a low concentration and so permits the accumulation of virus during the first few minutes of feeding. Evidence that such virus-inhibitory substances exist in both vector and non-vector insects has been given by several workers, *e.g.* fluid from crushed *Myzus persicæ* inactivates *Hyoscyamus* virus 3 (Hamilton, 1935); fluid from macerated aphides and leaf-hoppers, including the clover leaf-hopper *Aceratagallia sanguinolenta*, inhibits tobacco Mosaic virus and several others (Black, 1939*b*); while extracts from non-vector caterpillars similarly inhibits tobacco Mosaic virus and tobacco Necrosis virus (Smith, 1941). How or where the virus is brought into contact with the inhibitory factor is unknown; nor is there any information as to whether the inhibition is a direct action on the virus or on the plant tissue, but, however that may be, the effect is to render the virus innocuous.

The Group II type of transmission is characteristically found amongst those viruses which are either non-inoculable by needling infective sap into a healthy plant or in which this is only accomplished with difficulty; there is a latent period after feeding in which the insect is unable to transmit the virus, but thereafter it becomes infective and may remain virulent during its whole life. This latent or "incubation" period was explained by Rand and Pierce (1920) as being the time required for multiplication of the virus, in the insect, up to the concentration needed for effective inoculation into a plant. There is definite evidence that such a multiplication does occur in at least one animal virus (Merrill and Ten Broeck, 1935), but with plant viruses the position is much less satisfactory. Nevertheless, it is difficult to explain how the leaf-hopper vector of maize Streak can still be capable of causing infection nine weeks after once feeding on an infected plant for only fifteen seconds, unless one assumes an intervening period of multiplication (Storey, 1939*a* and *b*). Similarly, it is easier to explain in this way the fact that the vector (*Macrosteles divisus*) of Aster Yellows requires an incubation period of from ten to nineteen days before it is able to transmit the disease to a healthy plant (Kunkel, 1926). With respect to the last disease, Kunkel (1937) has also shown that by exposing the insect to a temperature of 31° to 32° C. it might become permanently non-infective, but that if the exposure be short it would regain its virulence after a longer or shorter period in which it was not able to transmit. This, in Kunkel's view, is only understandable if this period is required for a slow multiplication of the virus after it had largely been inactivated by the high temperature. Black (1941*c*) supports the view that the incubation period represents the time required for multiplication of the virus of Aster Yellows. He fed the vector for two days on plants infected with the disease and then transferred them to healthy plants, from which batches were removed at intervals, macerated, and their body-fluid inoculated into healthy insects; these insects being tested later for their power to induce the disease in healthy asters. Black found that insects macerated before the fourth day of the incubation period gave no infection, whereas those macerated on the twelfth day were infective even when the juice was diluted 1 in 1000. Bawden (1950), however, has pointed out that Black obtained more successful inoculations at a dilution of 1 in 1000 than at 1 in 100 or 1 in 10, so that the degree of dilution could be no indication of virus multiplication; while, on the contrary, the increasing success obtained with the inoculations as the incubation period progressed strongly suggested the influence of an inhibitor within the insect which gradually lost its potency. Indeed, Black (1939*b*) had himself described such an inhibitor in the body-fluid of the clover leaf-hopper. Further, the fact that Black's "control" insects, fed for long periods on infected asters, were strikingly more infective than the "test" insects which fed for only one or two days on infected plants, suggests that the virus content of the insect is largely determined by the length of feeding time rather than on any multiplication of the virus. There are other cogent arguments against the multiplication hypothesis. It has been shown, for instance, that in the case of sugar-beet "Curly-Top" the amount of virus imbibed by the vector determines the length of time the vector remains in an infective condition (Freitag, 1936; Bennett and Wallace, 1938); on the other hand, it has little or no effect on the length of the incubation (latent) period within the insect. Thus Freitag (1936) and Storey (1939*a* and *b*) pointed out that this latent period begins from the time the insect *leaves* the infected plant, and not from the moment it starts to imbibe the virus; an insect which has been reared entirely on a plant infected with a "persistent" virus is still unable to infect another plant until after the expiry of the normal incubation period—a fact which does not fit any too well into a theory of virus multiplication.

Certainly, multiplication of virus is not always necessary, for Bennett (1935) proved, by feeding the leaf-hopper *Eutettix tenellus* on infective sap from Curly-Top of sugar-beet, that infection followed after the normal incubation period when the infected sap was diluted ten thousand times, the presumption being that natural feeding on an infected plant would provide the insect with ten thousand times more virus than was required for infection. He suggested, therefore, that there was no multiplication of the virus, but that it was stored in the blood (body fluid) or some internal organ of the insect and only released gradually to the salivary glands, from whence it reached the stylet and so was injected into plant tissues during feeding. Storey (1932, 1933) has shown in his work on maize Streak and sugar-beet Curly-Top that the virus must enter the body fluid as a necessary preliminary to infection of a plant, and thus has arisen the hypothesis that the latent or " incubation " period is simply the time needed for these organs to become infected. The fact that most workers have failed to demonstrate the presence of any virus in salivary glands, and that Bennett and Wallace (1938) found less virus in these organs than in other parts of the infected insect, suggests that the salivary glands are intermittently fed with virus and that their rapid exhaustion explains the irregularity often found in insect transmission of viruses. The problems are intriguing and much remains to be done before an adequate account can be given of what happens to the virus during the period in which the infected insect is unable to transmit to a healthy plant. How intriguing the explanations may be is illustrated by an observation by Storey (1933), that the insect vector of maize Streak could be made virulent by injecting into it sap from an infected plant, whereas direct inoculation from plant to plant failed. This suggested to him the possibility that the virus passed through a cycle of development in which one form, produced within the plant, was accepted by the insect vector which in turn modified its nature so that it became inoculable to a plant. On this view, the " incubation " period represented the time taken for the conversion of the virus into its new form. He recognised, however, that if this were the case, plants should be susceptible to virus inoculated by needle from the crushed tissues of the insect vector, and presumably an insect would be immune from virus extracted in the same way from a vector. In point of fact, the results he obtained were directly opposed to the theory, for he successfully inoculated insects with vector blood but failed to infect plants, and in a later summary (Storey, 1939*b*) he states that amongst all the plant viruses there is no evidence to suggest that any developmental change does occur.

(3) Potato Aphid Vectors.—Potato viruses are spread under field conditions and the rate of spread will obviously be affected by any factors which influence the breeding, feeding, movement and survival of the insect vectors over the winter; of these vectors, aphides or " green-fly," as they are variously termed, are by far the most important (page 258).

Ecology of Aphides (particularly Myzus persicæ) *in Relation to Transmission of Viruses in the Field.*—For efficiency as a vector, the conditions must be such as to ensure survival of the aphid in sufficient numbers over the winter. They must facilitate an early arrival on a potato crop containing virus-infected plants, the rapid breeding up of large colonies and the constant movement of individuals (alatæ or apteræ) within the crop, thus giving opportunities for imbibing virus and transmitting it to healthy plants. For the dissemination of viruses from one infected crop to another, flights by alatæ may be required.

(i) *Over-Wintering.*—Survival over the winter is usually assured by the depositing of eggs within the bud-axils of hard-wood trees or, in the case of some species of aphides, in sheltered sites on hardy herbs. Jacob (1941) has been unable to confirm Theobald (1926) that eggs of *M. persicæ* are deposited on brassicæ; nor has there been any confirmation of his statement that eggs are to be found on potato tubers, though apteræ of this species as well as of *Myzus pseudosolani* and *Macrosiphum euphorbiæ* occur in early spring on sprouting tubers. This latter fact may be important if some of the tubers are virus-infected, and many cases of heavy disease attacks in the young growing crop can be explained in this way. Further, W. M. Davies (1932) showed that sprout infestation might, under favourable weather conditions, account for the initial aphid infestation of the growing crop, for in separate instances colonies of *Myzus persicæ*, *Myzus circumflexus* and *Macrosiphum solanifolii* on the sprouts had at least a few individuals alive on the shoots when these appeared above ground.

Sprout infestation of tubers in storage (usually in " chitting " houses) is only one example of the over-wintering of apteræ under sheltered conditions; most potato aphides may, for instance, be found as apteræ on many plants in heated glass-houses throughout the winter. Of importance, however, to the question of initial infestation of field crops of potatoes is W. M. Davies' (1934) discovery that *M. persicæ* survived the winter as apteræ on winter field brassicæ, such as savoys, and that the early infestation of the potato crop usually varied in intensity according to the degree of proximity of such winter brassicæ (1937, 1938). This is confirmed by the observations of Jacob (1941), who also considers it probable that years of high aphid infestation of potatoes follow winters when widespread hibernation on brassicæ has occurred, and that low infestations follow winters when few or no *M. persicæ* survive on winter brassicæ.

More recently, attention has been directed to the importance of root-clamps as a means of over-wintering. Broadbent and Hull (1947) and Broadbent *et al.* (1949) have reported that *Myzus persicæ*, *Hyperomyzus* (*Rhopalosiphoninus*) *staphyleæ* (Koch) (Fig. 47), and *Aulacorthum* (*Macrosiphum*) *solani* (Kalt)—*Myzus pseudosolani* (Theob) commonly occur in mangold clamps in many parts of the British Isles, but that only *Myzus ascalonicus* Doncaster has been found infesting clamped swedes. So far as *M. persicæ* is concerned the degree of infestation (and incidentally, the keeping power of the roots), appears to be directly related to the thoroughness with which the roots are " topped " at clamping time. Thus, when all foliage and petioles were stripped off there was no aphid infestation and only 3 per cent. of roots rotted; when some 3 in. of green leaf-bases were left on the roots, 8 per cent. rotted and 5 per cent. became infested, while the effect of clamping untopped roots was to cause 12 per cent. rot and 8 per cent. aphid infestation. It is clear that this may form an important method of aphid over-wintering, especially during severe winters, and that it may have serious effects upon the degree of infestation of the summer crops (*e.g.* potato and sugar-beet) with repercussions on the extent of the spread of virus diseases. Broadbent and Hull (1947), for instance, state that in 12 square miles of Lincolnshire they found 26 mangold clamps still unopened in April and May, of which 12 were infested with *M. persicæ*; at least six of these clamps were still unused in June. So far, no success has followed attempts to control clamp infestation by (i) blowing B.H.C. dust into the straw covering of the clamp or (ii) dusting the roots with either derris powder or with 3 per cent. nicotine dust applied at the rate of 1 lb./ton of mangolds.

(ii) *Migration from the Winter Host to Potato.*—Davies and Whitehead (1935) consider that winter brassicæ and other cruciferous plants are the main source of the initial infestation of *M. persicæ* on potato, whereas Ris Lambers (1938), in Holland, regards these as of less importance than the hardwood and glasshouse winter host-plants, a view which is shared in Germany by Störmer (1938). In any case the potato crop will normally become infested by means of alate progeny of the stem-mothers which take to flight from May onwards, so that the meteorological conditions affecting flight will have a marked influence on the date and degree of initial infestation. W. M. Davies (1935, 1936, 1937) showed, both by laboratory tests and field observations, that the most favourable conditions require the co-incidence of a temperature reaching 65° F., a relative humidity of not more than 70 per cent., and a wind speed of less than five miles per hour ; in other words, a warm, dry and relatively still atmosphere. Broadbent (1949) has added considerably to our knowledge of the factors affecting aphid flight. He showed, among other facts, that flight was more frequent in young (one to four days after metamorphosis) aphids than in adults, and that it was temporarily stimulated by starvation ; flight declined rapidly at light intensities below 100 f.c. and ceased with darkness, while after a period of flying aphids were less likely to respond by flight to good flying conditions than were others who had spent the previous day in feeding. Changes in relative humidity only temporarily affected aphid flight ; a higher humidity retarding and a lower one increasing it. After adjusting themselves to the change aphides flew readily at all humidities tested between 50 and 100 per cent. with temperatures below 80° F. (26·7° C.) ; the combination of high humidity and high temperature (90° F.—32·2° C.) sometimes inhibited flight, while flight frequency was greater under fluctuating pressure than under constant pressure. Davies and Whitehead (1935) observed that hot, dry conditions not only directly facilitated flight but, by causing the colonised cruciferous weeds to wilt and die, greatly increased the proportion of alatæ produced, and

Thomas and Vevai (1940) have shown that the factors which stimulate the production of large numbers of alatæ appear to be (*a*) large fluctuations in daily temperature, (*b*) a large percentage of dry sunny days tending towards drought conditions (particularly in May), and (*c*), correlated with (*a*) and (*b*), low relative humidities. Davies and Whitehead (1938) found that alatæ have no difficulty in detecting and colonising even isolated plants at a distance of at least a quarter of a mile, and probably much farther.

(iii) *Movement within the Potato Crop.*—So long as conditions are favourable for flight, the winged migrants are in constant movement from plant to plant, during which viviparous female larvæ are deposited to form the nuclei of future colonies. The migrants of *M. persicæ* show perhaps even greater mobility than other species, for Davies (1932) noted that they only paused on each plant long enough to deposit a single larva, though later in the season this species also deposited several at a time, as is usual with aphides. It was evident from Broadbent's (1949) experiments on the factors affecting aphid flight (*cf.* above) that optimum conditions were likely to be found within a crop, and this has now been demonstrated (Broadbent, 1950) by comparing the climatic conditions above a crop of potatoes with those found at varying levels within the crop (*i.e.* the micro-climate or ecoclimate). As compared with the temperature recorded outside the crop (within the screen) the maximum within the crop was from 0° F. to 13° F. higher and, over a period of eleven weeks, averaged 6° F. higher ; the crop minimum was 2° F. lower and the average daily temperature range was 8° F. higher—the average daily mean temperature in the crop over a period of five weeks being 2·2° F. higher than in the screen. By day, humidity was higher in the crop than in the screen, the average difference at the minima being 5 per cent. in relative humidity and 7° F. in dew point ; with a dew point, at night, 2° F. lower than in the screen. Both temperature and humidity were greatly affected by wind speeds and this, within a crop, altered every few seconds though it rarely exceeded 3 miles/hr. even when the wind-speed two metres above the crop averaged 15 miles/hr. So far, only voluntary movement has been discussed, but it should be borne in mind, as Broadbent has shown, that conditions favourable for flight often exist within and immediately above a potato crop, although strong winds may be blowing only a few feet higher; alatæ on the wing within the crop may therefore easily be caught in strong air-currents and be carried involuntarily for considerable distances.

There is also a good deal of evidence that even the apterous adults display unsuspected powers of movement within a crop. Davies (1932) found that 84 per cent. of *Macrosiphum solanifolii* (*euphorbiæ*) and 73 per cent. of *Myzus persicæ* changed their site within twenty-four hours, and of these at least 50 per cent. had moved to other leaves. Similarly, Ris Lambers (1938) reports that after 70 per cent. of plants had been infested no alatæ could be found, but within a further twelve days fully 99 per cent. of the crop had become colonised. This movement of apteræ must therefore be of some importance once the foliage of neighbouring plants come in contact. Czerwinski (1943) agrees that apteræ move very frequently but only, he says, to a few of the nearest plants; and Broadbent *et al.* (1950*a*) regard this as confirming their view that apteræ play little part in the spread of viruses, even within a crop. Many, as yet imperfectly understood, factors are obviously operating to modify any such generalisation, including complex virus/insect/plant relationships, the relative proportions of alatæ and apteræ, and the varying incentives to movement which may be very different in the two forms.

Nevertheless, it seems certain that the spread of viruses usually shows a closer correlation with alatæ numbers and mobility than with the wingless forms (Whitehead (1943)). Doncaster and Gregory (1948) conclude, from the observed spread of Leaf Roll and Rugose Mosaic (virus "Y") within a crop, that plants close to the source of infection are most likely to contract infection and that the chances of this occurring decline rapidly with increasing distance, and Gregory and Read (1949) have crystallised this relationship in the empirical expression Log $1 = a + bx$ ($1 =$ the number of infective punctures at a distance x from the source after a given time, while a and b are constants for any one set of field conditions but liable to vary independently with the disease and the season). In other words, it is recognised that factors which modify the simple relationship suggested by Doncaster and Gregory are usually operating, and field experiments can be devised to study their nature and influence. On *a priori* grounds, for instance, one would expect that the distribution from a single source would be very different in the case of a " non-persistent " virus such as virus " Y " in which the insect vector is immediately infective after some two minutes' feeding, but which quickly requires replenishment, and a " persistent " one such as Leaf Roll in which the insect retains the virus for many days but is unable to transmit it to a healthy plant for the first forty hours or so after even prolonged feeding on the source of infection. This, and other factors were certainly operating in field experiments carried out by Broadbent *et al.* (1950*a*) in which batches of potted King Edward potatoes were exposed, for periods of about a fortnight each, to equal chances of Leaf Roll and virus " Y " infection from a nearby field crop of Majestic potatoes. They found that even a few feet of isolation from the main crop produced very different data on virus transmission to the potted plants. Thus, (i) the total spread within the main crop only trebled the initial infection, whereas 22·4 per cent. of the healthy, potted plants contracted infection, suggesting that the winged spring migrants were less active than in Doncaster and Gregory's (1948) trials in a similar " ware " district, for the latter workers ascribe most infection within a crop to this cause ; to some extent, however, the disparity of spread within the crop and the potted plants may have been due, as Van der Plank (1948) says, to the (potted) plants being exposed in an isolated row instead of in the middle of the main crop ; (ii) the main spread within the crop was of Leaf Roll, which suggests fairly prolonged feeding with intermittent short flights by alatæ ; (iii) the potted plants did not become infected until the maturing main crop discouraged further feeding by the alatæ bred up within the crop, and the migration to the winter hosts had begun ; under such conditions one would expect a heavy infestation of the younger, potted, plants (Moericke, 1941) ; (iv) contrary to what happened in the main crop, the chief spread to the potted plants was of virus " Y," for 20·5 per cent. became infected as compared with 1·9 per cent. infected by Leaf Roll. Among factors which might have contributed to this result were (*a*) the greater susceptibility to " Y "-infection shown by King Edward as compared with Majestic (Bawden and Kassanis, 1946) ; (*b*) the greater restlessness of alatæ leaving the main crop as compared with the spring migrants after becoming established within reach of abundant food and (*c*) an increased ability on the part of *Macrosiphum solanifolii* (*M. euphorbiæ* Thomas) to transmit virus " Y." The conditions on a seed-growing farm in a pastoral area are, of course, quite different. Davies (1934) and Davies and Whitehead (1935, 1938) have shown that in such cases the spring migration is both small and late, and that only an infinitesimal proportion of individuals arrive on the potato crop in an infective condition ; the virus usually being that of Leaf Roll. Also, Broadbent *et al.* (1950*a*) state that migrants which soon find hosts are likely to infect more plants than those which have flown a considerable distance. The disease foci are also few in number and a very heavy " build-up " of aphid population would be required to give anything approaching the rate of disease increase found in " ware " districts. In some seed areas early crop maturation expedites the dispersal migration.

(iv) *Multiplication within the Potato Crop and Migration to the Winter Host Plants.*—Warm sheltered conditions, with abundance of food, result in an extremely rapid breeding up of " lice " from the viviparous apteræ deposited by the alate migrants (and successive generations), to reach a maximum usually by the end of July. The same conditions, however, are favourable for the development of aphid parasites and predator insects, and their activity causes a sharp drop in aphid numbers until they, in turn, are reduced in numbers by the dearth of aphides. Such aphides as escape their enemies then again reproduce to give rise to a late summer (September) peak somewhat lower than that in July. With the maturation of the potato crop, food becomes short for the aphid population, and the rate of production of alatæ (continuous as it has been throughout the summer) shows a sudden rise. Many of the earlier produced alatæ will already have taken advantage of the summer optimum conditions for flight in order to migrate to any neighbouring brassicæ or root-crops, on which generations of apteræ continue to develop until the following spring unless the winter conditions are too adverse for survival. Opportunities for flight are less common in autumn, but when they do occur migration of alatæ takes place to many kinds of food plants as well as to certain hardwood winter-hosts such as the peach, for many workers have shown that migration is not a purposeful flight to a winter-host, directed by smell or any form of sense-perception (Profft, 1939; Broadbent, 1949*a*; Kennedy, 1950). After a long or short period of feeding, flight is resumed but, as Kennedy (1950) has pointed out, many more take to flight after feeding on a plant unsuitable for over-wintering the eggs, *e.g.* the spindle-tree (*Euonymus europæa*), than do so from a suitable one. Hence the arrival on suitable hardwood trees, such as the peach, of *M. persicæ* in numbers which Kennedy estimated at tens of thousands per day on a four-foot high tree, completely overshadows the relatively small number leaving the tree and creates an illusion of directed flight. Nor are all the hardwood trees recorded as winter hosts equally suitable for over-wintering eggs, and Ris Lambers (1946) states that, in Holland, although *M. persicæ* will oviposit on almost all species of *Prunus*, eggs will only hatch and give rise to spring colonies on the peach (*P. persica* Batsch). In Canada, Gorham (1941) says this aphid commonly over-winters on the Canadian wild plum (*P. nigra* Ait) which, however, is not a European species. In Great Britain, Broadbent (1949*a*) has recorded spring colonies arising from eggs on peach, nectarine (*P. persica* Stokes, var), and the ornamental almond-peach (*P. amygdalo-persica* (West Rehd), but neither Broadbent nor Doncaster and Gregory (1948) found colonies in spring on cherry (*P. cerasus* L) although eggs had been laid the previous autumn. On these hardwood hosts alate functional females are produced which pair with alate males, produced either on the summer or winter host plants, and then deposit eggs within sheltered sites such as bud-axils. It will be seen, therefore, that the number of eggs (and consequently stem-mothers and their alate progeny) developing on the hardwood trees in spring, is definitely influenced by the weather conditions of the previous autumn, whereas this is far less true of the alatæ bred up on winter brassicæ, since these plants may have been colonised at any time during the previous summer.

(4) CONTROL OF VIRUS DISEASES IN POTATO CROPS.—(A) GENERAL.—We have seen that three conditions, operating together, bring about a rapid and progressive degeneration of potato stocks by the spread of virus diseases. These conditions are :—

(i) Presence of diseased plants within, or in close proximity to, an otherwise vigorous potato crop.

(ii) Presence of aphid vectors of virus diseases.
(iii) Conditions favourable for the rapid multiplication and movement of the aphides.

If not more than any two of these conditions occur within a potato area there will be little spread of disease and therefore of degeneration. The occurrence of diseased plants is largely within the control of the grower since they arise primarily from the planting of infected tubers ; it is the business of the seed producer to ensure, as far as is practicable, that no infected tubers are included in his produce, whilst it is for his customer, who produces for the " ware " market, to take precautions against the contamination of this seed from his own partially infected stocks. On the other hand, the arrival of vectors and the rate of breeding up, and movement, of the insects are determined by meteorological factors wholly beyond control, and no amount of care on the part of a grower will do more than slightly to counteract the effect of these climatic hindrances to the maintenance of the health of his potato crops. Hence, for this reason and because of the intricacy of the problems involved, the production of healthy seed is a specialist's job rather than a sideline in the production of ware for the table.

The special problems of the seed-grower and the " ware " grower are discussed later, but some aspects of the maintenance of the health of potato stocks are equally important to both. This is particularly true of the serious effects which may result from the presence of groundkeepers.

(a) *Groundkeepers*, *Volunteers* or *Self-setts*, as they are variously termed, are important both as potential sources of virus diseases from which the new crop may become infected, and as a frequent cause of admixture of varieties. Doncaster and Gregory (1948) surveyed some fifty fields and found that the survival of groundkeepers on arable land averaged from 2000 to 7000 per acre in the first crop after potatoes, and fell to from 500 to 800 per acre in the third year ; which was the average interval before another potato crop occupied the field. Hence the new crop on the average had a 5 per cent. admixture of groundkeepers. The number varied according to the type of intermediate cropping between the successive occupation of the land by potatoes ; thus the largest number of groundkeepers were usually found in root crops and the smallest number in land seeded down to short ley, with cereals in an intermediate position; but whatever the rotation practised, some groundkeepers could invariably be found up to at least four or five years lapse of time. Although the insect infestation of groundkeepers growing among roots may be heavy, it is uncommon to find aphides on such potatoes in grass or cereals. Hence neither Rugose Mosaic (virus "Y") nor Leaf Roll increases much, in groundkeepers, over the infection initially present in the parent crop. From this it follows that groundkeepers from a healthy parent crop are not usually important as a factor in degeneration, although their presence may easily

TABLE XXIX

Infection of Scotch Majestic from Up-to-Date Volunteers, 1943

From Doncaster and Gregory (1948)

	Conditions of Progeny in 1944 (per cent.).			
	Rugose Mosaic.	Rugose Mosaic. Leaf Roll.	Leaf Roll.	Healthy.
Area contaminated with Volunteers (1943) . .	5·5	73·5	17·5	3·5
Area approx. 150 yds. from contaminated area .	2·5	0·0	6·3	91·0

ruin any hope of certification because an attempt to reach the necessary standard of *purity* of type may involve heavy roguing. Survivors from a diseased crop may, of course, be the cause of an abnormally large increase in disease in the new crop. This is well illustrated by a case quoted by Doncaster and Gregory (1948) in which a part of a crop of the variety Majestic occupied land which had carried a crop of Up-to-Date two years previously. The Up-to-Date groundkeepers represented 23 per cent. of the crop on the "contaminated" portion of the field and proved to be heavily infected; 55 per cent. having Rugose Mosaic, and 27 per cent. having secondary Leaf Roll, including 12 per cent. with mixed infection. The Majestic crop on the "uncontaminated" area showed only 0·2 per cent. Rugose Mosaic and 0·25 per cent. Leaf Roll, but on the contaminated area the majority of the Majestic plants developed either Leaf Drop Streak (first-year symptoms of virus "Y" infection) or primary Leaf Roll, or both. The foregoing Table XXIX shows the effect of the proximity of this reservoir of disease on the health of the Majestic crop the following year.

(b) *Number of New Infections arising from the proximity of one Infector Plant.*—Broadbent and Gregory (1948) added a fourth year's observations to the survey work of Doncaster and Gregory (1948) and noted the wide variation in the number of new infections which were attributable to spread

TABLE XXX

(Adapted from Broadbent and Gregory (1948))

Number of New Infections ascribed to One Infector (adjusted to a Plot of 720 Plants)

	Rugose Mosaic.	Leaf Roll.
"Seed" Areas—		
Cockle Park (Northumberland)	0·4	0·04
Aberystwyth (Cardigan)	0·2	0·90
Bangor (Caernarvonshire)	0·3	0·3
"Ware" Areas—		
Sutton Bonington (Leicester)	1·2	5·2
Newport (Shropshire)	5·2	6·6
Kirton (Lincolnshire)	1·3	2·6
Rothamsted (Herts)	1·6	6·3
Reading (Berkshire)	9·6	8·9
Cambridge	7·0	10·1
East Malling (Kent)	2·7	2·3

from each infected plant. As might be expected, this variation occurred from centre to centre in any one year, and from year to year in any one centre. Nevertheless, it is of interest to quote the spread of infection per unit infected plant in a typical year, at centres which can be grouped according to whether or not they are in an area reputedly suitable for healthy seed-production.

Too much should not be read into records obtained in any one year, but Table XXX clearly illustrates the well-known fact that in some areas there is very little spread of virus diseases, even when diseased infector plants are, as in the work of Doncaster and Gregory (1948) and Broadbent and Gregory (1948), deliberately planted in close proximity to the healthy crop. On the other hand, it shows the devastating effect that the same number of infector plants may have on healthy crops in typical " ware " growing districts.

(c) *Factors, beyond the Control of the Grower, which influence the Spread of Virus Diseases.*—It has already been stressed that it is an over-simplification to assume that differences in the spread of virus diseases merely reflect differences in the number of aphid vectors present, although that is important; it would not, for instance, explain why Gregory and his colleagues found that (in 13 " ware " growing centres) 69 per cent. of the virus " Y " infections, and only 48 per cent. of Leaf Roll, reached the tubers of Majestic crops before the end of July; nor why there was little subsequent increase in the amount of Rugose Mosaic although frequently—in association with a high initial aphid attack—there was a *late* increase in Leaf Roll. Rather is it true to emphasise that many factors which influence the *activities* of the aphid vectors determine the amount of virus spread, *cf.* Dickson *et al.* (1949). These factors, which are discussed later, were first studied in the pioneer work of W. Maldwyn Davies in North Wales. Some of the factors are topographical but most can be summed up as " climate." From a study of the spread of virus " Y " in some 40 localities in Denmark, Hansen (1941) concluded that there was a high negative correlation between the incidence of the disease and both the relative humidity and number of days rainfall in June, but not with the amount of precipitation measured in millimetres. He also found a high positive correlation between disease incidence and the mean temperature in July; which was to be expected since a similar correlation existed between the temperature and the number of *Myzus persicæ* generations. Hansen states that the number of *Myzus persicæ* increased during the early part of 1939 on a logarithmic scale, the average daily logarithmic increase being 0·0912 at 16·8° C. Murphy and Loughnane (1937) studied the spread of Leaf Roll over a period of ten years near Dublin, which district can be regarded as typical of the " ware " growing areas of eastern Ireland. They found that seasons could be separated into three groups according to the percentage of plants which became infected within 10½ ft. from a known infector; these being (1) not more than 15 per cent.; (2) not more than 50 per cent.; and (3) not more than 75 per cent. Most of the spread was believed to take place within the six weeks from the end of May to early July, and Murphy and Loughnane correlated this spread with the rainfall and temperature during the month of June. The least spread occurred in years with an excessively wet June which restricted aphid increase, and this was reinforced by very dry weather in July which hardened the plants, or by a continuance of the wet conditions. Moderate spread occurred with low rainfall and high temperatures in June, which favoured the aphides but tended to ripen the plants prematurely. What is particularly significant is the statement by these authors that maximum spread was the result of *normal* rainfall and temperature in June, which permitted rapid growth of the potato plants and simultaneous increase in the aphid vectors of Leaf Roll. The converse is equally true, viz. healthy seed can only be grown with confidence in areas in which the *normal* climate discourages aphid activity, without at the same time being too adverse for the potato crop.

(B) CLIMATIC FACTORS AND SEED GROWING.—Fortunately, suitable climatic conditions for healthy seed production are to be found in more areas than was formerly supposed, including, in addition to the greater part of Scotland, the northern part of Ireland, the moorlands of Cumberland, Devon and Cornwall, and the uplands and coastal areas of Wales. In North Wales, Whitehead, Currie and Davies (1932) found that successful seed production depended not on altitude or the absence of aphid vectors, but rather on the prevalence of bleak windy conditions on the seed farm, and the maturation of the haulms before any great development in the aphid population occurred; these conditions being most often found in coastal areas. Davies (1934) described a technique to enable comparisons to be made in the number of aphides present in potato crops. Thus, by regarding the compound leaf as the unit, and taking 100 leaves at random as the crop was traversed, he found that successful seed farms never carried a population of more than 20 *Myzus persicæ* per 100 leaves, whereas this "Index," as it was called, reached 1000 per 100 leaves on some occasions on unsuccessful farms, and always exceeded 100 per 100 leaves. The time at which the count is made for this purpose is all-important, since the object is to estimate the more immediate effect of the initial migration rather than the cumulative effect of migration and shelter, which facilitates breeding, or the prevalence of parasites and predators which greatly reduce the aphid population. In normal years migration may finish about mid-July, so that the index figure should be arrived at by the end of that month; in forward or backward seasons the count may have to be made up to one month earlier or later respectively. Davies (1938) found during a survey of eastern Scotland that the aphid population fluctuated from one district to another, and apparently for similar reasons as had been found to obtain in North Wales. It was clear, also, that the number of *Myzus persicæ* might exceed 20 per 100 leaves without necessarily condemning the area for healthy seed production, provided that mobility was reduced by the prevalence of strong winds. The ordinary grower, without expert knowledge, cannot identify aphid species with certainty, but as a very rough guide it may be assumed that the vector species *Myzus persicæ* will ordinarily not exceed 15 per cent. of the aphid population. *Macrosiphum euphorbiæ* (particularly when the flower heads are heavily infested) may amount to 75 per cent. of the total aphides present, although occasionally the predominant species is *Aphis rhamni*. The proportion of *M. persicæ*, however, tends to increase (at least in North Wales, and possibly elsewhere) as the season advances. Broadbent (1950*a*) has analysed the results of experiments in different parts of England and Wales from 1941 to 1947 on the spread of potato Leaf Roll and Rugose Mosaic. He concluded that Leaf Roll spread was correlated with the number of alate *M. persicæ* caught on sticky-traps throughout the potato-growing season; that there was some correlation with the maximum count of *M. persicæ* per 100 leaves but this probably reflected the correlation between trapped aphides and the number per 100 leaves. The spread of Rugose Mosaic (potato virus "Y") was correlated to a lesser degree with number of *M. persicæ*, perhaps because other aphid species are often vectors. With both diseases higher correlations were obtained when the infected plants were dispersed among the healthy crop than when they occurred in a row. Broadbent is of the opinion that it is possible to predict the average health of potato stocks in the following year from average trap data, and further work may enable the health of individual stocks to be predicted.

The climatic conditions determining the population and activities of the aphid vectors of potato viruses in North Wales (and hence the probable suitability of certain areas for seed-potato production), have proved equally applicable to other parts of the British Isles, *i.e.* as shown by Davies (1938) for eastern Scotland, Staniland (1943) for Devon and Cornwall, Jacob (1944) for the four northern counties of England, Broadbent (1946) for north-west Derbyshire, and Fidler (1949) for north-east Yorkshire. But the British Isles have a typically cool, moist, maritime climate, and it is to be supposed that the more the climate of a country diverges from this type, the less assurance we can have that similar criteria of temperature, humidity, and wind velocity will apply in judging the potentiality of a district for healthy seed-potato production ; Bald and Norris (1943), for instance, emphasise that at Canberra the population of *Myzus persicæ* is depressed by hot, dry weather, as well as by heavy rains which directly destroy the aphides. Much attention has been given to this problem in South Africa by Van der Plank (1944*a* and *b*). He finds that while the British criteria apply reasonably well along a narrow, barren strip of the west coast ; in the continental climate of the interior it is the very high temperatures and low humidities which check the flight of the aphid vectors of virus diseases. At both extremities of the environmental scale potatoes—but not aphides—will thrive, and it is in the intermediate climates that high aphid infestation can be expected. He states that when the average daily maximum temperature in summer is 32° C. (89·6° F.) *M. persicæ* virtually disappears. At Kimberley, winter rains which favour aphides are negligible and the rising temperature in early spring, with a resulting dryness of atmosphere, keeps aphides in check so effectively that two crops of potatoes can be grown per year with little risk of virus transmission ; counts over three seasons, for instance, gave an average for *M. persicæ* of 1·1 per 100 leaves, the highest being 3·6 per 100 leaves in April, when the danger of virus spread was almost past. As criteria for healthy seed-potato production in a hot, dry climate, Van der Plank suggests (1) a mean, maximum temperature, in summer, of 90° F., (2) a daily range of not less than 28° to 35°, and (3) the prevalence of strong, hot and dry, land-winds. On the other hand, under cool maritime conditions, a mean maximum temperature of 65° F. or less, and a daily range of, at most, 13° during June, are to be desired. He considers that reliance on a June temperature test of the suitability of an area for seed-potato production has advantages over an aphid count, not only in respect of the saving in time, but because it is not affected by the often remediable proximity of brassicæ or other winter hosts; also, since it is a test of the climatic conditions governing the flight of *M. persicæ*, it measures the tendency to migrate—a much more reliable test of suitability than is afforded by a count of the total number of aphides present; *cf.* also, Dickson *et al.* (1949).

THE PROBLEM FOR THE SEED GROWER.—Even in the best areas the seed grower will be wise to remember that many virus-infected plants will certainly be present in his neighbourhood, and that in some seasons there may be an unusual increase in aphid population capable of spreading diseases in his stocks. Precautions are therefore necessary to safeguard the health of the seed-tubers he proposes to sell.

(a) *Roguing out of Diseased Plants.*—The grower should have little difficulty in deciding whether "roguing" out diseased plants is effective in maintaining the health of his potato stocks, and should regard the degree of effectiveness as some measure of the suitability of his farm for seed production. It is certainly not worth the trouble in most "ware" growing areas (Broadbent *et al.*, 1950), and Doncaster and Gregory (1948) consider it unlikely to be effective if, on the average, a virus disease more than doubles itself in a season (*cf.* Table XXX). With a lower rate of increase than this, however, efficient roguing should, in most seasons, enable a grower consistently to maintain the health of his stocks within the limits of one or other of the Certification standards. Thus, Whitehead (1943) showed that roguing was effective over a period of fourteen years (1928-1941) in maintaining the health of some 59 potato stocks of a number of varieties, in certain areas of North Wales. One typical case (Sharpe's Express) was traced from its original source near Holyhead (where it showed 0·3 per cent. total virus infection) through 50 farms where roguing was practised, with the result that 14 crops were shown to have developed more than 1 per cent. of total virus infection, but in only three of these cases had the disease increased to more than 3 per cent. Doncaster and Gregory (1948) consider that, in districts where there is no spread at all, the Leaf Roll and Rugose Mosaic diseases will automatically eliminate themselves because fewer tubers than normal are produced in the second and subsequent years of infection, and they quote Gram (1922) as claiming that this has in fact occurred in coastal areas of Jutland. There is, however, no proof of any such *progressive* deterioration in yield from an infected plant and, even if this is conceded, roguing will ensure elimination within one season. The first step is to remove all plants, together with their tubers, which are recognisable as being virus-infected, an operation which can be carried out when the crop is being rogued for trueness to type and the elimination of undesirable plants such as wildings and bolters. Such virus-infected plants are infective before symptoms are visible, but in good seed areas they can usually be recognised before there is any migration of alate aphides to them. To be effective, all roguing should be completed before any appreciable aphid colonisation occurs, in order both to eliminate sources of disease and to avoid distribution of the aphides through disturbing the crop during roguing. The more important virus diseases requiring to be eliminated if the health of the stocks is to be maintained are shown in Table XXXI.

Little difficulty will be experienced except with regard to the milder symptoms of Mosaic, but all plants in which a mottle is clearly discernible should be removed. The effect on the ultimate health of stocks—both on the seed farm and when the produce is grown for ware—of such mottled plants as are allowed to remain will differ markedly according to whether the cause of the mottle is virus " X " (*e.g.* in Kerr's Pink), virus " A " (*e.g.* in Golden Wonder) or virus " Y " (*e.g.* in Epicure). So long as varieties such as these deservedly popular sorts are grown there can be little hope of completely eradicating viruses " X," " A " or " Y." Aucuba Mosaic (virus " G ") is common but can safely be ignored ; if, however, there is any indication of spread under field conditions, it is probable that the symptoms are due to the complex F+A which, in association, are aphid-transmitted, and such plants should be rogued out.

(b) *Pre-planting Precautions.*—The removal of an unusually large number of plants showing virus symptoms should be taken as an indication that the previous year was favourable for the spread of disease and as pointing to the need for a change of seed. For this purpose, nothing but the best seed obtainable from the best districts is good enough for planting. Before planting, the opportunity afforded by the routine examination of seed for the presence of scabs, Black Scurf, Blight, Blackleg, etc., should be seized to reduce still further the incidence of certain viruses in the seed stock. This is made possible by the fact that viruses " F," " G " and " A,"

TABLE XXXI

Virus Diseases Important in Causing Degeneration

Disease.	Due to Virus(es).	Distribution as far as known.
Leaf Roll	Leaf Roll	A significant cause of rejection of stocks for certification in S.E. Scotland, becoming less important from east to west and from south to north. A main cause of degeneration in England and Wales, but said to be negligible in Eire.
The " Mosaics " including—		
(i) Mosaic	X or A or Y	" X " is widely distributed over the whole British Isles, some varieties being 100 per cent. infected. " A " is very common in certain varieties, more popular in Scotland and Ireland than in England or Wales ; its distribution in the two latter countries is not known but is probably common.
(ii) Streak	Y	"Y," in its first-year symptoms of Streak, is very common in east and south-east England ; is said to be " not uncommon " in Eire. Generally not common in Scotland but, in its second-year form of Rugose Mosaic, is prevalent in S.W. Scotland and occurs also in Wales.
(iii) Severe Mosaic	Y or X+Y or X+A or X+F	The complexes X+Y and X+A are the chief causes of severe Mosaic in the British Isles, with a distribution determined by that of their constituent viruses.

together with complexes of which these viruses form a part, induce a *necrosis of tubers* in certain varieties which are given in Chapter XXVI (pages 450, 453) and Chapter XXVII (page 501). Samples of tubers of any of these varieties should therefore be cut, and if more than a very occasional one is found affected with necrosis, the stocks should be rejected for planting.

(c) *Planting Plans.*—Just as viruses can be arranged into groups according to the method of transmission (page 494 *et seq.*), so potato varieties fall into groups, the members of which show distinctive reactions to some viruses. Following Cockerham (1939), the characteristics of these groups are :—

Group I. Varieties lethally necrotic to viruses " A " and " X " ; these including Arran Crest, Ninetyfold, King Edward VII, Craigs Defiance, Craigs Royal, Craigs Snow-white, International Kidney and Epicure. Such varieties, when *artificially* infected with either of the two viruses by *grafting*, become so severely necrotic in the foliage that the plant dies. In the *field* this extreme susceptibility protects the plant against systemic infection, for the cells in the immediate neighbourhood of the point of infection are at once killed and provide an obstacle across which the virus cannot spread to healthy tissue ; the practical effect is a form of *field immunity* from attack by either virus, which can be put to use by planting any one of these varieties between others liable to infection from either virus " X " or virus " A."

Group II. Varieties lethally necrotic to virus " A," but non-lethal to virus " X " ; amongst which are Kerr's Pink, Doon Star, Great Scot, Eclipse, Sharpe's Express, Redskin, Duke of York, British Queen, Up-to-Date, Gladstone and Ballydoon (Cockerham, 1939). To these, according to Murphy (1938), are to be added Alannah, Arran Peak, Dunbar Standard, International Kidney, Rhoderick Dhu and Ulster Monarch. (Additional ones will be found in Table XXXIII, pages 684-5.) In these varieties virus " A " will not occur under field conditions, nor will the complex X+A (Crinkle), but any mosaic will be due to " X " or " Y " or to the complex X+Y (Rugose Mosaic).

A few varieties, necrotic to virus " A," are affected only in the growing tips of the shoot ; this form of Top Necrosis being distinguished as " apical " Top Necrosis. Amongst the varieties showing apical Top Necrosis are Epicure and Arran Crest in Group I and Duke of York and Eclipse in Group II (Scott, 1938).

Group III. Varieties lethally necrotic to virus " X " but non-lethal to virus " A." No popular commercial variety shows this form of reaction, so that for practical purposes this group can be ignored.

Group IV. Varieties non-lethal to viruses " A " and " X." Cockerham (1939) subdivides this group into (*a*) and (*b*), of which sub-group (*a*) includes the three varieties Golden Wonder, Arran Chief and Catriona, all of which are very commonly infected with virus " A." The remaining varieties non-lethal to the two viruses are placed in the sub-group (*b*); these include Majestic, Arran Banner, Arran Pilot, Arran Consul, Ally, King George, Dunbar Cavalier, Arran Comrade and Arran Luxury (Cockerham, 1939). Mosaic in any of these varieties may be due to "X," "A" or "Y," whilst Severe Mosaic will be caused by complexes of two or more of these viruses or by virus "Y" alone. Appendix II (Table XXXIII) should be consulted for the reaction of other varieties.

In planning the order in which his potatoes should be planted, the seed grower will be guided by the reaction to be expected of each variety to prevalent viruses, by the probability of it already having one virus of a complex present, and by the extent to which insect transmission is to be expected in the light of previous experience. It would clearly be folly to plant, say, Majestic containing virus "X" alongside Golden Wonder with a slight mottle due to virus "A," for there may be mutual transference of viruses by contact of foliage (X) and by aphides (A), with the result that both varieties would show, in the following year, an amount of the Severe Mosaic complex (X+A) corresponding to the prevalence of the insect vector in the current season. If, however, they were grown in different fields or were separated by as wide a belt as possible of some variety in group I, lethally necrotic to both "X" and "A," the risk of either variety contracting the complex would be greatly minimised and perhaps obviated altogether in really good seed-growing areas. In less suitable areas in which there may be an appreciable aphid population on the move, it will probably be advisable to restrict the planting to not more than three carefully selected varieties, of which one could be chosen from group I to act as a break between the other two varieties.

(d) *Destruction of Tops.*—In good seed-growing areas the aphid infestation may occur so late in the season that little transmission of viruses is possible before the foliage matures. As a precaution, though, against a somewhat earlier aphid attack than usual it may be advisable to destroy the foliage, and hence the aphides, by spraying with sulphuric acid. This destruction of the foliage not only prevents further movement of the virus to the tubers, but has the additional advantage of protecting the tubers against the effects of a late attack of Blight.

THE PROBLEM FOR THE WARE GROWER.—The essential difference in the conditions obtaining in the ware-growing districts from those found in the seed-growing areas is the prevalence of aphid vectors in the former and the difficulty of controlling them.

(a) *Precautions in the "Chitting" House.*—Sprouting tubers are very liable to become infested with aphides, which in this way may cause a very serious spread of virus disease in the stocks. Tubers should be stored under clean, well-ventilated conditions and should be dusted with nicotine sulphate, applied by means of hand-bellows, as a further precaution against aphid infestation of the developing sprouts.

(b) *Precautions at Planting Time.*—In the field the first precaution of great importance is to avoid planting on land not thoroughly cleared of "groundkeepers" or "volunteer" tubers persisting in the soil from a previous crop; such plants will probably be of a different variety from the new crop as well as possibly acting as nuclei for the spread of virus diseases, and so render nugatory all other precautions which may be taken. When a change of seed is found to be necessary, by far the best plan is to use nothing but new seed or, if this is impossible, the new seed should be isolated as far as is practicable to minimise the risk of infective aphides reaching the crop. Under conditions where aphides are usually numerous, it is unlikely that efficient isolation can be obtained stocks, whether or no the intervening distance is planted with "field immune" varieties; the additional precaution should therefore be taken of closely surrounding the crop to be protected by a tall crop such as oats; mangolds and swedes are colonised by *Myzus persicæ*, and are therefore not suitable. If the acreage to be planted with new seed is too large for efficient protection the grower should plant a plot, sufficient to supply his needs for seed in the following year, under the conditions of isolation suggested.

(c) *Precautions during Growing Season.*—Roguing for purity (page 91) and to prevent the spread of disease should be a matter of routine on all potato crops, and this is not less true of spraying or dusting to prevent loss from Blight (page 343 *et seq.*). Very occasionally this last operation involves risk of serious foliage damage by copper poisoning when carried out on plants covered with punctures during an exceptionally heavy aphid or other insect infestation. The prolongation of plant growth as a result of spraying may also prolong the period of aphid infestation, and hence increase the risk of late virus infection of some of the tubers. This is of no importance unless seed is to be saved from the crop, but even in this case the increasing use made by ware growers of acid-spraying to prevent tuber infection with Blight will afford equal protection against virus infection. Alternatively, the crop destined for seed should be lifted not later than the end of July in southern areas, and allowed to " green " on the surface of the soil before storage.

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APPENDIX I

FUNGICIDES

I. FOLIAGE TREATMENT AGAINST BLIGHT

(*a*) Foliage Protection

Bordeaux Mixture.—Ingredients for 40 gallons.

4 lb. copper sulphate (bluestone).
5 lb. fresh hydrated lime.
40 gallons water.

(i) The first step is to make up a solution of the bluestone, which should be of 98 per cent. purity and in powder or granular form. To do this, suspend a fine sack containing 4 lb. of the bluestone over a *wooden* barrel containing 35 gallons of clean water, so that the sack is just below the surface. If allowed to stand overnight all the bluestone will have dissolved, and after thorough stirring the solution will be ready for use the following morning. Alternatively, the bluestone can be dissolved quickly in a known small quantity of hot water and made up to 35 gallons with cold water.

(ii) Add 5 lb. of commercial hydrated lime (freshly purchased in paper bags) to 5 gallons of clean water in a bucket, and stir well.

(iii) Pour the solution of hydrated lime through a gauze or muslin strainer into the bluestone solution, which is kept stirred to ensure thorough mixing.

(iv) Free copper in the mixture may cause severe scorching of the potato foliage, so before use the solution should be tested by either dipping a piece of blue litmus paper into it or by holding the blade of a pocket-knife or a clean bright wire nail into the solution for a few minutes. If the litmus paper turns pink or the metal is tarnished the presence of free copper is indicated and should be corrected by the addition of more hydrated lime.

So long as the solutions are not mixed they will keep indefinitely, but once mixed, the mixture tends to form precipitates on standing and should be used within twenty-four hours or its efficiency rapidly deteriorates. From 100 to 120 gallons of spray are required per acre, so that hogsheads of 54 gallons capacity will provide convenient receptacles. Alternatively, a stock solution of copper sulphate can be prepared in a wooden barrel by dissolving 2 lb. of copper sulphate for every gallon of water used. When required, draw off 2 gallons of the solution into a hogshead containing 33 gallons of water, then proceed to add the hydrated lime solution as indicated above.

Burgundy Mixture.—Ingredients for 40 gallons.
4 lb. copper sulphate (bluestone).
5 lb. commercial washing soda.
40 gallons water.

The method of preparation is similar to that of Bordeaux Mixture. The two sprays are equally efficient in most areas, but in industrial districts where the atmosphere may be contaminated with acid gases there is less risk of scorching the foliage if Bordeaux Mixture is used.

Proprietary Copper Sprays.—Many efficient substitutes for home-made Bordeaux or Burgundy Mixtures are now obtainable; they usually have the advantage of requiring only the addition of water to a powder immediately before use.

Dry Dusts.—For convenience, and particularly when access to water is difficult, dry dusts may be used in place of wet sprays. These dusts contain some compound of copper such as the carbonate and should be purchased ready-made. They are less persistent and therefore less effective than wet sprays, whilst the cheaper rate of application is more than offset by the fact that at least four and often more applications are required. It should be remembered that it is not so much the amount of powder applied per acre but the amount of copper which determines the effectiveness of the treatment; a guarantee should therefore be obtained that the powder contains not less than 15 per cent. (and preferably 20 per cent.) of metallic copper, none of which should be in the "free" form capable of injuring the foliage. Further, the efficacy of the treatment depends upon the leaves receiving a complete coating of the powder on both surfaces. This, in turn, depends on the fineness of division of the particles of dust, so that a guarantee is required that at least 85 per cent. of the powder will pass through a 100-mesh sieve. Finally, the dusting should be carried out in the early morning whilst the leaves are still covered with dew; the powder should be delivered upwards with nozzles producing an almost impalpable floating dust. The rate of application should vary from about 10 lb. of powder per acre for the first application up to double that amount for the later treatments (*cf.* further details under "Blight," page 334).

(*b*) Foliage Destruction

This can be accomplished by the use of corrosive liquids such as copper sulphate or sulphuric acid; a mixture of copper sulphate (3 per cent.) and common salt (1 per cent.) is now frequently used, while tar distillate wash is also used on a limited scale at present; other substances have been tried, *e.g.* sodium chlorate and di-nitro-ortho-cresol, but their use has not yet progressed beyond the experimental stage.

Copper sulphate of 1·5 per cent. strength (6 lb. dissolved in 40 gallons of water) or 2 per cent. (8 lb. per 40 gallons water), applied with an ordinary spraying machine, will destroy the leaves, and hence the Blight fungus. The green haulms, however, are scarcely affected and continue to supply nutriment to the tubers, the yield of which is therefore not so greatly reduced as would be the case by total destruction of the tops. Sometimes new foliage develops which may have to be resprayed with copper sulphate or even with acid.

Sulphuric acid (oil of vitrol) of 10 per cent. strength (4 gallons of commercial concentrated oil of vitriol in 40 gallons of water) completely destroys all the tops. It must be applied from a spraying machine fitted with a glass or lead-lined container at the rate of from 100 to 120 gallons per acre. The *acid* should be added slowly to the *water* and the spray directed downwards on to the foliage from a coarse nozzle. Gloves to protect the hands and goggles for the eyes should be worn throughout the operation, and afterwards the container and nozzles should be washed out with water to which has been added a little washing soda. Finally, the sprayer should be rinsed with clean water. Sometimes the acid is applied without dilution with water and is then atomised through a very fine nozzle to produce the finest of misty clouds. This requires only about one-tenth the amount of liquid, and of course dispenses with the labour of carrying water.

Although acid spraying can be carried out by the farmer, there are advantages in arranging for the work to be done by a specialist firm on contract.

The mixture of copper sulphate and common salt and the tar distillate wash are applied with the ordinary sprayer and so far have given satisfactory results, although the foliage is not killed so rapidly as with sulphuric acid. The tar distillate wash has an advantage in that it is less wearing on the machines than copper sulphate.

Lifting should be delayed for at least a week, and preferably a fortnight, after the destruction of the tops. This ensures that most disease spores in the soil will be dead and that there will be little danger of tubers becoming infected at lifting time (*cf.* further details under "Blight," page 334).

II. SEED-TUBER DISINFECTION AGAINST DISEASE

Although much effort has been expended by many workers since the pioneer investigations of Bolley (1891) and Arthur (1897), we have yet to find the ideal method of treatment against seed-tuber borne diseases. Of the first substances tried, formaldehyde is volatile and its effects are therefore not persistent, whilst mercuric chloride, although persistent, is very poisonous to human beings and livestock. The time required for treatment also had to be reckoned in hours until the expedient of maintaining the liquid at 48° C. to 50° C. (118° F. to 122° F.) was tried, and the time was further reduced by the addition to the mercuric chloride of sufficient concentrated hydrochloric acid to make the acidulated liquid 0·1 per cent. in strength (*i.e.* one part of acid by volume to 1000 parts of the mercuric chloride solution). Various other substances have been tested, and in particular other inorganic salts of mercury, but there has been little or no advance made until the discovery in recent years of the efficacy of organic mercurial compounds. Those in common use to-day are proprietary substances which are practically instantaneous in effect and persistent, but are poisonous to human beings and animals. Although most of the tests have been carried out with a view to controlling Common Scab or Black Scurf, it is probable that successful treatment against the latter would be equally efficient in controlling other tuber-borne diseases. The time at which the tubers are treated is of great importance. Whereever practicable this should be done at lifting time, the chief difficulty being that this involves the immediate grading of the crop to separate out the seed. The efficiency of treatment diminishes with increasing delay after lifting, and the operation

TABLE XXXII

Treatments for Seed-Tuber Borne Diseases.

Substance.	Strength.	Duration.	Controls.
Formaldehyde. Cold	1 in 240	1½-2 hrs.	Common Scab (Chap. XXIV)
,, ,,	1 ,, 240	8 hrs.	Black Scurf (Chap. XXI)
,, ,,	1 ,, 100	¼-½ min.	Dry-Rot (Chap. XXII) and probably other tuber-borne diseases
,, Hot (48° C.-50° C.)	1 ,, 240	5 mins.	Common Scab
Formaldehyde. Hot	1 ,, 240	10 mins.	Black Scurf but reduces sprouting
Mercuric Chloride (Corrosive Sublimate). Cold	1 ,, 1000	1½-2 hrs.	Common Scab and kills most sclerotia of Black Scurf; Blight (Chap. XXIII) and Skin Spot (Chap. XXII)
,, ,, ,, ,,	1 ,, 500	2 hrs.	Black Scurf
,, ,, ,, ,,	1 ,, 1000	5 mins.	Common Scab
Hot. (48° C.-50° C.)	1 ,, 500	5 mins.	Silver Scurf (Chap. XXII)
,, ,, ,, ,,	1 ,, 1000	10 mins.	Common Scab and Black Scurf
Acidulated Mercuric Chloride. Cold (0·1 per cent. acid)	1 ,, 3000	2 hrs.	Common Scab and Black Scurf
,, ,, ,, ,,	1 ,, 10,000	16 hrs. (overnight)	,, ,, ,, ,,
,, ,, ,, ,,	1 ,, 1000	5 mins.	Black Scurf
Proprietary Organic Mercurials	1 ,, 1000 (or as directed)	½-1 min.	Common Scab, Black Scurf, Blight, Dry-Rot and Skin Spot

should in no case be delayed for more than two months. The above table has been compiled for the assistance of growers from those claims by research workers which appear to have been substantially proved. It should be remembered, however, that the use of proprietary substances involves some risk of essential ingredients being changed without notice, unless care is taken to purchase only from firms of established repute, whose products have been approved under an official scheme of the Ministry of Agriculture and the Department of Agriculture for Scotland (1943). The procedure in treating tubers is simple and only requires the provision of a suitable container for the liquid in which boxes of seed-tubers can be immersed; a draining board from which the excess liquid can drain back into the container is an economy, whilst the whole operation should be carried out in a place inaccessible to children or animals. Dipping tanks should be of wood, iron or concrete. If there is no preliminary washing of the soil-encrusted tubers a disagreeable sludge soon accumulates which must be removed, and the solution replenished, to avoid loss in activity (Foister and Wilson, 1943). It must be admitted, however, that the many practical difficulties involved in the manipulation of "liquid-dips" for large quantities of tubers have prevented their use on any but a small scale; it is possible that the widespread adoption of seed-tuber treatment will have to wait upon the discovery of an efficient non-poisonous dust, containing a volatile fungicidal ingredient.

APPENDIX II

DESCRIPTIVE NOTES OF SOME COMMON COMMERCIAL VARIETIES

THE following descriptions of varieties and sprouts have been compiled from observations made during many seasons and should prove valuable to those engaged in the potato industry.

In studying these descriptions the reader should note: (1) where parts are described as coloured, green is excluded; (2) it has been found impossible to describe all colour tones appearing on varieties and sprouts, and therefore some of the terms used are conventionalised; (3) faint colouring of the foliage parts sometimes does not appear; (4) branching, except when occurring freely, may also not appear on every plant; (5) the bud is described at an early stage and not when about to open; (6) the even and uneven junctions of the leaflet lobes have reference only to the pair of lateral leaflets next the terminal leaflet; where no specific mention is made of this character it may be assumed that both types of lobes appear in approximately equal numbers in the varieties concerned; (7) when leaflets are described as folded, the two sides bend above the mid-veins; (8) the general position of the eyes refers to the apical eye and its cluster; (9) all characters are described for plants in the height of their vigour; in youth, as in age, a number of these vary; (10) the omission of a character from a description indicates that the character has little diagnostic value for that variety; and (11) the notes on diseases in stocks have reference to Scottish conditions.

The behaviour of the varieties towards certain viruses is described. The writers are indebted to Dr G. Cockerham, Scottish Society for Research in Plant Breeding, Edinburgh, for the notes dealing with the reaction of varieties to the common viruses "A," "X" and "Y," and also for Table XXXIII at the end of the descriptions which, in addition to the above-mentioned viruses, sets out the reactions of varieties to viruses "B" and "C" and to the virus of Leaf Roll.

Except where otherwise stated, all varieties described are immune from Wart disease.

DESCRIPTIONS OF POTATO VARIETIES

ALLY (D. MACKELVIE)

MATURITY.—*Early Maincrop.*

TUBER.—Round to oval (flat); skin slightly lemon and somewhat rough; on exposure very faint red-purple develops at the eyes of most tubers, but some may remain green; eyes small, shallow, saucer-shaped, few, close together and generally on the shoulder; flesh white; sprouts pink.

FOLIAGE.—Haulm of medium height, upright but spreading slightly; stems green with little branching; wings straight; leaf rather open, broad, fairly short and slightly rigid; leaflets dark grey-green, hairy, with a thick appearance, long, broad, pointed and fairly flat; towards maturity the leaflets become rather glossy; secondary leaflets rounded and inconspicuous, generally none between terminal and last pair of laterals. Terminal often joined to laterals.

FLOWER.—White, not very frequent; anthers lemon and malformed; buds green with a pink tinge, inflorescence stalk often long.

REMARKS.—Cropping: good; cooking quality: rather poor; keeping quality: fairly good; bolters occur; second growth in the form of cracking often appears; slightly resistant to Blight; non-necrotic to viruses " A " and " X "; susceptible to virus " Y "; Mosaics common in stocks; fairly susceptible to Common Scab. This variety is only grown on a small scale now.

ARRAN BANNER (D. MACKELVIE)

MATURITY.—*Early Maincrop.*

TUBER.—Round (slightly flattened); heel often indented; skin white, turning green on exposure, and, at most, developing only very faint colour at the eyes and lenticels; eyes shallow, saucer-shaped, generally on the shoulder, medium to deep in large tubers; flesh white; sprouts pink.

FOLIAGE TYPE.—Great Scot.

FOLIAGE.—Haulm tall, vigorous and upright; stems strong, branching, slightly mottled purple, especially at nodes; wings slightly waved, particularly at top of stems; leaf large, open and slightly drooping; midrib slightly coloured at bases of leaflet stalks; midribs of young leaves coloured; leaflets medium green, dull, fairly large, broad, flat and wrinkled; secondary leaflets numerous and often borne on leaflet stalks which are long; terminal leaflet droops.

FLOWER.—White, infrequent; buds dark and rather pointed, hairs not adpressed; inflorescence and flower stalks short.

REMARKS.—Cropping: extremely good; cooking quality: fairly good; keeping quality: fairly good; non-necrotic to viruses " A " and " X "; virus " X " common in stocks; has some resistance to virus " Y "; severe Mosaics not very common in stocks; susceptible to Skin Spot and Skin Necrosis; very resistant to Dry Rot.

ARRAN BARD (D. MACKELVIE)

MATURITY.—*Early Maincrop.*

TUBER.—Oval ; skin white, netted ; on exposure, blue-purple develops at the eyes ; eyes shallow and on the point ; flesh white ; sprouts blue.

FOLIAGE.—Haulm of medium height, spreading ; stems coloured purple, especially at the base ; nodes green ; wings only slightly waved ; leaves large, fairly open with some colour on midribs and leaflet stalks ; leaflets medium to dark green, large and rather flat ; leaflet lobes uneven ; secondary leaflets small and not numerous.

FLOWER.—Blue-purple, tipped white, fairly frequent ; berries occur freely.

REMARKS.—Cropping : good ; cooking quality : good ; keeping quality : fairly good ; non-necrotic to viruses " A " and " X " ; mild Mosaics common in stocks ; susceptible to Leaf Roll, virus " Y " and Dry Rot. This variety does not seem to be establishing itself on the market.

ARRAN CAIRN (D. MACKELVIE)

MATURITY.—*Late Maincrop.*

TUBER.—Long oval ; skin white, remaining almost entirely green on exposure, although occasionally faint red-purple may develop ; eyes shallow ; flesh white or very slightly lemon ; sprouts pink.

FOLIAGE TYPE.—President.

FOLIAGE.—Haulm tall, vigorous and spreading ; stems coloured, strong and branching freely ; wings waved ; leaf markedly open and rigid ; midrib coloured at bases of leaflet stalks ; leaflets medium green, dull, slightly upwards folded and wrinkled ; secondaries small and not numerous, generally no secondaries between terminal and last pair of laterals.

FLOWER.—Dark red-purple with large white tips ; large and fairly numerous ; star slightly coloured ; anthers orange, often not forming symmetrical column ; buds dark and blunt ; inflorescence stalks long.

REMARKS.—Cropping : good ; cooking quality : fair ; keeping quality : fairly good ; necrotic to viruses " A," " B " and " C " ; non-necrotic to virus " X " ; susceptible to virus " Y " ; Leaf Roll common in stocks ; prone to second growth. Very few stocks of this variety are now grown.

ARRAN CHIEF (D. MACKELVIE). (NON-IMMUNE)

MATURITY.—*Early Maincrop.*

TUBER.—Round to short oval (slightly flattened) ; skin white, usually with a purple spot at the heel during the growing season ; on exposure, a little blue-purple usually develops at the eyes and sometimes also at the lenticels ; eyes medium, generally just on the shoulder, and deep in large tubers ; flesh white ; sprouts blue.

FOLIAGE TYPE.—Great Scot.

FOLIAGE.—Haulm upright and tall with rigid tops ; stem mottled purple, branching slightly at tops ; wing distinctly waved ; leaf moderately open and rather rigid ; leaflets medium to dark green, dull, broad, slightly upwards folded, with waved margins ; leaflet lobes even ; terminal leaflet not so drooping as in Great Scot; secondary leaflets fairly numerous and often on leaflet stalks.

FLOWER.—White, with green tips, infrequent; anthers malformed and pale; buds mainly pale green, blunt with short sepals; inflorescence and flower stalks short.

REMARKS.—Cropping: very good; cooking quality: floury, very good; keeping quality: very good; wildings and bolters occur; non-necrotic to viruses "A" and "X"; viruses "X" and "A" common in stocks; susceptible to virus "Y"; Mosaics common in stocks.

ARRAN COMRADE (D. MACKELVIE)

MATURITY.—*Second Early.*

TUBER.—Round (somewhat flat); skin very white; on exposure, a little blue-purple usually develops at the eyes, but some tubers may turn green only; eyes shallow, generally on the shoulder; flesh white; sprouts blue.

FOLIAGE.—Haulm of medium height, upright but spreading slightly, compact, with drooping tops, especially towards maturity; stems little branched, rather hairy and only faintly coloured; wings straight; leaf fairly open and drooping; leaflets medium to dark green, slightly upwards folded; top leaflets dull and soft; secondary leaflets fairly numerous, rather narrow, pointed, and sometimes on leaflet stalks.

FLOWER.—White, occurring freely; inflorescence stalk long; anthers orange; buds green, tinged light brown, hairy and blunt; in the early stages the white tip of the bud is prominent.

REMARKS.—Cropping: moderate, high proportion of medium and small tubers; cooking quality: fair; keeping quality: fair; very susceptible to Blight; non-necrotic to viruses "A" and "X"; has some resistance to virus "Y"; Mosaics and Leaf Roll common in stocks; fairly susceptible to Spraing and Internal Rust Spot. The variety is now grown only on a small scale.

ARRAN CONSUL (D. MACKELVIE)

MATURITY.—*Early Maincrop.*

TUBER.—Oval (blunt); heel often indented; skin white, remaining almost entirely green on exposure, although very faint red-purple may develop at the eyes; eyes medium, deep in large tubers, and generally on the point; flesh white to very pale lemon; sprouts pink.

FOLIAGE TYPE.—Tall Duke of York.

FOLIAGE.—Haulm tall and open; stems branching freely and slightly coloured; wings straight; leaf markedly open and long; leaflets medium green, flat (except on top foliage), long and narrow, with long stalks; leaflet lobes even; secondary leaflets often numerous, small, often projecting upwards and frequently borne on leaflet stalks.

FLOWER.—White, infrequent; anthers yellow; buds dark, hairy, pointed and dropping readily; sepal tips fairly long; inflorescence and flower stalks short.

REMARKS.—Cropping: very good, high proportion of ware; cooking quality: fair; keeping quality: excellent; growth slow; fairly resistant to Blight; susceptible to Blackleg; non-necrotic to viruses "A" and "X"; very susceptible to virus "Y"; very susceptible to Leaf Roll, the effects of which are severe; susceptible also to Net-Necrosis; the variety also frequently suffers from Powdery Scab; bolters occur.

ARRAN CREST (D. MACKELVIE)

MATURITY.—*First Early.*

TUBER.—Round, heel generally indented; skin white, pale red-purple developing at and about the eyes on exposure; eyes medium to deep, eyebrows often raised; flesh white; sprouts pink.

FOLIAGE TYPE.—Low-growing Epicure.

FOLIAGE.—Haulm of low to medium height, spreading; stem slightly coloured, especially at base, hairy and branching slightly; wings mainly straight; leaf very open, long and rigid; leaflets medium to dark green, long, narrow, flat, pointed and glossy, with a slightly wrinkled surface, stalks long; secondaries pointed and not numerous.

FLOWER.—White, rare; buds small, coloured and dropping readily; inflorescence and flower stalks short.

REMARKS.—Cropping: fairly good; cooking quality: fair; keeping quality: fair; very susceptible to Common Scab; necrotic to viruses "A" and "X"; fairly susceptible to virus "Y." Severe Mosaic common in stocks. The variety is now grown only on a small scale.

ARRAN LUXURY (D. MACKELVIE)

MATURITY.—*Second Early.*

TUBER.—Long oval, thick; skin white; on exposure, red-purple develops about the eyes while the remaining surface may become mottled; eyes shallow, mainly on the point; flesh white; sprouts pink.

FOLIAGE TYPE.—May Queen.

FOLIAGE.—Haulm of medium height and spreading; stems branching; wings slightly waved; leaf open and fairly rigid; leaflets medium green, dull, with long stalks; terminal leaflet well clear of last pair of side leaflets; secondary leaflets seldom appear between terminal and last pair of leaflets.

FLOWER.—Absent; buds purple with green markings, hairs numerous and upstanding.

REMARKS.—Cropping: good; cooking quality: good; keeping quality: fair; necrotic to virus "B"; non-necrotic to virus "X"; virus "X" and Leaf Roll common in stocks. The variety is now grown only on a small scale.

ARRAN PEAK (D. MACKELVIE)

MATURITY.—*Early Maincrop.*

TUBER.—Oval, thick; skin slightly lemon and netted; heel sometimes tinged purple; on exposure, blue-purple develops rapidly at and about the eyes, while the remaining surface often becomes mottled; eyes shallow and often on the point; flesh white; sprouts blue.

FOLIAGE.—Haulm tall and slightly spreading; stems strong, mottled purple, branching slightly; wings green, broad and waved; leaf open, midrib slightly coloured at base and bases of leaflet stalks; leaflets medium green, dull and rather flat (except on top foliage); leaflet stalks long; secondary leaflets large, pointed, projecting upwards and often borne on leaflet stalks; secondary leaflets seldom appear between terminal and last pair of leaflets; sulphury tops common.

FLOWER.—White, large and profuse; backs of petals sometimes coloured; anthers orange; style thin; buds fairly dark, sepal tips reflexed, stamens occasionally protrude; inflorescence and flower stalks long and strong; berries occur.

REMARKS.—Cropping: very good; cooking quality: fairly good; keeping quality: very good; necrotic to virus "A"; non-necrotic to virus "X"; susceptible to virus "Y"; virus "X" common in stocks; appears very resistant to Dry Rot.

ARRAN PILOT (D. MACKELVIE)

MATURITY.—*First Early.*

TUBER.—Long oval, often tapering at both ends; skin white; on exposure, blue-purple develops fairly rapidly at and about the eyes, while the remaining surface may become mottled; eyes shallow and on the point; eyebrows long; flesh white; sprouts blue.

FOLIAGE TYPE.—May Queen.

FOLIAGE.—Haulm of low to medium height, spreading, and straggling towards maturity; stems fairly numerous, tinged purple and branching; wings slightly waved; leaf fairly short, open and moderately rigid; midrib slightly coloured at base and bases of leaflet stalks; leaflets dark green, slightly upwards folded, broad, with a thick appearance, and margins often waved; terminal often overlapped; leaflet lobes generally uneven; blotches on foliage are common; secondary leaflets few and small.

FLOWER.—Blue-purple, tipped white, small, infrequent and often concealed by foliage; style long; anthers orange; buds fairly dark, stigma and stamens often protrude; inflorescence and flower stalks short.

REMARKS.—Cropping: very good; cooking quality: fair; bolters and semi-bolters very common; rather resistant to Common Scab but fairly susceptible to Powdery Scab; susceptible to Dry Rot; non-necrotic to virus "X"; necrotic to viruses "A" and "B"; virus "X" common in stocks; susceptible to virus "Y," the effects of which are severe; Mosaics common in stocks.

ARRAN SIGNET (D. MACKELVIE)

MATURITY.—*Second Early.*

TUBER.—Long oval (flat); skin very white, sometimes tinged purple in parts; on exposure, blue-purple develops rapidly at and about the eyes, while the remaining surface becomes mottled; eyes very shallow and mainly on the point; flesh very white; sprouts blue.

FOLIAGE TYPE.—Rigid Duke of York.

FOLIAGE.—Haulm low, compact and spreading; stems fairly thick, mainly green, faintly coloured at tops, branching freely; wings broad and only slightly waved; leaf long, markedly open and rigid; midrib coloured at base and bases of leaflet stalks; leaflets light green, flat, long and pointed; mid vein of young leaflet coloured; leaflet lobes uneven; secondary leaflets not numerous, generally no secondaries between terminal and last pair of laterals.

FLOWER.—White and frequent; backs of petals often coloured, especially in bud stage; anthers yellow-orange; buds dark, hairy, blunt, sepal tips often reflexed; berries occur.

REMARKS.—Cropping: very good; cooking quality: fairly good; bolters and semi-bolters occur; susceptible to Blight; non-necrotic to viruses "A" and "X"; susceptible to virus "Y," the effects of which are severe; very susceptible to Leaf Roll; Mosaics common in stocks. This variety does not cut well for seed and is not being grown to any great extent now.

ARRAN VICTORY (D. MACKELVIE)

MATURITY.—*Late Maincrop.*

TUBER.—Round (somewhat flat) and irregular; skin purple; eyes medium to deep; eyebrows long; flesh white; sprouts blue.

FOLIAGE TYPE.—Kerr's Pink.

FOLIAGE.—Haulm upright and tall; stems mottled purple, branched at tops; wings slightly waved and usually coloured; leaf fairly open with purple midrib; leaflets medium to dark green, glossy, broad, pointed and rather flat; leaflet stalks coloured; terminal drooping; secondary leaflets frequent and pointed, and sometimes on leaflet stalks.

FLOWER.—Creamy white, not very numerous; anthers pale yellow, and often malformed; ovary-interior coloured; buds dark, hairy (hairs adpressed), pointed, with long sepal tips; inflorescence and flower stalks short.

REMARKS.—Cropping: good; cooking quality: excellent; keeping quality: very good; somewhat resistant to Blight; very resistant to Dry Rot; non-necrotic to viruses "A" and "X"; has some resistance to virus "Y" and Leaf Roll; virus "X" common in stocks. This variety is much more popular in Ireland than in Great Britain.

ARRAN VIKING (D. MACKELVIE)

MATURITY.—*Early Maincrop.*

TUBER.—Oval, heel end slightly indented; skin white; on exposure, the tuber greens quickly, developing a faint red-purple at the eyes and lenticels, a colour which may diffuse elsewhere, the eye centres may remain green; eyes medium, on shoulder; flesh white; sprouts pink; stolons rather long.

FOLIAGE TYPE.—Tall-growing Arran Pilot.

FOLIAGE.—Haulm tall, upright with characteristic crowded tops; stems thick, fairly numerous, branching freely, especially at tops, tinged purple particularly at bases, also coloured underground; nodes swollen, green; wings wide, waved; leaf of average length, close, fairly rigid, midrib pink at base and bases of leaflet stalks; leaflet light to medium green, matt, thick, wrinkled, terminal round, stalk often tinged pink; parts of young leaves and midribs of young leaves often pink; secondary leaflets rounded, inconspicuous, often hidden by the leaflets.

FLOWER.—Frequent, small red-purple, tipped lighter in colour; anthers orange; with age, the flower sometimes becomes almost polypetalous; inflorescence and flower stalks short, tinged brown, appearing to arise from a rosette of leaves; pedicels above cork ring short; buds frequent, dark, blunt; anthers and style protrude from the bud; floral parts not hairy and the hairs present are mainly adpressed.

REMARKS.—This variety, like Arran Pilot, develops blotches on the leaflets. Cropping: good; cooking quality: very good; keeping quality: good. Stocks almost invariably affected with virus "X." This latter feature and the long stolons are disappointing characters. The variety is not widely grown.

BALLYDOON (McGILL & SMITH LTD.)

MATURITY.—*Late First Early.*

TUBER.—Oval; skin white, turning green and developing only very faint red-purple at the eyes on exposure; eyes shallow, often on the point; flesh white; sprouts pink.

FOLIAGE TYPE.—British Queen.

FOLIAGE.—Haulm of medium height, spreading, but slightly more upright than British Queen; stems mainly green, slightly branching and hairy; wings fairly straight; leaf fairly open and rigid; leaflets medium to dark green, broad, glossy and slightly upwards folded; terminal often joined to lateral leaflets and not so round as in British Queen; secondary leaflets fairly numerous and rounded.

FLOWER.—White, large and profuse; anthers orange; buds lightly coloured, blunt with green tips; inflorescence and flower stalks long and mainly green; berries occur.

REMARKS.—Cropping: good; cooking quality: fairly good; keeping quality: fairly good; rather susceptible to Blight; non-necrotic to virus "X"; necrotic to viruses "A," "B" and "C"; stocks usually fairly free from Leaf Roll and Mosaics. The acreage under this variety is now receding.

BEN LOMOND (A. PATON)

MATURITY.—*Second Early.*

TUBER.—Oval; skin white; on exposure, purple develops about eyes; eyes shallow, mainly on the point; flesh white; sprout blue.

FOLIAGE TYPE.—Great Scot.

FOLIAGE.—Haulm of medium height and compact; stem tinged blue-purple at base and above nodes; wings fairly straight; leaf rather close; leaflets large, medium to dark green, glossy; leaflet lobes uneven; terminal leaflet droops; secondary leaflets conspicuous and rounded.

FLOWER.—White, frequent; buds dark.

REMARKS.—Cropping: fairly good, tubers often numerous and small; cooking quality: fair; keeping quality: fairly good; bolters occur; necrotic to virus "A"; non-necrotic to virus "X"; Leaf Roll and mild Mosaics common in stocks; rather susceptible to Dry Rot. The trade—and thus the acreage—in this variety is now small.

BRITISH QUEEN (A. FINDLAY). (NON-IMMUNE)

MATURITY.—*Second Early.*

TUBER.—Oval to oval (pointed); skin white; on exposure, pale red-purple develops at and about the eyes and the remaining surface may become mottled; eyes medium and generally on the point; eyes on sides of tuber have often long raised eyebrows; flesh white; sprouts pink.

FOLIAGE.—Haulm of medium height, vigorous and spreading; stems tinged brown, darker at bases, and branching freely; branches rigid; wings broad and slightly waved; leaf open and rigid; leaflets medium to dark green, glossy, broad, and slightly upwards folded; end pair does not overlap the terminal which is round and cordate at the base; secondary leaflets fairly numerous and rounded, but not very large.

FLOWER.—Creamy white, large and profuse; anthers yellow-orange; inflorescence stalks long and bronze coloured; buds dark and blunt.

REMARKS.—Cropping: good; cooking quality: floury, very good; keeping quality: fair; bolters occur; susceptible to Blight and Blackleg; necrotic to viruses "A," "B" and "C"; non-necrotic to virus "X"; virus "X" common in stocks; severe Mosaics uncommon; Leaf Roll common; rather susceptible to Internal Rust Spot and Common Scab.

Some Synonyms are: Maid of Auchterarder, McPherson's Early, Pioneer, Pioneer Queen and English Beauty.

CATRIONA (A. FINDLAY)

MATURITY.—*Second Early.*

TUBER.—Long oval (often flattened); skin slightly yellow, blue-purple at and about the eyes; colour in the cork; eyes very shallow and on the point; flesh soft, tinged lemon; sprouts blue.

FOLIAGE TYPE.—May Queen.

FOLIAGE.—Haulm of medium height, compact, spreading and vigorous; stems branching freely, coloured, especially at tops; wings waved; leaf fairly close and rigid; leaflets dark green, with waved margins, slightly upwards folded and broad, the last pair tending to curl round terminal; leaflet lobes generally even; secondary leaflets numerous.

FLOWER.—Light blue-purple, tipped white, fairly frequent; anthers yellow, not forming a symmetrical column; style long; buds dark, hairy and globular, stamens protruding; pedicel above cork ring short; inflorescence and flower stalks fairly short and coloured.

REMARKS.—Cropping: good; cooking quality: good; keeping quality: poor; bolters occur; very susceptible to Blight, Gangrene and Dry Rot; necrotic to virus "B"; non-necrotic to viruses "A" and

"X"; virus "A" almost invariably in stocks; has some resistance to virus "Y"; Mosaics common in stocks; fairly susceptible to Spraing and Internal Rust Spot. This variety is grown mainly for the garden trade.

CONFERENCE (POLLOCK)

MATURITY.—*Early Maincrop.*

TUBER.—Oval, sometimes irregular; skin white, on exposure, the tubers turn green and develop only very faint purple; flesh white; eyes shallow; sprouts pink. Greened tubers frequently show white dots under the skin.

FOLIAGE.—Medium height and spreading; stems fairly numerous, green, although a little colour may develop towards maturity, little branching; wings only slightly waved; leaf dark green, close, the last pair of laterals not overlapping the terminal; leaflet rather flat, fleshy with a rough appearance, lobes even; secondaries numerous and rather rounded.

FLOWER.—White; freely formed; anthers orange; style long; stigma bilobed; inflorescence stalks green, slightly tinged brown; buds usually coloured.

REMARKS.—A new variety about which little is known at present; cooking quality reported to be fairly good; keeps very well.

CRAIGS ALLIANCE (SCOTTISH SOCIETY FOR RESEARCH IN PLANT BREEDING)

MATURITY.—*First Early.*

TUBER.—Oval, slightly flat; skin white, on exposure, colouring red-purple at eyes and lenticels at rose end; flesh white; eyes shallow; sprouts pink.

FOLIAGE TYPE.—Craigs Defiance.

FOLIAGE.—Medium height, open; stems fairly numerous and slightly bronzed, sometimes assuming a zig-zag appearance; nodes green and swollen; wing small and straight; leaf long and open, drooping; mid-rib green; leaflet of average size, slightly upwards folded, glossy, lobes uneven, terminal rounded; secondary leaflets fairly numerous, small and pointed.

FLOWER.—Flower white and infrequent; buds usually drop.

REMARKS.—Cropping: good; cooking quality: good, better than Arran Pilot; necrotic to viruses "A" and "B"; non-necrotic to virus "X." This recently-introduced variety may prove to be a substitute for Arran Pilot; being new, its commercial characters have not yet been fully tested.

CRAIGS BOUNTY (S.S.R.P.B.)

MATURITY.—*Late Maincrop.*

TUBER.—Long oval to kidney, inclined to be flat; skin white and netted; on exposure, the tuber greens only slowly and, if any colour develops, it is a faint red-purple located at the rose end, eyes and lenticels;

eyes shallow, saucer-shaped, mainly on the point; sprouts pink; stolons very long.

FOLIAGE TYPE.—Robust Up-to-Date.

FOLIAGE.—Haulm of medium height, strong, bushy, providing a very good cover; stems green, sometimes coloured at leaf axils, branching profusely; nodes green, not swollen; wings thin and only slightly waved; leaf very long, broad, open, fairly rigid, midrib of young leaf may show some colour; leaflet large, somewhat blunt, light green, matt, wrinkled, thick, slightly upwards folded, usually with uneven lobes; terminal rounded and not overlapped; leaflet stalks have two parallel lightly-coloured lines; secondary leaflets not numerous, small, rounded.

FLOWER.—Fairly frequent, small, red-purple, tipped white; anthers yellow to orange and often irregular; style long; stigma sometimes brown; inflorescence stalk slender, tinged brown, often appearing to arise from a rosette of leaves, branches short; pedicels light green; buds dark, blunt, stigma often protrudes; hairs on inflorescence and flower stalks and on buds short and inconspicuous.

REMARKS.—Cropping: very good; cooking quality: only fair; keeping quality: good. Non-necrotic to viruses "X," "A" and "B," necrotic to virus "C." Resistant in the foliage to and probably immune from Blight strains "A" and "C." Owing to the long runners, green tubers often appear in the lifted crop. The variety is unlikely to become a popular one.

CRAIGS DEFIANCE (S.S.R.P.B.)

MATURITY.—*Early Maincrop*.

TUBER.—Oval to long oval, flat; skin white; on exposure, red-purple develops at and about the eyes, while the remaining surface becomes mottled; eyes shallow and mainly on the point; flesh white; sprouts pink.

FOLIAGE TYPE.—Great Scot.

FOLIAGE.—Haulm medium to tall; upright, spreading only slightly; stems branching freely, often zig-zag in form, mottled light reddish brown; nodes with less colour; wings slightly waved; leaf open, rather rigid, with some colour at the bases of petioles; leaflets medium to dark green, young leaflets dull, older leaflets rather glossy, pointed, margins often waved and slightly upwards folded; leaflet lobes generally uneven; secondaries usually small, broad and not numerous.

FLOWER.—Red-purple, tipped white, fairly numerous but lasting only for a short time; anthers orange; inflorescence stalk fairly long and slightly coloured, leafy bracts common; buds dark, blunt and not hairy, stamens often protrude, sepal tips rather long.

REMARKS.—Cropping: very good; cooking quality: good; keeping quality: only fair, the variety sprouts very rapidly in early spring; necrotic to viruses "A," "B," "C" and "X"; susceptible to virus "Y." During the war and post-war period this variety has done fairly well in the Mediterranean Area and it has, in consequence, some value for export purposes.

CRAIGS ROYAL (S.S.R.P.B.)

MATURITY.—*Second Early.*

TUBER.—Oval to long oval, slightly flat; parti-coloured pink, colour in the cork; white tubers often appear; eyes shallow; flesh white to pale lemon; sprouts pink.

FOLIAGE TYPE.—Craigs Defiance.

FOLIAGE.—Haulm of medium height and rather open; stems not numerous, green, with slight tinge of colour on internodes; nodes mainly green and slightly swollen; wings narrow and slightly waved; leaf medium to long, broad and fairly open, slightly rigid, midrib lightly coloured at bases of leaflet stalks; stipule-like growths slightly hairy on the upper surface; leaflet large, broad, slightly upwards folded, lobes unequal, terminal rounded, medium to dark green, glossy with a thin appearance; leaflet stalks fairly long and lightly coloured in the young leaves; secondary leaflets not numerous, medium in size and rounded, often borne on the leaflet stalks.

FLOWER.—Red-purple, tipped white, rarely observed; styles short; buds drop readily.

REMARKS.—Cropping: very good; cooking quality: very good; keeping quality: appears to be good. Necrotic to viruses "X" and "A." Susceptible to Blight. Although this variety is a second early, it bulks very early and may be used as a first early.

CRAIGS SNOW-WHITE (S.S.R.P.B.)

MATURITY.—*Maincrop.*

TUBER.—Oval to kidney, sometimes slightly indented at heel end; skin white; on exposure, a faint red-purple may develop about the eyes but some tubers may remain green; eyes shallow; flesh white; sprouts pink.

FOLIAGE.—Haulm of medium height, spreading, providing very good cover; stems green with faint brown internodes, branching mainly at the tops; stems coloured below ground; wings fairly large, rather straight but waved at the tops; nodes green and slightly swollen; leaf of average size, rather wide, rather close, terminal drooping, midrib green with slight colour at the base of leaflet stalks; sulphury tops common; stipule-like growths large; leaflet light green, matt, medium to large, margins slightly waved, mid-vein green; leaflet stalks light brown; terminal round, cordate and not overlapped; leaflet lobes generally uneven; secondary leaflets not numerous, small and rounded; usually no secondary leaflets occur between the terminal and first pair of laterals.

FLOWER.—White, frequent, large; occasionally a pink tinge may appear; anthers orange, anther column sometimes irregular; styles short; flower sometimes almost polypetalous; pedical above cork ring long and green; inflorescence stalk long and bronzed with adpressed hairs; buds brownish-green with green base.

REMARKS.—Cropping: very good; cooking quality: fair; keeping quality: appears to be good. Necrotic to viruses "X," "A," "B" and "C," but appears to be very susceptible to virus "Y." Resistant in the foliage to and probably immune from Blight strains "A," "C" and "D," not, however, resistant in the tuber. Susceptible to Dry Rot. The variety sometimes shows a few runners outside the drills. Its greatest weakness is its susceptibility to virus " Y," the effects of which are less serious than in most varieties. This susceptibility, however, will prevent the variety ever becoming a popular one.

DARGILL EARLY (GARDINER)

MATURITY.—*Second Early.*

TUBER.—Kidney (pear-shaped); skin pale yellow; on exposure, red-purple may develop at eyes; eyes shallow, mainly on the point, those on the sides having raised eyebrows; flesh yellow; sprouts pink.

FOLIAGE.—Haulm of medium height, spreading; stem tinged red-purple; wing wide, slightly waved; leaf open with a little colour at base and bases of leaflet stalks; leaflets dark green, crinkled, glossy, slightly folded, arched, more or less at right angles to the midrib and with waved margins; leaflet stalks long, often with secondaries; secondaries numerous and well developed.

FLOWER.—Light red-purple, tipped white, seldom formed; flower stalk short.

REMARKS.—Cropping: fair; cooking quality: good; stocks very frequently affected with Mosaic; bolters and wildings occur. The tall types found in this variety are usually the relatively healthy plants, the lower growing plants appearing to be invariably infected with virus " Y " to which the variety has some resistance; non-necrotic to virus " X "; necrotic to virus "A." Very little of this variety is now grown.

DI VERNON (A. FINDLAY)

MATURITY.—*First Early.*

TUBER.—Long oval; skin slightly yellow, mottled blue-purple at eyes and rose end; colour in the cork; eyes very shallow and on the point; flesh tinged lemon; sprouts blue.

FOLIAGE TYPE.—Dwarf Gladstone.

FOLIAGE.—Haulm low to medium in height, spreading; stem branching and mottled purple; wings waved and green; leaf open and drooping; leaflets dark green, glossy, thin, fairly narrow with waved margins; the last pair of leaflets tends to overlap the terminal; secondary leaflets small and numerous; towards maturity, the margins of the leaflets frequently curl upwards.

FLOWER.—Blue-purple, tipped white, not very numerous; anthers yellow-orange; buds very dark, blunt, with reflexed sepal tips; inflorescence stalks long and purple tinged; flower stalks rather short.

REMARKS.—Cropping: fair; cooking quality: very good; keeping quality: poor; susceptible to Dry Rot; resistant to Common Scab; bolters and semi-bolters occur; non-necrotic to virus " X "; necrotic to virus " A "; has some resistance to virus " Y "; virus infection is often shown more by foliage reduction than by mottling; Leaf Roll fairly common in stocks; foliage variations common. The variety is grown mainly for the garden trade.

DOON BOUNTY (McGILL & SMITH, LTD.)

MATURITY.—*Second Early.*

TUBER.—Oval ; skin white ; on exposure, red-purple may develop at and about the eyes ; eyes medium, mainly on the point ; flesh white ; sprouts pink.

FOLIAGE.—Haulm tall, with only a few thick stems ; stems strong, branching and slightly mottled reddish brown ; nodes green ; wings broad and waved ; leaf long and open ; leaflets medium green, fairly glossy, arched, slightly upwards folded and with a rough appearance ; leaflet lobes generally even ; leaflet stalks long ; secondaries not numerous and frequently none on midrib between terminal and last pair of leaflets.

FLOWER.—White, large and profuse ; backs of petals may be coloured ; anthers orange and often malformed ; buds dark ; berries occur ; pedicel above cork ring long ; flower stalk long, coloured and much branched.

REMARKS.—Cropping : very good. Necrotic to virus "A" ; non-necrotic to virus "X." Very little of this variety is now grown ; indeed, Doon Bounty never did establish a place for itself on the market.

DOON EARLY (McGILL & SMITH, LTD.)

MATURITY.—*First Early.*

TUBER.—Oval (blunt), rather square at heel, which is often slightly indented ; skin white, remaining green on exposure ; eyes medium to deep ; eyebrows often raised ; flesh white ; sprouts pink.

FOLIAGE TYPE.—Robust Witchhill.

FOLIAGE.—Haulm of medium height, spreading slightly ; stems strong, fairly hairy and mainly green with little branching ; wings straight ; leaf open and somewhat rigid ; leaflets light green, long, fairly broad and pointed, slightly upwards folded ; secondary leaflets not numerous.

FLOWER.—White, fairly numerous ; anthers orange ; styles short ; buds light green ; inflorescence stalks short ; berries occur occasionally.

REMARKS.—Cropping : very good ; cooking quality : rather poor ; earlier than Epicure ; tubers become very large and coarse if left to maturity ; necrotic to viruses "A" and "B" ; non-necrotic to virus "X." Somewhat resistant to Common Scab. The acreage under this variety has never been large and very little of it is now grown.

DOON EIRE (McGILL & SMITH, LTD.)

MATURITY.—*Maincrop.*

TUBER.—Oval to Kidney ; skin parti-coloured pink, coloured at rose end and eyes, colour in the cork ; eyes shallow ; flesh white ; sprouts pink.

FOLIAGE.—Haulm fairly strong, tall and upright with a slight spread ; stems green, with some colour at bases and tops ; wings broad and wavy ; leaves large, long and medium close, the top leaves often being sulphury ; leaflets light green, wrinkled and dull, the edges of top leaflets often bronzed ; leaflet stalks long, often carrying secondaries ; secondaries fairly numerous, large and inclined to be rounded.

FLOWER.—White, large, numerous ; anthers orange ; style long ;

inflorescence and flower stalks long and coloured ; buds coloured ; berries occur freely.

REMARKS.—The cropping and cooking characters of this variety are satisfactory. However, it is a poor keeper and is very susceptible to Blight and Virus diseases. Virus " X " is very common. The variety is now found mainly as a rogue.

DOON STAR (McGILL & SMITH, LTD.)

MATURITY.—*Early Maincrop.*

TUBER.—Oval, rather square at the heel which is often slightly indented ; skin white, blue-purple developing, particularly about the eyes, on exposure ; eyes shallow ; flesh slightly pale lemon ; sprouts blue.

FOLIAGE.—Haulm upright and tall ; stem branching and mottled purple ; wings straight ; leaf open and rigid ; midrib slightly coloured at base and bases of leaflet stalks ; leaflets medium to dark green, dull, smooth, narrow, rather flat and pointed, with light green mid vein ; leaflet lobes uneven ; secondary leaflets fairly numerous, small and rounded. Young growth often sulphury.

FLOWER.—White, not very numerous ; anthers orange ; buds dark and blunt ; inflorescence and flower stalks fairly short ; berries occur.

REMARKS.—Cropping : good ; cooking quality : good ; keeping quality : poor ; bolters and wildings occur ; susceptible to Dry Rot, Gangrene and Blight ; susceptible to Internal Rust Spot ; rather resistant to Common Scab ; non-necrotic to virus " X " ; necrotic to virus " A " ; susceptible to virus " Y " ; virus " X " common in stocks. Owing to its susceptibility to Dry Rot and Gangrene, particularly the former, this variety has rapidly lost its popularity.

DR McINTOSH (J. HARPER)

MATURITY.—*Early Maincrop.*

TUBER.—Long-oval to kidney, skin white ; on exposure, the tuber greens relatively rapidly and develops a faint red-purple colour at eyes and lenticels, the colour diffusing slightly over the remainder of the surface ; eyes shallow and mainly on the point ; flesh white ; sprouts pink.

FOLIAGE TYPE.—British Queen.

FOLIAGE.—Haulm of medium height, compact, spreading, providing excellent cover ; stems not thick, mainly green, branching, at tops ; wings wavy ; leaf long, close, somewhat rigid, midrib green ; leaflet thin, slightly upwards folded, medium green, glossy ; secondary leaflets numerous, small, rounded, not conspicuous, often there are no secondary leaflets on the midrib between the terminal and first pair of laterals.

FLOWER.—White, profuse ; anthers deep orange ; inflorescence and flower stalks long, slightly tinged brown ; buds frequent, dark, hairy, with hairs outstanding ; berries occur freely.

REMARKS.—Cropping : very good ; cooking quality : good, improving with keeping ; keeping quality : good. Necrotic to virus " A " but not to " X " and is thus subject to mild Mosaics. This variety is not subject to second growth in any form and cracked tubers do not appear. It appears to be unable to withstand drought well.

DUKE OF YORK (MIDLOTHIAN EARLY) (SIM). (NON-IMMUNE)

MATURITY.—*First Early.*

TUBER.—Long oval to pear-shaped, thick; skin yellow and rough; on exposure, pale red-purple develops at the eyes; eyes very shallow and on the point; flesh yellow; sprouts pink.

FOLIAGE.—Haulm of low to medium height, spreading and often straggling; stems with little colour, hairy and branching; wings straight but sometimes waved at tops; leaf long, open and drooping; leaflets light to medium green, dull, rather flat, thick, fairly narrow, long and rather blunt; secondary leaflets fairly numerous, rather small and round.

FLOWER.—White, seldom formed; anthers pale and malformed; buds lightly coloured with long green tips; inflorescence stalk generally short and appearing to arise in a leaf axil or a rosette of leaves; flower stalks short.

REMARKS.—Cropping: good; cooking quality: very good for an early; suceptible to Blight; bolters, semi-bolters and wildings occur; necrotic to viruses " A " and " C "; non-necrotic to virus " X "; viruses " B " and " X " common in stocks; susceptible to virus " Y "; Mosaics and Leaf Roll fairly common in stocks.

DUNBAR ARCHER (C. T. SPENCE)

MATURITY.—*Late Maincrop.*

TUBER.—Short-oval; skin white, often purple at heel end; on exposure, develops a faint blue-purple colour at eyebrows and lenticels but the eye centres usually remain green, the colour diffusing elsewhere; white dots develops a faint blue-purple colour at eyebrows and lenticels but the eye shaped and slightly on the shoulder; flesh white; sprouts blue; stolons tinged purple.

FOLIAGE TYPE.—Dunbar Standard.

FOLIAGE.—Haulm tall and upright; stems very strong and branching freely, purple at the base and leaf axils with a diffuse colour throughout; wings very wavy; leaf medium in size, fairly open, fairly rigid, midrib slightly coloured at bases of leaflet stalks and generally carrying two parallel lines of colour; stipule-like growths small; leaflet medium to dark green, somewhat matt, slightly upwards folded, lobes mainly even, terminal rounded, not overlapped, lateral leaflets fairly broad and pointed; petiole carries two parallel lines of colour; secondary leaflets fairly numerous, rounded, not large.

FLOWER.—White, fairly profuse; anthers orange; style long, not twisted as in Dunbar Standard; flower stalk short, tinged light brown, hairs outstanding, especially in young stalks, the stalk appears to arise from a rosette of leaves; buds dark; berries sometimes occur.

REMARKS.—Cropping: good; cooking quality: very good; keeping quality: good; necrotic to viruses " A " and " B "; susceptible to virus " Y " but has some resistance to Leaf Roll. The acreage planted under this variety is not large.

DUNBAR CAVALIER (C. T. SPENCE)

MATURITY.—*Early Maincrop.*

TUBER.—Oval ; skin white and rather rough ; eyes and neighbourhood pink ; colour in cork, generally rather diffuse ; eyes fairly shallow and often on the shoulder ; eyebrows on sides of tuber long ; flesh white ; sprouts pink.

FOLIAGE.—Haulm medium height to tall, upright, spreading slightly later ; stems lightly coloured, branching at tops ; wings mainly straight ; leaf open and rigid, often pointing upwards ; midribs of young leaves often coloured at bases of leaflet stalks ; leaflets dark grey-green, dull, small but rather broad and flat ; leaflet lobes generally uneven ; secondary leaflets fairly numerous, small and rounded.

FLOWER.—Red-purple, tipped white, profuse, star coloured ; pleasantly scented ; anthers orange ; style very thin and short ; buds dark and blunt ; abscission ring highly coloured.

REMARKS.—Cropping : fairly good ; cooking quality : good ; keeping quality : good ; non-necrotic to viruses " A " and " X " ; susceptible to virus " Y " ; Mosaics and Leaf Roll very common in stocks. This variety is now almost completely off the market but it is sometimes found as a rogue.

DUNBAR ROVER (C. T. SPENCE)

MATURITY.—*Second Early.*

TUBER.—Oval ; skin white ; on exposure, faint red-purple may develop at and about the eyes ; eyes fairly shallow ; flesh white ; sprouts pink.

FOLIAGE.—Haulm tall, vigorous and upright ; stems thick, strong, green, pink towards maturity and branching at tops ; wing straight, but slightly waved on top foliage ; leaf open and large ; leaflets medium to dark green, long, broad, rather flat and pointed ; leaflet lobes generally even ; leaflet stalks long ; secondary leaflets large and numerous, often borne on leaflet stalks.

FLOWER.—White, large and profuse ; anthers yellow-orange ; buds fairly dark ; sepal tips long.

REMARKS.—Cropping : good ; cooking quality : very good ; keeping quality : good ; not so susceptible to Blight as British Queen ; necrotic to viruses " A " and " C " ; non-necrotic to viruses " X " and " B "; virus " X " common in stocks ; susceptible to virus " Y."

DUNBAR STANDARD (C. T. SPENCE)

MATURITY.—*Late Maincrop.*

TUBER.—Long oval ; skin white, turns almost entirely green on exposure, only very faint red-purple may develop at the eyes ; eyes shallow ; flesh white ; sprouts pink.

FOLIAGE TYPE.—Kerr's Pink.

FOLIAGE.—Haulm very tall, upright, vigorous and rigid ; stems very strong, branching, branches upright, and slightly coloured ; wings broad and almost straight ; leaf rigid and fairly close ; leaflets very large, dark green, dull, slightly wrinkled, slightly upwards folded and ending in sharp points ; margins of young leaflets sometimes waved ; secondary leaflets large, but not always appearing between terminal and last pair of leaflets.

FLOWER.—White, not numerous ; anthers yellow to yellow-orange and not forming a symmetrical column ; style short and twisted ; buds green with pink tinge, sepal tips reflexed ; in the young stages the white tip of the bud is conspicuous ; inflorescence and flower stalks fairly short, with adpressed hairs.

REMARKS.—Cropping : very good ; cooking quality : very good ; keeping quality : good ; rather late ; necrotic to virus " A " ; non-necrotic to virus " X " ; has some resistance to virus " Y " ; effects of Leaf Roll severe ; susceptible to Dry Rot and Common Scab. The most serious fault is the late maturity.

ECLIPSE (SIR JOHN LLEWELYN) (HARRIS). (NON-IMMUNE)

MATURITY.—*Late First Early.*

TUBER.—Oval to oval (pointed), and slightly flattened ; heel often slightly indented ; skin white ; on exposure, pale or faint red-purple develops at and about the eyes ; greened tubers often show white dots under skin ; eyes shallow and generally on the point ; flesh very white ; sprouts pink.

FOLIAGE.—Haulm of medium height and somewhat spreading ; stems branching, pink in colour and solid before maturity ; nodes usually green ; wings slightly waved and not so darkly coloured as the stem ; leaf fairly open, rather rigid and short ; leaflets light to medium green, dull, fairly flat, small and rather broad ; the end pair of leaflets generally overlaps the terminal asymmetrically ; leaflet lobes usually uneven ; there is a pink tinge at the bases of the leaflet stalks and on the margins of the leaflets in the early stages of growth ; secondary leaflets not numerous, small and rounded.

FLOWER.—White, small and infrequent ; anthers pale yellow and often malformed ; buds hairy and dark pink ; the inflorescence stalk is fairly short and generally appears to arise at a leaf axil.

REMARKS.—Cropping : good ; cooking quality : poor ; keeping quality : fairly good ; bolters, semi-bolters and other variations occur frequently ; several types of wildings also appear ; necrotic to viruses " A " and " C " ; non-necrotic to virus " X " ; virus " X " common in stocks ; susceptible to virus " Y " ; mild Mosaics very common in stocks ; fairly susceptible to Common Scab.

EDZELL BLUE

MATURITY.—*Second Early.*

TUBER.—Round (somewhat flat), rather irregular ; heel often indented ; skin purple ; eyes medium to deep, eyebrows distinct ; flesh snow-white ; sprouts blue.

FOLIAGE TYPE.—Duke of York.

FOLIAGE.—Haulm of low to medium height and spreading ; stems with little branching, mottled purple with colour more pronounced at leaf axils ; wings straight ; leaf open, long and drooping ; midrib purple at base and bases of leaflet stalks ; leaflets grey-green, dull, rather flat, long and fairly narrow ; leaflet lobes generally uneven ; secondary leaflets fairly numerous.

FLOWER.—White, small, sometimes with a tinge of blue-purple, occurring fairly freely ; anthers yellow-orange ; buds dark and blunt ; ovary-interior purple ; pedicel above cork ring short ; inflorescence and flower stalks fairly short.

REMARKS.—Cropping : good ; cooking quality : very good ; keeping quality : poor ; bolters occur ; susceptible to Dry Rot ; resistant to Common Scab ; non-necrotic to virus " X " ; necrotic to viruses " A," " B " and " C " ; fairly resistant to virus " Y " ; mild Mosaics common in stocks. The variety is now grown only in gardens.

EPICURE (CLARK). (NON-IMMUNE)

MATURITY.—*First Early.*

TUBER.—Round (irregular), heel generally indented ; skin white, turning pink on exposure ; eyes mainly just on the shoulder, deep and usually with raised eyebrows ; flesh white ; sprouts pink.

FOLIAGE TYPE.—King Edward.

FOLIAGE.—Haulm upright, rather robust and tall for an early ; stems pink, not hairy, little branching ; wings broad, mainly green and slightly waved ; leaf fairly close ; leaflets dark green, glossy, long, rather narrow and slightly upwards folded ; the last pair of leaflets have waved margins and point forwards, overlapping the terminal, which droops ; secondary leaflets fairly numerous and often large.

FLOWER.—White, not frequent ; anthers generally malformed and pale yellow ; buds fairly dark and blunt with green tips ; sepal tips reflexed ; very few hairs on style.

REMARKS.—Cropping : excellent ; cooking quality : fair ; keeping quality : good for an early ; bolters and semi-bolters occur ; this variety is more resistant to frost than any other early ; very susceptible to Common and Powdery Scabs. Dry Rot uncommon ; necrotic to viruses " A " and " X " ; susceptible to virus " Y " ; Leaf Roll and Mosaics uncommon in stocks. Owing to its capacity to recover from frost damage, this variety has so far no rivals in the Scottish early areas.

GLADSTONE (MCGILL & SMITH LTD.)

MATURITY.—*Early Maincrop.*

TUBER.—Oval ; skin often rough, white with pink at eyes and neighbourhood ; colour in the cork and rather diffuse ; eyes shallow and often on the point ; flesh white ; sprouts pink.

FOLIAGE TYPE.—Tall Di Vernon.

FOLIAGE.—Haulm of medium height and upright ; stems lightly coloured, especially at bases of leaves, and branching slightly at tops ; wings straight and not broad ; leaf open and rather drooping ; leaflets dark green, glossy, rather small, with a thin appearance and slightly upwards folded ; leaflet margins often curl upwards ; young leaves are coloured at base of midrib and at bases of leaflet stalks ; terminal leaflet droops ; secondary leaflets small and numerous with margins curled upwards.

FLOWER.—White, large and profuse; anthers orange; buds dark and blunt with conspicuous white tip; inflorescence and flower stalks long and mainly green; berries occur, frequently stippled with white dots.

REMARKS.—Cropping: good; cooking quality: very good at the beginning of the season, falling off later; keeping quality: very good; bolters occur; tubers often hollow; necrotic to virus "A"; non-necrotic to virus "X"; susceptible to virus "Y"; Leaf Roll common; severe Mosaics uncommon; a non-infectious rolling in the basal leaves frequently appears in dry years and is stated to be due to boron deficiency.

Note.—Red Gladstone is a red tuber variant of Gladstone.

GOLDEN WONDER (BROWN)

MATURITY.—*Late Maincrop.*

TUBER.—Long oval to pear-shaped; skin russet; eyes shallow, frequently on the point and often with slightly raised eyebrows; flesh white to pale lemon; sprouts blue; scale leaves sometimes blue.

FOLIAGE.—Very upright, tall and vigorous; stems few and stout, branched at tops, mainly green but coloured at bases; wings broad and only slightly waved; leaf open and rather rigid; leaflets medium green, markedly wrinkled and slightly upwards folded; leaflet lobes generally even; secondary leaflets fairly numerous and blunt.

FLOWER.—Purple, distinctly white-tipped and freely formed; anthers yellow-orange; buds blunt, bases green.

REMARKS.—Cropping: fair; cooking quality: excellent; keeping quality: excellent; wildings occur; very resistant to Common Scab; tubers resistant to Blight; prone to slug attack; susceptible to Net-Necrosis and Internal Rust Spot; non-necrotic to viruses "A" and "X"; virus "A" invariably in stocks; susceptible to virus "Y"; Mosaics and Leaf Roll common in stocks, effects severe.

Note.—Langworthy is identical with Golden Wonder except that the tuber skin is white.

GREAT SCOT (MAIR)

MATURITY.—*Early Maincrop.*

TUBER.—Round (slightly flattened), heel generally indented; skin slightly lemon, but white at the eyes during growing season; faint pink may develop at eyes on exposure, but tubers may turn only green; eyes shallow to medium, saucer-shaped and generally on the shoulder of tuber; flesh white; sprouts pink.

FOLIAGE.—Haulm medium tall and upright; stems lightly coloured, especially at bases of leaves, darker at bottoms; wings straight; leaf fairly open, slightly drooping; terminal leaflet drooping; leaflets dark green, broad, glossy, with a thin appearance and slightly upwards folded; leaflet lobes generally even; secondary leaflets fairly numerous and rounded.

FLOWER.—White, infrequent; anthers pale yellow and generally malformed; buds small, dark and rather blunt; inflorescence and flower stalks short.

REMARKS.—Cropping: very good; cooking quality: fairly good; keeping quality: fairly good; bolters and wildings occur; rather susceptible to Blight and Blackleg; appears very resistant to Dry Rot; necrotic to virus "A"; non-necrotic to virus "X"; virus "X" fairly common in stocks; fairly susceptible to virus "Y"; obvious Mosaics rare; somewhat resistant to Leaf Roll.

HOME GUARD (HOWIE)

MATURITY.—*First Early.*

TUBER.—Oval; skin white; on exposure, faint colour may develop at the eyes; eyes shallow to medium, generally on shoulder; flesh white; sprout blue.

FOLIAGE TYPE.—Ballydoon.

FOLIAGE.—Haulm of medium height; stems numerous and green but may be coloured at bases towards maturity, little branching; nodes swollen; wings not pronounced and almost straight; little axillary growth; leaf open; leaflets dark green and glossy; leaflet stalks long; leaflet lobes uneven; terminal roundish; secondaries fairly numerous, heart-shaped and often cupped.

FLOWER.—White; seldom formed; buds infrequent and dropping readily.

REMARKS.—Cropping: good; cooking quality: good; keeping quality: fairly good, although sprouting very rapidly; necrotic to viruses "A" and "B"; non-necrotic to virus "X." Stated to be susceptible to lime-induced manganese deficiency. The acreage has increased much in recent years.

IMMUNE ASHLEAF

MATURITY.—*First Early.*

TUBER.—Pear-shaped; skin slightly lemon; on exposure, blue-purple develops rapidly at and about the eyes, the remaining surface becoming mottled; eyes on point of tuber shallow, those on sides, often with slightly raised eyebrows; flesh yellow; sprouts blue; scale leaves sometimes blue.

FOLIAGE TYPE.—Duke of York.

FOLIAGE.—Haulm of medium height, spreading; stems branching slightly and lightly coloured at maturity; wings straight and narrow; leaf open, markedly long, broad, and drooping; leaflets light green, long, fairly narrow, thin, pointed and slightly upwards folded; leaflet lobes generally even; slight colour at base of leaflet stalks and midribs in young growth; terminal leaflet is sometimes joined to a lateral leaflet or leaflets; secondary leaflets narrow, projecting upwards and often on leaflet stalks.

FLOWER.—Light blue-purple and large; anthers yellow-orange; buds dark and blunt; contracted cyme type of inflorescence.

REMARKS.—Cropping: fair; cooking quality: good; non-necrotic to viruses "A" and "X"; virus "A" almost invariably in stocks; susceptible to virus "Y"; Mosaics common in stocks, effects severe. Immune Ashleaf is synonymous with the German variety Juli. The acreage grown now is very small indeed.

INTERNATIONAL KIDNEY (R. FENN)

MATURITY.—*Early Maincrop.*

TUBER.—Long oval; skin pale yellow; on exposure, blue-purple develops rapidly at and about the eyes and the tuber surface becomes mottled; eyes shallow, eyebrows distinct; flesh white to lemon; sprouts blue.

FOLIAGE.—Medium height to tall, upright; stems dark and branching; wings straight and coloured; leaf fairly close; leaflets dark green, glossy, blunt, wrinkled with waved margins; secondaries large, round and numerous; terminals drooping, often joined to last pair of side leaflets.

FLOWER.—Small, white, not frequent; anthers pale yellow, malformed; stigma protruding; buds dark; inflorescence stalk generally short and appearing to arise in a rosette of leaves or at leaf axil.

REMARKS.—This variety is grown commercially on a large scale only in the Channel Islands. It is very susceptible to Blight but seems rather resistant to Leaf Roll and Mosaics. Necrotic to viruses "A" and "X"; resistant to virus "Y"; virus "C" almost invariably in stocks.

KERR'S PINK (HENRY)

MATURITY.—*Late Maincrop.*

TUBER.—Round (somewhat flat and often irregular), heel often indented; skin pink; eyes usually medium, but sometimes deep and generally on the shoulder; flesh white; sprouts pink.

FOLIAGE.—Haulm upright, vigorous and very tall; stems thick and strong, branched mainly at tops, and coloured; wings slightly waved and usually coloured; leaf rather large, rigid and fairly close; midrib coloured; leaflets dull, medium to dark green, large, broad, pointed and slightly upwards folded; leaflet lobes generally even; secondary leaflets fairly numerous, pointed, slightly projecting upwards and sometimes on leaflet stalks.

FLOWER.—White and freely formed; anthers yellow; buds dark and pointed; ovary-interior pink.

REMARKS.—Cropping: very good; cooking quality: floury, very good; keeping quality: good; several types of wildings occur; appears very susceptible to Skin Spot and Powdery Scab; necrotic to viruses "A" and "B"; non-necrotic to virus "X"; virus "X" almost invariably in stocks; has some resistance to virus "Y"; stocks very free from severe Mosaics.

KING EDWARD VII. (BUTLER). (NON-IMMUNE)

MATURITY.—*Early Maincrop.*

TUBER.—Oval to pear-shaped; skin white, splashed pink at eyes and neighbourhood; colour in the cork, coloured parts clearly defined; surface smooth; eyes shallow, generally just on the shoulder; flesh white; sprouts pink.

FOLIAGE.—Haulm erect and tall with crowded tops; stems branched and lightly coloured; wings straight and not broad; leaves fairly open and rather drooping; leaflets dark green, glossy, long, narrow and slightly upwards folded with waved margins; leaflet lobes generally uneven; young leaflets small, narrow and twisted forward, the last pair fitting round the terminal; terminal sometimes joined to lateral leaflets; secondary leaflets fairly numerous and small.

FLOWER.—Red-purple, small, and seldom formed; anthers pale yellow and malformed; buds pink and pointed; inflorescence and flower stalks short.

REMARKS.—Cropping: fairly good; cooking quality: good, retains its colour better than most varieties after boiling; keeping quality: very good; bolters, wildings and many variations occur; very susceptible to Blight; rather resistant to Common Scab; susceptible to Skin Spot which may result in "blind" tubers; necrotic to viruses "A" and "X"; susceptible to virus "Y"; Mosaics and Leaf Roll uncommon in stocks.

Note.—Red King is a variation of King Edward and has almost whole-coloured red tubers.

KING GEORGE V. (BUTLER)

MATURITY.—*Second Early.*

TUBER.—Oval to oval (pointed); skin white, although occasionally colour appears at the heel and rose ends; on exposure, pale red-purple develops at the eyes; eyes of medium depth and on the point; those on the sides of the tuber have raised eyebrows; flesh white; sprouts pink.

FOLIAGE TYPE.—British Queen.

FOLIAGE.—Haulm of medium height, spreading, not so rigid as British Queen; stems tinged red-purple and branching vigorously; wings broad and only slightly waved; leaf open and drooping; hairs on midrib less upright than in British Queen; leaflet medium green, soft, broad, slightly upwards folded and dull; the end pair does not overlap the terminal, which is round and cordate at the base; secondaries fairly numerous.

FLOWER.—White, numerous, but not so numerous as in British Queen; anthers often pale and malformed; inflorescence and flower stalks long and bronzed; buds dark.

REMARKS.—Cropping: good; cooking quality: poor; keeping quality: fair; non-necrotic to viruses "A" and "X"; susceptible to virus "Y"; virus "X" and Leaf Roll common in stocks. This variety is now grown only on a small scale.

MAJESTIC (A. FINDLAY)

MATURITY.—*Early Maincrop.*

TUBER.—Long oval to pear-shaped; skin white; on exposure, pale red-purple usually develops at the eyes but sometimes tubers show practically no colour; eyes shallow and on the point; flesh white; sprouts pink.

FOLIAGE TYPE.—British Queen.

FOLIAGE.—Haulm of medium height and spreading, less rigid and more open than that of British Queen; stems branching, especially at base, only lightly coloured; wings straight; leaf open and slightly drooping; mid-ribs of young leaves coloured; leaflets medium green, flat, pointed and rather narrow; stalk and lower part of mid vein of young leaflet coloured;

leaflet lobes generally uneven ; terminal long, fairly narrow and not cordate ; secondary leaflets fairly numerous, small and rounded.

FLOWER.—Creamy white, profuse ; anthers orange ; buds pink and blunt ; sepal tips fairly long ; inflorescence and flower stalks long ; berries occur.

REMARKS.—Cropping : excellent ; cooking quality : fair to good ; keeping quality : very good ; does not cut well for seed ; second growth in the form of cracking common ; bolters, wildings and other variants occur ; fairly susceptible to Blight, Dry-Rot and Common Scab ; non-necrotic to viruses " A " and " X " ; virus " X " common in stocks ; susceptible to virus " Y " ; Mosaics and Leaf Roll fairly common in stocks. An outstanding and consistent cropper.

MAY QUEEN (SADLER). (NON-IMMUNE)

MATURITY.—*First Early.*

TUBER.—Long oval (often irregular) ; skin white ; on exposure, faint blue-purple may develop at the eyes, but some tubers may remain green ; eyes shallow and on the point ; eyes on sides often with raised eyebrows ; flesh white and soft ; sprouts blue ; scale leaves sometimes faint blue.

FOLIAGE TYPE.—Dull, dark British Queen.

FOLIAGE.—Haulm of low to medium height, spreading and vigorous ; stems branching, especially at the base, slightly coloured ; wings waved ; leaf fairly open and long ; leaflets dark to medium green, fairly glossy, long, upwards folded and margins waved ; the last pair of leaflets curls over the terminal ; secondary leaflets show considerable variation.

FLOWER.—Light blue-purple, with large tips of white, occurring freely ; anthers orange ; flower parts irregular ; inflorescence and flower stalks long ; buds purple and globular ; few hairs on style.

REMARKS.—Cropping : good ; cooking quality : fair ; keeping quality : poor ; bolters and semi-bolters occur ; very susceptible to Blight and Dry-Rot ; necrotic to viruses " A " and " B " ; non-necrotic to virus " X " ; susceptible to virus " Y " ; Mosaics common in stocks. This tender variety requires very careful handling.

NINETYFOLD (CLARK). (NON-IMMUNE)

MATURITY.—*First Early.*

TUBER.—Oval (pointed) ; skin white ; on exposure, very faint red-purple may develop at the eyes ; eyes on point shallow, those on the sides often with long and raised eyebrows ; flesh very white and soft ; sprouts pink.

FOLIAGE TYPE.—Duke of York.

FOLIAGE.—Haulm of low to medium height, spreading ; stems hairy, slightly tinged pink towards maturity, branching ; wings almost straight ; leaf long, open and drooping ; leaflets light green, long, narrow, often flat and slightly wrinkled ; the last pair of leaflets overlaps the terminal asymmetrically ; yellow Aucuba (virus " G ") spotting in leaves common ; secondary leaflets fairly numerous and blunt, but not conspicuous.

FLOWER.—White, rarely formed ; anthers generally pale yellow and malformed ; buds fairly dark, sepal tips long and green ; inflorescence stalks generally appear to arise in a rosette of leaves or at a leaf axil.

REMARKS.—Cropping: good; cooking quality: poor; keeping quality: poor; very susceptible to Blight and Dry-Rot; necrotic to viruses "A" and "X"; susceptible to virus "Y"; stocks fairly free from virus diseases; Aucuba Mosaic (virus "G") throughout stocks. Bolters and semi-bolters uncommon. This tender variety requires very careful handling.

ORION (SMITH)

MATURITY.—*Early Maincrop.*

TUBER.—Short-oval; slightly indented at heel end; skin white; on exposure, blue-purple develops at the rose end, particularly at the eyes the centres of which do not become so dark, and the remaining tissue may become slightly coloured, more especially at the lenticels; eyes saucer-shaped, shallow to medium; flesh lemon; sprouts blue.

FOLIAGE TYPE.—Great Scot.

FOLIAGE.—Haulm upright and of medium height, providing good cover; stems green with bronze tinge, branching; wings green and waved; nodes green; axillary growth plentiful; leaf average in size and width, rather close, drooping slightly, midrib slightly coloured only in young leaves; stipule-like growths small; leaflet of average size, terminal rounded, lateral leaflets not very broad and tapering markedly towards the tip, slightly upwards folded, lobes mainly uneven, medium to dark green in colour, glossy; leaflet stalks and mid-veins green; secondary leaflets frequent, fairly narrow and pointed; secondary leaflets may appear on the leaflet stalks.

FLOWER.—Frequent, white, backs of petals tinged purple in early stages; anthers yellow to orange; with age, the flower becomes almost polypetalous; inflorescence and flower stalks average in length and slightly bronzed; buds frequent, brownish, hairs outstanding.

REMARKS.—Cropping: very good; cooking quality: good; keeping quality: good. Necrotic to virus "B." Resistant to and probably immune from Blight strains "A," "C" and "D" in the foliage and fairly resistant in the tuber. In certain seasons, slight gemmation may occur; infection tests suggest that this variety is susceptible to Dry Rot. Orion was the first real Blight-resistant variety to be marketed in Britain. Mild Mosaics are now common in stocks. The acreage is not extending.

PENTLAND ACE (SCOTTISH SOCIETY FOR RESEARCH IN PLANT BREEDING).

MATURITY.—*Second Early.*

TUBER.—Long oval; skin white, developing pink coloration on exposure; flesh pale lemon; eyes shallow to medium; sprouts pink.

FOLIAGE TYPE.—Bushy Craigs Defiance.

FOLIAGE.—Haulm of medium height, upright; stems thin, round, mottled bronze, branched, straggling towards maturity; wings small, straight or occasionally waved at top; leaf small, midrib tinged brown at bases of leaflet stalks; leaflets small to average size, rounded, thick, dark green, slightly glossy, slightly rough; secondary leaflets small and not numerous.

FLOWER.—Pink, small, infrequent; buds small, tinged pink, slightly hairy; inflorescence stalks green, inconspicuous.

REMARKS.—Cropping: good; cooking quality: good; necrotic to viruses "X," "A" and "B" and field-immune from Blight strains "A," "B" and "C."

PURITAN. (NON-IMMUNE)

MATURITY.—*First Early.*

TUBER.—Oval (pointed); skin white; on exposure, very faint red-purple may develop at the eyes; eyes medium and generally on the point; eyes on sides often with long and raised eyebrows; flesh very white and soft; sprouts pink.

FOLIAGE TYPE.—Duke of York.

FOLIAGE.—Haulm of low to medium height, spreading; stems branching and slightly tinged pink towards maturity; wings slightly waved; leaf open, long and semi-rigid; midrib slightly coloured at bases of leaflet stalks; leaflets light green, fairly glossy, long, fairly narrow, rather flat, margins sometimes curl upwards at maturity; the last pair of leaflets overlaps the terminal, generally asymmetrically; secondaries very small and not numerous.

FLOWER.—White, fairly frequent; anthers yellow-orange; buds dark at bases with fairly long, green sepal tips.

REMARKS.—Cropping: fairly good; cooking quality: fair; keeping quality: poor; very susceptible to Blight and Dry-Rot; non-necrotic to viruses "A" and "X"; susceptible to virus "Y"; virus "X" common in stocks. This tender variety requires very careful handling.

RECORD

MATURITY.—*Maincrop.*

TUBER.—Round to oblong, slightly flat; skin white with a yellow tinge, a faint blue-purple flush may be found at the rose end and usually at the heel end; on exposure, a blue-purple colour develops at the rose end, eyes and lenticels, and may diffuse elsewhere; eyes shallow to medium; flesh yellow; sprouts blue.

FOLIAGE TYPE.—Up-to-Date.

FOLIAGE.—Haulm of medium height, compact and spreading; stems strong, branching, mottled pink at base and at leaf axils; nodes green; wing broad, waved; leaf long, fairly close, arched, midrib tinged pink; leaflet of average size, light to medium green, slightly rounded, waxy, the younger leaflets are slightly wrinkled, terminal leaflet drooping; secondary leaflets fairly numerous, of average size, pointed, leaflets often on leaflet stalks and some are directed towards the leaf base.

FLOWER.—White; anthers orange; inflorescence stalk bronzed at top; buds pink, frequent.

REMARKS.—Cropping: very good; cooking quality: good; keeping quality: reputed to be good. This Dutch variety has not been tested to determine its reaction to viruses but, as mosaics occur in stocks, it is evidently non-necrotic to virus "X." At present, the variety is grown mainly for the crisp trade.

REDSKIN (W. B. POLLOCK)

MATURITY.—*Early Maincrop.*

TUBER.—Round, heel often indented ; skin pink ; eyes fairly shallow and generally on the shoulder , flesh pale lemon ; sprouts pink.

FOLIAGE.—Haulm upright and tall ; stems fairly strong and coloured without much branching ; wings broad and slightly waved ; leaf open and fairly rigid ; midrib coloured at base and bases of leaflet stalks ; leaflets medium green, dull, broad and flat (except on the top foliage) ; mid veins of young leaflets coloured at bases ; young leaflets may also be coloured at bases ; secondary leaflets sometimes large but not very numerous.

FLOWER.—White, frequent ; anthers orange ; buds dark ; ovary-interior pink ; inflorescence and flower stalks long ; berries may occur.

REMARKS.—Cropping : good ; cooking quality : good ; keeping quality : good ; necrotic to virus " A " ; non-necrotic to virus " X " ; virus " X " ; common in stocks ; susceptible to virus " Y " ; rather susceptible to Common and Powdery Scabs.

ROYAL KIDNEY (A. FINDLAY). (QUEEN MARY.) (NON-IMMUNE)

MATURITY.—*Second Early.*

TUBER.—Long oval to pear-shaped (somewhat flat) ; skin white ; on exposure, red-purple develops rapidly at and about the eyes, while the remaining surface becomes mottled ; eyes shallow, often on the point ; flesh white ; sprouts pink.

FOLIAGE TYPE.—King Edward.

FOLIAGE.—Haulm of medium height to tall, upright and spreading later ; stems not robust and generally not branched, sometimes lightly coloured at base and bases of leaves ; wing slightly waved ; leaf fairly open and rather drooping ; midribs of leaves coloured at base and bases of leaflet stalks in the young stages ; leaflets medium green, broad, slightly upwards folded, with a soft appearance ; top foliage dull and drooping ; secondary leaflets not numerous and often projecting upwards.

FLOWER.—Absent, stalks short ; buds green at base, dropping readily.

REMARKS.—Cropping : moderate ; cooking quality : fair ; keeping quality : good ; susceptible to Blight ; appears rather resistant to Common Scab ; non-necrotic to viruses " A " and " X " ; viruses " X " and " B " common in stocks ; mild Mosaics common ; severe Mosaics uncommon. This variety has done well in the Mediterranean area and in Teneriffe and is, thus, used mainly for export.

SHARPE'S EXPRESS (NON-IMMUNE)

MATURITY.—*Late First Early.*

TUBER.—Pear-shaped, sometimes curved ; skin white ; on exposure, pale red-purple develops at the eyes ; greened tubers often show white dots under skin ; eyes on the point shallow, those on the sides having sometimes raised eyebrows ; flesh slightly lemon ; sprouts pink.

FOLIAGE.—Haulm upright to spreading and of medium height, with dense apical foliage ; stems often tinged pink and generally unbranched ; wing slightly waved ; leaf long and close ; leaflets medium to dark green, glossy, cordate, markedly upwards folded, slightly wrinkled and pointed ; the last pair of leaflets often curls round the terminal ; secondary leaflets very numerous, giving the leaf a crowded appearance, and folded upwards.

FLOWER.—Deep red-purple with small white tips not profuse ; anthers yellow ; buds lightly coloured ; inflorescence and flower stalks short.

REMARKS.—Cropping : fair ; cooking quality : good ; keeping quality : fairly good ; bolters, semi-bolters and wildings occur ; somewhat resistant to Blight for an early ; susceptible to Dry Rot ; necrotic to viruses " A," " B " and " C " ; non-necrotic to virus " X " ; virus " X " common in stocks ; susceptible to virus " Y."

STORMONT DAWN

MATURITY.—*Early Maincrop.*

TUBER.—Short-oval, skin white ; on exposure, a very faint colour may develop at the eyes and lenticels but often no colour is seen ; eyes shallow, mainly on the point ; flesh white, tinged pale lemon ; sprouts faint pink.

FOLIAGE.—Haulm medium to tall, giving good cover ; stems slightly tinged brown at internodes, darker at the base, branching vigorously at the tops ; nodes not swollen ; axillary growth marked ; wings broad, waved ; leaf open, rigid, midrib green ; leaflet broad, blunt, medium to light green, matt, with a thick appearance, slightly upwards folded, terminal rounded ; secondary leaflets not frequent, small and rounded ; midrib between terminal and first pair of laterals generally without secondary leaflets.

FLOWER.—White, frequent ; anthers orange ; style long ; inflorescence stalk long with short branches, generally appearing to arise in leaf axil or rosette of leaves, green, hairs adpressed ; buds frequent, green, not very hairy, hairs outstanding ; stigma and anthers protrude at an early stage.

REMARKS.—Cropping : very good ; cooking quality : stated to be good ; keeping quality : fairly good. Usually free from second growth symptoms. Slightly resistant to Blight. Resistant to Dry Rot. As this variety contracts Mild Mosaics in the field, it is evidently non-necrotic to virus " X." The acreage planted is now contracting.

SUTTON'S ABUNDANCE (CLARK)

MATURITY.—*Early Maincrop.*

TUBER.—Oval to round, somewhat flat ; skin white ; on exposure, blue-purple develops at and about the eyes ; eyes shallow and usually just on the shoulder ; eyebrows long and distinct. During the growing season the heel end shows a blue-purple coloration. Flesh white. Sprouts blue.

FOLIAGE TYPE.—Great Scot.

FOLIAGE.—Haulm tall, strong and upright ; stem branching and becoming purple tinted, particularly at leaf bases ; wing fairly broad and slightly waved; leaf close and slightly drooping; leaflets dark green, glossy, broad, rather flat and overlapping; leaflet lobes generally uneven; secondary leaflets numerous, round and well developed, giving the leaf a close appearance.

FLOWER.—White, large and numerous; stigma bilobed style long; anthers yellow orange; buds dark, sepal tips slightly reflexed; pedicel above cork ring long; inflorescence and flower stalks long.

REMARKS.—Cropping: good; cooking quality: floury, very good; keeping quality: good; susceptible to Blight; necrotic to virus "A"; non-necrotic to virus "X"; has some resistance to virus "Y"; stocks fairly free from obvious virus diseases. Abundance no longer holds an important place on the market.

THE ALNESS (SCOTTISH SOCIETY FOR RESEARCH IN PLANT BREEDING)

MATURITY.—*Second Early.*

TUBER.—Oval to round (rather thick); skin white; some faint colour may develop, but most tubers turn green only on exposure; eyes shallow; flesh white; sprouts pink.

FOLIAGE.—Haulm of medium height, spreading; stems hairy, slightly coloured, little branching; wings almost straight; leaf fairly close and somewhat rigid; leaflets medium green, large, broad and rather flat; the last pair of leaflets does not overlap the terminal; leaflet lobes generally uneven; secondary leaflets often small and inconspicuous; terminal leaflet rather long and not overlapped.

FLOWER.—White, fairly numerous; anthers orange; inflorescence and flower stalks strong; buds dark; berries occur.

REMARKS.—Cropping: good; cooking quality: good; rather susceptible to Blight; necrotic to virus "A"; non-necrotic to virus "X"; very susceptible to virus "Y"; Leaf Roll common in stocks. This variety never established a good position on the market.

ULSTER CHIEFTAIN (CLARKE)

MATURITY.—*First Early.*

TUBER.—Oval, very slightly indented at heel end; skin very white; on exposure, does not green rapidly and faint blue-purple develops only slowly at eyes, lenticels and sometimes elsewhere on the surface; eyes shallow to medium and on shoulder; flesh white; sprouts blue.

FOLIAGE TYPE.—Herald.

FOLIAGE.—Haulm low growing, not robust, rather compact but spreading later; stems not thick, hairy at base, purple at base and underground towards maturity; wings straight and narrow; leaf fairly large, open and drooping with green midrib; leaflets medium green, large, rather flat with slightly waved margins and with a thick appearance; terminal round; lobes generally uneven; secondary leaflets small.

FLOWER.—White, rare; inflorescence stalks generally inconspicuous.

REMARKS.—Cropping: very good; cooking quality: fair; very susceptible to Blight and Dry Rot; non-necrotic to virus "X"; necrotic to viruses " A " and " B " ; the foliage is not robust and does not always fill the drill, sometimes allowing weed growth ; the variety evidently requires fairly rich land.

ULSTER CROMLECH (CLARKE)

MATURITY.—*Early Maincrop.*

TUBER.—Short-oval to round, heel often indented ; skin white, purple at heel end ; on exposure, a blue-purple colour develops at eyes and neighbourhood and also at the lenticels, the colour diffusing slightly over the remainder of the tuber surface but the eye centres may remain green ; white dots can be observed under the skin of greened tubers ; eyes shallow, mainly on shoulder ; flesh white ; sprouts blue ; stolons long and slightly coloured.

FOLIAGE.—Haulm upright, tall, bushy, spreading ; stems thick, rather solid, branching vigorously, somewhat zig-zag in form, slightly stippled purple at leaf bases and upper internodes ; axillary growth frequent ; wings fairly broad and wavy ; leaf close, rather rigid, coloured at base ; leaflet large, medium to dark green, glossy, thick, flat except on apical leaves, terminal round ; secondary leaflets not numerous, often large and round.

FLOWER.—White, numerous, medium in size ; anthers yellow to orange ; style fairly long ; inflorescence stalk long, tinged slightly brown, hairs adpressed ; buds frequent, base green, remainder tinged brown, hairs adpressed.

REMARKS.—Cropping : very good ; cooking quality : stated to be very good ; keeping quality : fair ; very susceptible to Blight. This is a new Irish variety about the commercial and other characters of which not much is known. The reports from New Zealand are good.

ULSTER ENSIGN (CLARKE)

MATURITY.—*Second Early.*

TUBER.—Oval to kidney ; skin white, pink about rose end and eyes ; colour in the cork ; eyes shallow and apical ; flesh white ; sprouts pink.

FOLIAGE TYPE.—Gladstone.

FOLIAGE.—Haulm of medium height, open ; stems with little branching, slightly purple at the base, internodes slightly coloured especially near the leaf axils ; nodes mainly green ; wings waved slightly at the top but straight below ; leaf rather open, terminal drooping, midrib coloured at base ; stipule-like growths small ; leaflet dark green, glossy, of average size, lobes even, terminal rounded, margins slightly fluted ; secondary leaflets numerous and small, leaflets often found on the petioles.

FLOWER.—White, large, not freely formed ; anthers yellow to orange, sometimes twisted ; styles short ; flower stalks appearing to arise in a rosette of leaves ; cork ring coloured ; buds dark ; berries occur.

REMARKS.—This is a new Irish variety and not much is known about its commercial characters yet. It appears to be a good cropper, but is reputed to suffer badly from Blight if grown as a second early. It should be lifted early. Resistant to Dry Rot. The variety produces bolters very freely.

ULSTER PREMIER (CLARKE)

MATURITY.—*First Early.*

TUBER.—Long oval to kidney, not thick ; pink at the rose end and at eyes, colour in cork ; eyes at rose end shallow and almost on shoulder ; the remaining eyes may be medium deep ; green tubers often show white dots under the skin ; flesh white ; sprouts pink.

FOLIAGE.—Haulm low to medium in height, upright at first and spreading later ; foliage sparse ; stems not numerous, purple at extreme base but otherwise green ; bases of stems very hairy ; wings narrow and only very slightly waved ; leaf rather close, medium size, midrib green ; leaflets medium to dark green, glossy, broad, slightly upwards folded, lobes mostly even ; terminal leaflet drooping, sometimes fused with laterals ; secondary leaflets fairly frequent, round and not pointed.

FLOWER.—White and numerous ; anthers orange ; buds pink at base ; berries occur.

REMARKS.—This is a new Irish variety about the commercial and other character of which little is known. The tubers are attractive and the cooking and keeping qualities are reputed to be very good.

ULSTER PRINCE (CLARKE)

MATURITY.—*First Early.*

TUBER.—Kidney ; skin white ; eyes shallow and few ; on exposure, blue-purple rapidly develops ; flesh white ; sprouts blue.

FOLIAGE.—Haulm low and medium in height, spreading later ; top growth flat ; stems mainly green, although faint pink may appear at the base ; wings straight ; leaf close and drooping ; leaflets waxy, light green, long, oblong, slightly wrinkled with uneven lobes ; terminal leaflet slightly overlapped ; secondaries round and few, there being often none on the midrib between the terminal and the last pair of leaflets.

FLOWERS.—Large, white, numerous ; anthers orange ; berries occur.

REMARKS.—Cropping : very good. Susceptible to Dry Rot. This is a new Irish variety about the commercial and other characters of which little is known. It is reputed to produce marketable ware tubers earlier than Arran Pilot and Ulster Chieftain.

ULSTER SUPREME (CLARKE)

MATURITY.—*Late Maincrop.*

TUBER.—Oval ; skin white ; on exposure, little, if any, colour develops ; eyes shallow to medium, on shoulder and sunk close to the eyebrow ; flesh white ; sprouts faint pink ; stolons fairly long.

FOLIAGE.—Haulm of medium height, spreading ; stems branching vigorously, particularly at tops, slightly coloured at leaf axils ; wings of medium width, wavy and green ; leaf of average size, close, fairly wide and rigid, midrib green ; stipule-like growths small ; leaflets of average size, terminal round, laterals broad and cordate, medium to dark green in colour, glossy, slightly upwards folded, with lobes generally even ; secondary leaflets average in size and frequency, rounded.

FLOWER.—Light blue-purple, tipped white, not frequent; anthers yellow, not forming a regular column; inflorescence stalks short, green; buds infrequent, lightly coloured, hairy and blunt.

REMARKS.—This is a new Irish variety about the commercial and other characters of which not much is known. It shows promise. The cooking quality is reputed to be very good. The variety is susceptible to Blight.

UP-TO-DATE (A. FINDLAY). (NON-IMMUNE)

MATURITY.—*Late Maincrop.*

TUBER.—Oval (somewhat flat), rather square at heel; skin white; remaining almost entirely green on exposure, only very faint red-purple may develop at the eyes; eyes shallow and generally on the point; flesh white; sprouts pink.

FOLIAGE.—Haulm of medium height to tall, vigorous and spreading; stems thick, branching freely and colouring towards maturity; wings slightly waved; leaf fairly open, long, spreading, rather rigid, lower leaves vigorous; midribs of younger leaves slightly coloured at their bases and at the bases of the leaflet stalks; leaflets light to medium green, long and broad, slightly upwards folded, the end pair markedly overlapping the terminal; leaflet lobes uneven; secondary leaflets fairly numerous, rounded and not generally large.

FLOWER.—Large, light red-purple, gradually lightening in shade towards the tip, but not distinctly white-tipped; blooms freely and for a long period; anthers yellow-orange; inflorescence and flower stalks long and thick; buds pink and slightly pointed.

REMARKS.—Cropping: excellent; cooking quality: fairly good; keeping quality: good; wildings and bolters occur; susceptible to Blight and Common Scab; necrotic to virus "A"; non-necrotic to virus "X"; viruses "B" and "X" almost invariably in stocks; susceptible to virus "Y"; effects of Leaf Roll not severe; stocks generally free from severe Mosaics.

Some synonyms are: Dalhousie, Factor, Glamis Beauty, Scottish Triumph and Tremendous.

Field-Marshal is identical with Up-to-Date except that the tuber has a russet skin.

VANGUARD (J. HARPER)

MATURITY.—*First Early.*

TUBER.—Round to oval, heel often indented; skin white; on exposure, faint red-purple may develop at the eyes; eyes medium, slightly on the shoulder; flesh white; sprouts pink.

FOLIAGE.—Haulm low growing, bushy; stems strong, branching and slightly mottled towards base; wing only slightly waved; leaf long, fairly rigid and open; leaflets medium green, dull, large and broad, slightly upwards folded and arched a little; leaflet lobes generally uneven.

FLOWER.—Red-purple, tipped white; infrequent; anthers orange.

REMARKS.—Cropping: very good; cooking quality: fair; bulks early, but tubers become coarse if left until mature; non-necrotic to viruses " A " and " X "; bolters occur; resistant to Common Scab. The acreage of this variety is now contracting.

WITCHHILL (BROWN)

MATURITY.—*First Early.*

TUBER.—Oval to long oval (flat); skin very white and smooth; on exposure, faint red-purple develops at eyes; eyes shallow and on the point; eyebrows sometimes slightly raised; flesh very white; sprouts pink.

FOLIAGE TYPE.—Duke of York.

FOLIAGE.—Haulm of medium height, spreading and compact; stems branching, numerous and not thick, faint colour developing towards maturity; wings not broad and slightly waved; leaf fairly open and drooping; leaflets fairly long, light to medium green with characteristic glossy, thin appearance; towards maturity the leaflet margins tend to curl upwards; secondary leaflets small and not numerous.

FLOWER.—Creamy white and seldom formed; anthers yellow; buds dark with green tips; sepals long; inflorescence stalk appears almost invariably terminal on a side shoot.

REMARKS.—Cropping: fair; cooking quality: fair; keeping quality: poor; bolters occur; very susceptible to Blight; non-necrotic to virus " X "; necrotic to virus " A "; viruses " B " and " X " almost invariably in stocks; susceptible to virus " Y." Witchhill is grown now mainly as a garden potato.

TABLE XXXIII

Reaction of Potato Varieties to Viruses

	Virus.				Y.		L.R.		Remarks.
	X.	A.	B.	C.	Inf.	Dis.	Inf.	Dis.	
Abundance	S	N	N	S	S	F.T.	S	S	...
Ally	S	S	S	N	S	S	S	F.S.	...
Alness	S	N	N	S	V.S.	S	V.S.	S	...
Angus Leader	S	S	N	N	S	F.T.	S	S	...
Arran Banner	S	S	S	S	F.S.	F.S.	F.S.	S	X common in stocks
Arran Bard	S	S	S	S	S	S	V.S.	V.S.	...
Arran Cairn	S	N	N	N	S	S	S	S	...
Arran Chief	S	S	N	S	S	S	S	S	X and A common in stocks
Arran Comrade	S	S	N	S	F.S.	F.S.	S	S	...
Arran Consul	S	S	S	N	V.S.	V.S.	V.S.	V.S.	...
Arran Crest	N	N	S	S	S	S	F.R.	F.S.	...
Arran Luxury	S	...	N	S	F.S.	S	F.S.	S	X common in stocks
Arran Peak	S	N	S	S	S	S	S	S	X common in stocks
Arran Pilot	S	N	N	S	S	V.S.	S	S	X common in stocks
Arran Signet	S	S	S	N	S	V.S.	V.S.	V.S.	...
Arran Victory	S	S	N	S	F.S.	F.T.	F.S.	F.T.	X common in stocks
Ballydoon	S	N	N	N	S	F.S.	S	S	...
Baron	S	N	S	S	F.S.	F.T.	S	S	...
Ben Lomond	S	N	N	S	...	F.S.	S	F.S.	...
Bishop	S	N	S	N	...	...	S	S	X common in stocks
British Queen	S	N	N	N	S	V.S.	S	S	X common in stocks
Catriona	S	S	N	S	S	F.T.	S	S	A almost invariably in stocks
Champion	S	S	S	S	F.R.	F.T.	F.R.	S	...
Craigs Alliance	S	N	N	S	S	S	S	S	...
Craigs Bounty	S	S	S	N	S	S	S	S	...
Craigs Defiance	N	N	N	N	S	S	S	F.S.	...
Craigs Royal	N	N	S	S	S	S	S	S	...
Craigs Snow-white	N	N	N	N	VS	S	S	S	...
Dargill Early	S	N	N	S	...	F.T.	F.S.	F.S.	Y common in stocks
Di Vernon	S	N	S	S	S	F.T.	S	S	...
Doon Bounty	S	N	S	N	...	...	...	...	...
Doon Early	S	N	N	S	F.S.	F.S.	S	S	...
Doon Pearl	S	N	N	S	S	F.T.	S	S	...
Doon Star	S	N	S	N	S	S	S	V.S.	X common in stocks
Duke of York	S	N	S	N	S	V.S.	S	S	X and B almost invariably in stocks
Dunbar Archer	S	N	N	S	S	S	S	F.T.	...
Dunbar Cavalier	S	S	S	S	S	S	V.S.	S	...
Dunbar Rover	S	N	S	N	S	V.S.	S	S	X common in stocks
Dunbar Standard	S	N	N	S	S	F.S.	S	S	...
Dunbar Yeoman	S	N	N	N	V.S.	V.S.	V.S.	V.S.	
Eclipse	S	N	S	N	S	V.S.	F.S.	S	
Edzell Blue	S	N	N	N	F.S.	F.S.	S	S	...
Epicure	N	N	S	N	S	S	F.S.	S	...
Gladstone	S	N	...	S	F.S.	S	V.S.	S	...
Golden Wonder	S	S	N	N	S	F.S.	S	V.S.	A invariably in stocks

TABLE XXXIII—*continued*

	Virus.				Y.		L.R.		Remarks.
	X.	A.	B.	C.	Inf.	Dis.	Inf.	Dis.	
Great Scot	S	N	S	S	S	F.S.	S	F.T.	X common in stocks
Herald	S	N	N	S	S	F.T.	S	S	...
Home Guard	S	N	N	S	...	...	...	...	...
Immune Ashleaf	S	S	N	N	S	S	S	S	A almost invariably in stocks
International Kidney	N	N	S	S	F.R.	F.T.	F.R.	S	C almost invariably in stocks
Kerr's Pink	S	N	N	S	F.S.	F.S.	F.S.	S	X almost invariably in stocks
King Edward	N	N	S	N	S	S	S	S	...
King George	S	S	S	N	S	S	S	S	X common in stocks
Majestic	S	S	S	N	S	S	S	F.S.	X common in stocks
May Queen	S	N	N	S	S	S	S	S	...
Ninetyfold	N	N	S	N	S	V.S.	S	S	Aucuba Mosaic (G) throughout stocks
Orion	S	...	N	...	...	...	...	...	X common in stocks
President	S	S	N	N	S	V.S.	S	V.S.	X common in stocks
Puritan	S	N	N	N	S	S	S	V.S.	...
Redskin	S	N	S	S	S	S	S	S	X common in stocks
Rhoderick Dhu	S	N	N	S	S	S	S	S	X common in stocks
Royal Kidney	S	S	S	N	S	S	S	S	X and B common in stocks
Sharpe's Express	S	N	N	N	S	V.S.	S	S	X common in stocks
Tinwald Perfection	S	S	S	S	S	S	S	S	X common in stocks
Ulster Chieftain	S	N	N	S	...	...	S	S	...
Ulster Monarch	S	S	N	S	...	...	S	S	...
Up-to-date	S	N	S	N	S	S	S	F.T.	X and B almost invariably throughout stocks
Vanguard	S	S	S	S	...	...	S	F.S.	...
Witchhill	S	N	S	N	S	V.S.	S	S	X and B almost invariably throughout stocks

Viruses X, A, B, C:
- N = necrotic reaction when infected by graft. (Indicates field-immunity.)
- S = ±mosaic symptoms upon infection. (Indicates susceptibility to infection in field.)

Virus Y and Leaf Roll:
- Inf. = relative susceptibility to infection.
  - V.S. = very susceptible.
  - S = susceptible.
  - F.S. = less susceptible.
  - F.R. = fairly resistant.
- Dis. = severity of disease.
  - V.S. = very severe.
  - S = severe.
  - F.S. = less severe.
  - F.T. = fairly tolerant.

Note.—The authors are very much indebted to Dr G. Cockerham, Scottish Society for Research in Plant Breeding, Craig's House, Corstorphine, Edinburgh 12, for permission to reproduce the above table.

TABLE XXXIV

Registration of Potato Varieties

List of varieties of potatoes registered by the Department of Agriculture for Scotland since the inception of the Registration Scheme in 1921

Year of Registration.	Name of Variety.	Raiser or Introducer.
1925	Arran Consul	Donald Mackelvie
1926	...	...
1927	Arran Banner	Donald Mackelvie
1927	Herald	McGill & Smith
1928	Arran Crest	Donald Mackelvie
1929	...	...
1930	Arran Pilot (A-581)	Donald Mackelvie
1931	...	...
1932	...	...
1933	...	...
1934	Doon Early (7268)	McGill & Smith, Ltd.
1934	Gladstone	McGill & Smith, Ltd.
1934	Alness (135(10))	Scottish Society for Research in Plant Breeding
1934	Redskin (772)	William Pollock
1935	Arran Peak (19363)	Donald Mackelvie
1936	Dunbar Rover (L. 89)	Charles T. Spence
1936	Dunbar Standard (A. 13)	Charles T. Spence
1938	Arran Bard (222/8)	Donald Mackelvie
1938	Craigs Defiance (451a(20))	Scottish Society for Research in Plant Breeding
1939	Vanguard (C65)	J. Harper
1939	Doon Bounty (1343)	McGill & Smith, Ltd.
1947	Orion (3(0))	A. T. Smith
1947	Craigs Royal (831(113))	Scottish Society for Research in Plant Breeding
1947	Craigs Snow-white (835a(4))	Scottish Society for Research in Plant Breeding
1948	Craigs Alliance (827a(185))	Scottish Society for Research in Plant Breeding
1951	Pentland Ace	Scottish Society for Research in Plant Breeding

TABLE XXXV

Varieties of Potatoes to which Lord Derby Gold Medals have been awarded

1916—Kerr's Pink and Lochar
1917—Ally
1918—No award
1919—Arran Comrade
1920—Rhoderick Dhu
1921—No award
1922—No award
1923—Ben Cruachan
1924—No award
1925—Arran Consul
1926—No award
1927—Arran Banner
1928—Arran Crest
1929—No award
1930—No award
1931—Arran Pilot
1932—Arran Cairn and Doon Pearl
1933—No award
1934—Arran Signet
1935—Gladstone
1936—Doon Early, Dunbar Standard and Redskin
1937—Dunbar Rover
1938—No award
1939—No award
1940—No award
1941—No award
1942—Doon Eire
1943—No award
1944—Arran Viking
1945—No award
1946—Craigs Bounty
1947—No award
1948—Ulster Supreme
1949—Craigs Royal

DESCRIPTIONS OF POTATO SPROUTS

VARIETY—ABUNDANCE

YOUNG SPROUT.—Green, tip blue-purple.

BASE.—Blue-purple ; thick ; moderately hairy, hairs short and woolly ; rootlets numerous.

MIDDLE PORTION.—Blue-purple, with green tinge ; moderately hairy, hairs adpressed ; short.

TIP.—Blue-purple, with green tinge ; fairly long, blunt ; young leaflets unfold.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ALLY

YOUNG SPROUT.—Green, tip tinged faint pink.

BASE.—Pale pink, not highly coloured, darker at lenticels ; moderately thick, tapering ; elongating later ; hairy ; rootlets very numerous ; stolons may appear ; scale leaves small and narrow.

MIDDLE PORTION.—Green ; not so hairy as base ; narrow.

TIP.—Faint brownish pink, tinged green ; pointed and small ; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—ARRAN BANNER

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Pink ; bulbous ; moderately hairy.

MIDDLE PORTION.—Green, with pink tinge ; moderately hairy ; hairs slightly adpressed.

TIP.—Green, with brownish pink tinge, becoming greener later ; large ; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN BARD

YOUNG SPROUT.—Green with blue-purple tinge.

BASE.—Blue-purple, lenticel centres lighter ; hairy ; thick, short and tapering ; rootlets not numerous.

MIDDLE PORTION.—Blue-purple, tinged green ; narrow ; hairs more numerous than on base.

TIP.—Blue-purple, tinged green ; long ; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN CAIRN

YOUNG SPROUT.—Green, tips pale pink.

BASE.—Very faint brownish pink, tinged green, darker at lenticels; not highly coloured; moderately thick; tapering; moderate to slightly hairy; scale leaves narrow and often small.

MIDDLE PORTION.—Green; narrow; not hairy.

TIP.—Brownish pink, tinged green; small and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN CHIEF. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple; thick and short; hairs very few and short; lenticel centres mostly coloured.

MIDDLE PORTION.—At first green, mottled blue-purple, later blue-purple with green tinge; short.

TIP.—Blue-purple, with green tinge; fairly long and blunt; young leaflets unfold very slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN COMRADE

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple; thick and short; hairy; lenticel centres sometimes white; rootlets numerous.

MIDDLE PORTION.—At first green, mottled blue-purple, later blue-purple with green tinge; short; very hairy.

TIP.—Blue-purple, greening slightly with age; blunt and rather short; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN CONSUL

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Brownish red, with green tinge, darker at lenticels; bulbous; hairs very few; rootlets few; scale leaves short and mainly green.

MIDDLE PORTION.—Green; very short; not hairy.

TIP.—Green, with brownish pink tinge; very short; pointed; young leaflets remain closed; more hairy than base.

RAPIDITY OF SPROUTING.—Very slow.

VARIETY—ARRAN CREST

YOUNG SPROUT.—Green, tips pink.

BASE.—Dark pink; thick, short and slightly tapering; hairy, hairs woolly; rootlets numerous; stolons may appear later.

MIDDLE PORTION.—Pink, tinged green; hairy, hairs slightly adpressed.

TIP.—Brownish pink, tinged green; fairly long; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate to rapid.

VARIETY—ARRAN PEAK

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple ; moderately thick and rather short ; slightly hairy.

MIDDLE PORTION.—Green, tinged blue-purple ; moderately hairy.

TIP.—Blue-purple, with green tinge ; very large ; leaflets unfold markedly ; upper surfaces of young leaflets tinged purple.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN PILOT

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple ; not thick ; tapering ; elongating rapidly ; slightly to moderately hairy, hairs short ; lightly coloured stolons may appear ; lenticel centres often white ; scale leaves blue-purple.

MIDDLE PORTION.—Green, mottled blue-purple ; long ; narrow ; not quite so hairy as base.

TIP.—Blue-purple ; young leaflets unfold markedly ; upper surfaces of young leaflets purple.

RAPIDITY OF SPROUTING.—Very rapid.

VARIETY—ARRAN SIGNET

YOUNG SPROUT.—Green, tips faint blue-purple or entirely green.

BASE.—Blue-purple, slightly tinged green ; not thick ; tapering ; hairy, hairs short ; lenticel centres often white ; scale leaves green, tinged purple ; stolons may appear.

MIDDLE PORTION.—Green, mottled blue-purple ; moderately hairy ; fairly long and narrow.

TIP.—Blue-purple, with green tinge ; pointed at first ; young leaflets unfold slightly later.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ARRAN VICTORY

YOUNG SPROUT.—Blue-purple, with little green.

BASE.—Blue-purple ; thick and tapering slightly ; moderately hairy, hairs short and rather adpressed ; lenticel centres coloured ; rootlets more numerous and scale leaves larger than in Edzell Blue.

MIDDLE PORTION.—Blue-purple, with faint green tinge ; fairly long ; hairy, hairs adpressed.

TIP.—Blue-purple, with slight green tinge ; fairly long and rather blunt ; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Fairly rapid.

VARIETY—ARRAN VIKING

YOUNG SPROUT.—Green, tips very faint pink.

BASE.—Pink, darker at the lenticels ; moderately thick and cylindrical, tapering towards the top ; hairy, hairs short ; scale leaves green and narrow ; stolons numerous.

Middle Portion.—Green with faint pink at the lenticels; fairly long and tapering; not hairy, hairs very short, not so hairy as base.

Tip.—Green with pink tip; small; pointed; young leaflets remain closed.

Rapidity of Sprouting.—Fairly rapid.

Variety—BALLYDOON

Young Sprout.—Green, sometimes tinged very faint pink.

Base.—Green, with faint pink tinge, darker at lenticels; moderately thick; very hairy, hairs long and woolly.

Middle Portion.—Green, very hairy.

Tip.—Green, tinged very faint pink; fairly long and blunt; rather hairy; young leaflets unfold; upper surfaces of young leaflets green.

Rapidity of Sprouting.—Fairly rapid.

Variety—BRITISH QUEEN. (Non-Immune)

Young Sprout.—Green, tips tinged pink.

Base.—Pale brownish pink to pink, with green tinge, not highly coloured; fairly thick; hairy to moderately hairy; lenticel centres sometimes white.

Middle Portion.—Green, with slight pink tinge; hairs rather adpressed; fairly long.

Tip.—Green, tinged reddish brown; fairly long and blunt; young leaflets unfold slightly.

Rapidity of Sprouting.—Moderate to fairly rapid.

Variety—CATRIONA

Young Sprout.—Dark blue-purple.

Base.—Blue-purple; moderately thick, tapering slightly; moderately hairy; some rootlets coloured; lenticel centres coloured; scale leaflets narrow.

Middle Portion.—At first blue-purple with green tinge, later blue-purple; not hairy; short.

Tip.—Blue-purple; long and blunt; young leaflets unfold slightly; upper surfaces of young leaflets tinged purple.

Rapidity of Sprouting.—Moderate.

Variety—CRAIGS ALLIANCE

Young Sprout.—Green, tips faint red-purple.

Base.—Faint red-purple, not highly coloured, darker at lenticels; thick to bulbous but not long; moderately hairy; rootlets not numerous.

Middle Portion.—Green, tinged red-purple; hairier than base; hairs adpressed; narrow.

Tip.—Green, tinged red-purple; large; young leaflets unfold.

Rapidity of Sprouting.—Fairly rapid.

Variety—CRAIGS BOUNTY

Young Sprout.—Green, tips pink.

Base.—Pink ; thick, tapering towards the top ; slightly hairy ; scale leaves tinged pink ; rootlets numerous.

Middle Portion.—Green, tinged pink ; slightly hairy ; narrow.

Tip.—Brownish green ; large ; hairs adpressed ; young leaflets remain closed.

Rapidity of Sprouting.—Moderate to slow.

Variety—CRAIGS DEFIANCE

Young Sprout.—Green, tip lavender.

Base.—Lavender, darker at lenticels; elongating and tapering markedly; hairs few ; rootlets not very numerous ; scale leaflets broad.

Middle Portion.—Green, tinged brownish red ; long and narrow ; hairs more numerous than on base.

Tip.—Brownish red, tinged green ; long ; young leaflets unfold markedly.

Rapidity of Sprouting.—Very rapid.

Variety—CRAIGS ROYAL

Young Sprout.—Green, tip tinged red-purple.

Base.—Lavender, darker at lenticels ; thick and short ; hairy, hairs adpressed ; scale leaves tinged red-purple ; rootlets not numerous and occasionally coloured.

Middle Portion.—Green, tinged red-purple ; thick, short and very hairy, hairs being adpressed.

Tip.—Green, tinged red-purple ; large ; young leaflets unfold.

Rapidity of Sprouting.—Fairly rapid.

Variety—CRAIGS SNOW-WHITE

Young Sprout.—Green, tip red-purple.

Base.—Red-purple ; thick ; hairs few : rootlets fairly numerous ; lenticel centres sometimes white ; stolens may appear.

Middle Portion.—Green, tinged red-purple ; short ; more hairy than base.

Tip.—Green, tinged red-purple ; young leaflets remain almost closed.

Rapidity of Sprouting.—Moderate.

Variety—CONFERENCE

Young Sprout.—Green.

Base.—Red-purple ; hairy ; thick ; rootlets fairly numerous ; scale leaves broad.

Middle Portion.—Green ; thick and hairy.

Tip.—Green ; large ; young leaflets unfold slightly.

Rapidity of Sprouting.—Moderate.

VARIETY—DI VERNON

YOUNG SPROUT.—Dark blue-purple.

BASE.—Blue-purple; moderately thick; tapering slightly; hairy; young rootlets often coloured; lenticel centres coloured; scale leaflets often broader than in Catriona.

MIDDLE PORTION.—At first blue-purple with green tinge, rapidly colouring to same tone as base; hairy, hairs adpressed.

TIP.—Blue-purple; very long and blunt; young leaflets unfold early and markedly; upper surfaces of young leaflets purple.

RAPIDITY OF SPROUTING.—Very rapid.

VARIETY—DOON BOUNTY

YOUNG SPROUT.—Green.

BASE.—Red-purple, darker at lenticels; hairs few; short and thick; rootlets not very numerous.

MIDDLE PORTION.—Green, tinged red-purple; more hairy than base, hairs rather adpressed; thick.

TIP.—Green, tinged reddish brown; long and blunt; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—DOON EARLY

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Very faint pink, tinged green; darker at lenticels; not highly coloured; thick; tapering; hairy; rootlets not very numerous.

MIDDLE PORTION.—Green; not so hairy as base; long and narrow.

TIP.—Green, tinged brownish pink; small and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Fairly rapid.

VARIETY—DOON STAR

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple; thick, tapering only at top; moderately to slightly hairy; lenticel centres coloured; rootlets not very numerous.

MIDDLE PORTION.—At first green, mottled blue-purple; later blue-purple with green tinge; rather narrow and short.

TIP.—Blue-purple; very short and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—DR McINTOSH

YOUNG SPROUT.—Mainly green, with faint pink tips.

BASE.—Pale pink; thick to moderately thick and cylindrical; hairy, hairs short; scale leaves usually green and narrow; lenticel centres often white; rootlets fairly numerous.

MIDDLE PORTION.—Green, tinged brown; fairly long; narrow; usually less hairy than base.

TIP.—Green, tinged brown; hairs few and adpressed; young leaflets unfold only very slightly or remain closed.

RAPIDITY OF SPROUTING.—Slow.

VARIETY—DUKE OF YORK. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Pale pink, tinged green, darker at lenticels, not highly coloured; moderately thick, tapering; very hairy; elongating rapidly.

MIDDLE PORTION.—Mainly green; very hairy.

TIP.—Green, with faint brownish pink tinge; fairly hairy; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Rapid.

VARIETY—DUNBAR ARCHER

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple, lenticel centres lighter in shade; thick and short; moderately hairy, hairs adpressed; scale leaves tinged purple, long and narrow; rootlets numerous.

MIDDLE PORTION.—Blue-purple, tinged green; long and narrow; more hairy than base, hairs adpressed.

TIP.—Blue-purple, tinged green; large; hairs adpressed; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Fairly slow.

VARIETY—DUNBAR CAVALIER

YOUNG SPROUT.—Green, tips pink.

BASE.—Lavender, with green tinge; coloured mainly at the bottom; lenticels highly coloured; moderately thick; tapering markedly; moderately to slightly hairy, hairs short; rootlets often coloured; scale leaflets pale brownish pink.

MIDDLE PORTION.—Green; narrow and long; not hairy.

TIP.—Green, with brownish pink tinge; small and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—DUNBAR ROVER

YOUNG SPROUT.—Green, tinged faint pink.

BASE.—Brownish pink to pink, tinged green, coloured mainly at the bottom; darker at lenticels; not highly coloured; rather thick and tapering; hairs few.

MIDDLE PORTION.—Green, not hairy; long.

TIP.—Green, with faint brownish pink tinge; rather pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—DUNBAR STANDARD

YOUNG SPROUT.—Practically green, only very faint pink may appear.

BASE.—Pale brownish pink, tinged green, coloured mainly at the bottom; not highly coloured; not thick; tapering; hairs few to moderate; lenticels rather flat; rootlets numerous at base.

MIDDLE PORTION.—Green; narrow; moderately to slightly hairy; long.

TIP.—Green, with very faint pink tinge; long and pointed; young leaflets open slightly.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—ECLIPSE. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips faint pink.

BASE.—Dark pink; at first moderately thick and tapering, later elongating; very hairy; scale leaflets small and narrow; numerous short stolons may appear.

MIDDLE PORTION.—Green, tinged faint pink; not so hairy as base; fairly long and narrow.

TIP.—Brownish red, with green tinge; small and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate to rapid.

VARIETY—EDZELL BLUE

YOUNG SPROUT.—Blue-purple.

BASE.—Blue-purple; very thick and short; hairy, hairs short; lenticel centres coloured; rootlets not so numerous as and scale leaves smaller than in Arran Victory.

MIDDLE PORTION.—Blue-purple, tinged green; hairy.

TIP.—Blue-purple; long and blunt; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Fairly rapid to moderate.

VARIETY—EPICURE. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips pink.

BASE.—Dark pink; thick and short; tapering slightly; moderately hairy to hairy, hairs short; stolons may appear.

MIDDLE PORTION.—At first green, later with pink tinge; fairly narrow; hairy.

TIP.—Pale brownish red, tinged green; short and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Fairly rapid.

VARIETY—GLADSTONE

YOUNG SPROUT.—Lavender, very little green.

BASE.—Lavender, tinged green; moderately thick and short; moderately to slightly hairy; hairs short and somewhat adpressed; lenticels darkly coloured; scale leaves faint brownish pink; some rootlets coloured.

MIDDLE PORTION.—Brownish red, tinged green; hairy, hairs adpressed.

TIP.—Brownish red, tinged green; large; young leaflets unfold markedly; upper surfaces of young leaflets slightly tinged brown.

RAPIDITY OF SPROUTING.—Slow.

VARIETY—GOLDEN WONDER

YOUNG SPROUT.—Green, tips faint blue-purple.

BASE.—Blue-purple; moderately thick and short; moderately hairy, hairs short.

MIDDLE PORTION.—Blue-purple, with green tinge; short.

TIP.—Blue-purple, with green tinge; fairly large and blunt; young leaflets unfold very slightly.

RAPIDITY OF SPROUTING.—Slow.

VARIETY—GREAT SCOT

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Pale brownish pink to pink, tinged green; lenticels darker; not highly coloured; bulbous; slightly hairy, hairs short.

MIDDLE PORTION.—Green, tinged faint pink; hairs adpressed.

TIP.—Green, with brownish pink tinge; large; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—HOME GUARD

YOUNG SPROUT.—Green, tip blue-purple.

BASE.—Blue-purple, lenticel centres may be lighter; moderately hairy; moderately thick and tapering.

MIDDLE PORTION.—Brownish purple, tinged green; more hairy than base; narrow.

TIP.—Green, tinged brownish purple; large; young leaflets unfold markedly.

RAPIDITY OF SPROUTING.—Very rapid.

VARIETY—IMMUNE ASHLEAF

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple, tinged green, not thick; tapering; hairy; lenticel centres often white.

MIDDLE PORTION.—At first green, mottled blue-purple, later more blue-purple; more hairy than base, hairs adpressed.

TIP.—Blue-purple; short and somewhat pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—INTERNATIONAL KIDNEY

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple; thick and tapering; hairs few.

MIDDLE PORTION.—At first green, mottled blue-purple, later blue-purple, tinged green.

TIP.—Blue-purple; pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—KERR'S PINK

YOUNG SPROUT.—Green, tips pale pink.

BASE.—Dark pink; thick and short; lenticel centres coloured; slightly hairy, hairs slightly adpressed.

MIDDLE PORTION.—Green, tinged pink; short and thick; hairs rather adpressed.

TIP.—Green, tinged reddish brown; fairly long; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—KING EDWARD. (NON-IMMUNE)

YOUNG SPROUT.—Lavender, very little green.

BASE.—Lavender, tinged green; lenticels dark; not thick; tapering; slightly hairy, hairs not adpressed; some rootlets coloured; scale leaflets pale lavender.

MIDDLE PORTION.—Pale lavender, tinged green; fairly narrow; not hairy.

TIP.—Reddish brown; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Fairly slow.

VARIETY—KING GEORGE

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Pink to dark pink; thick, hairy, hairs woolly.

MIDDLE PORTION.—Green; short and thick; hairy.

TIP.—Green, tinged brownish pink; short and blunt; moderately hairy; young leaflets do not unfold.

RAPIDITY OF SPROUTING.—Moderate to fairly rapid.

VARIETY—MAJESTIC

YOUNG SPROUT.—Green, tips tinged faint pink.

BASE.—Faint pink, darker at lenticels, not highly coloured; thick, short and tapering; hairy; rootlets fairly numerous.

MIDDLE PORTION.—Green; fairly narrow; hairy.

TIP.—Green, with faint pink tinge; fairly short and rather pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Fairly slow.

VARIETY—MAY QUEEN. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple ; moderately thick ; tapering ; elongating later ; very hairy, hairs woolly ; lenticel centres often white ; stolons may appear.

MIDDLE PORTION.—Blue-purple, with green tinge ; hairy ; fairly long.

TIP.—Blue-purple, with green tinge ; young leaflets unfold moderately ; upper surfaces of young leaflets purple tinted.

RAPIDITY OF SPROUTING.—Rapid.

VARIETY—NINETYFOLD. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips faint pink.

BASE.—Pink ; thick to moderately thick and tapering ; very hairy, hairs woolly ; small stolons may appear.

MIDDLE PORTION.—Green, with faint pink tinge ; hairy ; fairly long.

TIP.—Green, tinged brownish pink ; rather pointed ; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Rapid.

VARIETY—ORION

YOUNG SPROUTS.—Green, tips pink

BASE.—Red-purple ; thick and short ; slightly hairy ; lenticel centres sometimes white ; scale leaves tinged pink, short ; rootlets numerous.

MIDDLE PORTION.—Thick and short ; more hairy than base, hairs adpressed.

TIP.—Greenish brown ; hairs adpressed ; young leaflets open only slightly.

RAPIDITY OF SPROUTING.—Slow.

VARIETY—PENTLAND ACE

YOUNG SPROUT.—Green, tips pink.

BASE.—Dark pink ; moderately thick ; slightly to moderately hairy ; lenticel centres sometimes white ; scale leaves pink and often narrow.

MIDDLE PORTION.—Greenish brown ; hairy, more hairy than base ; hairs adpressed ; fairly narrow.

TIP.—Brown, with a green tinge ; large ; young leaflets unfold.

RAPIDITY OF SPROUTING.—Fairly rapid.

VARIETY—PURITAN. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips faint to very faint pink.

BASE.—Pale brownish pink, with green tinge ; thick to moderately thick and tapering ; hairy to very hairy ; elongating ; small stolons may appear.

MIDDLE PORTION.—Green ; moderately hairy ; fairly long.

TIP.—Green, tinged pale brownish pink ; fairly long ; pointed ; leaflets remain closed.

RAPIDITY OF SPROUTING.—Rapid.

VARIETY—RECORD

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple, lenticel centres lighter; thick to bulbous; not very hairy; scale leaves blue-purple and short; rootlets few.

MIDDLE PORTION.—Blue-purple, tinged green; short and fairly thick; hairy, much more so than base, hairs adpressed.

TIP.—Brownish purple, tinged green; hairs adpressed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—REDSKIN

YOUNG SPROUT.—Green, tips pale pink.

BASE.—Dark pink; lenticel centres coloured; moderately thick and short; slightly hairy.

MIDDLE PORTION.—Pink, with slight green tinge; short and thick; hairy, more hairy than base.

TIP.—Green, with brownish pink tinge; fairly long; young leaflets unfold slightly.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—ROYAL KIDNEY. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips faint pink.

BASE.—Pink, slightly tinged green; not thick; tapering; moderately hairy; elongating rapidly.

MIDDLE PORTION.—Green, with slight tinge of pink; slightly hairy; long and narrow.

TIP.—Green, tinged brownish pink; fairly long and pointed; young leaflets remain closed.

RAPIDITY OF SPROUTING.—Rapid.

VARIETY—SHARPE'S EXPRESS. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips faint pink.

BASE.—Pink to dark pink; moderately thick; tapering; moderately hairy; rootlets numerous; short stolons may appear.

MIDDLE PORTION.—Green, tinged pink; moderately hairy, hairs adpressed.

TIP.—Green, with reddish brown tinge; large; young leaflets open early and markedly; upper surfaces of young leaflets mainly green.

RAPIDITY OF SPROUTING.—Moderate to rapid.

VARIETY—STORMONT DAWN

YOUNG SPROUT.—Almost entirely green.

BASE.—Green, tinged faint red-purple, slightly darker at lenticels; thick and short; hairs very few; scale leaves green, short and broad; stolons may appear.

MIDDLE PORTION.—Green ; thick ; short ; not very hairy, more hairy than base.

TIP.—Green ; fairly large ; hairs adpressed ; young leaflets unfold only very slightly.

RAPIDITY OF SPROUTING.—Slow.

VARIETY—THE ALNESS

YOUNG SPROUT.—Green, tips tinged very faint pink.

BASE.—Pale brownish pink, tinged green ; not highly coloured, darker at lenticels ; thick ; tapering ; hairy.

MIDDLE PORTION.—Green, with slight pink tinge ; not so hairy as base ; long and narrow.

TIP.—Green, tinged brownish pink ; fairly long ; young leaflets may unfold slightly.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ULSTER CHIEFTAIN

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple ; lenticel centres often white ; thick and short ; hairy, hairs woolly ; scale leaves blue-purple, narrow and long ; rootlets fairly numerous.

MIDDLE PORTION.—Mainly green ; lenticels blue-purple ; hairy ; fairly narrow.

TIP.—Blue-purple ; large ; slightly hairy ; young leaflets usually remain closed.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—ULSTER CROMLECH

YOUNG SPROUT.—Green, tips blue-purple.

BASE.—Blue-purple ; thick ; very hairy, hairs woolly ; lenticel centres sometimes white ; stolons may appear.

MIDDLE PORTION.—Green, tinged blue-purple ; narrow ; not quite so hairy as base.

TIP.—Green, tinged blue-purple ; fairly large ; hairs adpressed ; young leaflets unfold only slightly.

RAPIDITY OF SPROUTING.—Fairly rapid to moderate.

VARIETY—ULSTER ENSIGN

YOUNG SPROUT.—Green, tip red-purple.

BASE.—Lavender, darker at lenticels ; hairy ; cylindrical and short ; rootlets sometimes coloured ; stolons sometimes appear.

MIDDLE PORTION.—Green, tinged red-purple ; very hairy, hairs mainly adpressed ; narrow.

TIP.—Green, tinged red-purple ; large ; hairy ; young leaflets unfold only slightly.

RAPIDITY OF SPROUTING.—Fairly rapid to moderate.

VARIETY—ULSTER PREMIER

YOUNG SPROUT.—Green, tinged red-purple.

BASE.—Light red-purple, darker at lenticels; not highly coloured; slightly hairy; cylindrical and only moderately thick; scale leaves narrow; rootlets numerous and sometimes coloured.

MIDDLE PORTION.—Mainly green; tinged red; more hairy than base.

TIP.—Mainly green; tinged red; fairly large; hairs adpressed; young leaflets open only very slightly.

RAPIDITY OF SPROUTING.—Fairly rapid.

VARIETY—ULSTER PRINCE

YOUNG SPROUT.—Green with blue-purple tinge.

BASE.—Blue-purple; hairy, hairs adpressed; moderately thick; rootlets numerous; scale leaves broad.

MIDDLE PORTION.—Blue-purple, tinged green; narrow; more hairy than base.

TIP.—Green, tinged blue-purple; long; young leaflets unfold.

RAPIDITY OF SPROUTING.—Rapid.

VARIETY—ULSTER SUPREME

YOUNG SPROUT.—Green, occasionally with very faint red-purple tip.

BASE.—Faint red purple; thick and cylindrical; moderately hairy; stolons may appear; rootlets frequent; scale leaves long and narrow; lenticel centres sometimes white.

MIDDLE PORTION.—Green, tinged red-purple; often more hairy than base; thick.

TIP.—Green; fairly large; young leaflets unfold only slightly or remain closed.

RAPIDITY OF SPROUTING.—Moderate.

VARIETY—UP-TO-DATE. (NON-IMMUNE)

YOUNG SPROUT.—Green, tips faint pink.

BASE.—Pale reddish brown, with green tinge; moderately thick and tapering slightly; hairs few; scale leaves narrow.

MIDDLE PORTION.—Green, tinged pink, narrow.

TIP.—Green, with reddish brown tinge; short; young leaflets may unfold slightly.

RAPIDITY OF SPROUTING.—Moderate to slow.

VARIETY—VANGUARD

YOUNG SPROUT.—Green, tips pink.

BASE.—Red-purple, tinged green, darker at lenticels; moderately hairy; thick.

MIDDLE PORTION.—Green with slight pink tinge; more hairy than base; short.

TIP.—Brownish red with green tinge; short; young leaflets unfold only slightly.

RAPIDITY OF SPROUTING.—Moderately rapid.

VARIETY—WITCHHILL

YOUNG SPROUT.—Green, tips very pale pink.

BASE.—Pale pink to pink, tinged green, darker at lenticels and bottom; not highly coloured; moderately thick and tapering; hairy; elongating later.

MIDDLE PORTION.—Green: fairly hairy; rather long and narrow.

TIP.—Green, tinged reddish brown; small and pointed; young leaflets do not unfold.

RAPIDITY OF SPROUTING.—Fairly slow.

TABLE XXXVI[1]

United Kingdom Potato Variety Acreages 1949 and 1950

Varieties	England		Wales		England and Wales		Scotland		Variety No.
	1949.	1950.	1949.	1950.	1949.	1950.	1949.	1950.	
First Early—	Acres.	Acres.	Acres.	Acres.	Acres.	Acres.	Acres.	Acres.	
1. Arran Pilot .	73,054	66,661	6,904	6,888	79,958	73,553	10,392	7,994	1
2. Ballydoon . .	1,067	535	60	20	1,127	555	143	27	2
3. Home Guard .	55,138	50,923	3,325	3,156	58,463	54,078	12,628	7,107	3
4. Ulster Chieftain	23,347	16,657	969	477	24,316	17,134	597	369	4
5. Vanguard . .	1,068	871	40	17	1,108	888	355	149	5
6. Duke of York .	5,016	4,562	42	70	5,058	4,632	2,245	1,923	6
7. Eclipse . .	11,203	9,412	174	137	11,377	9,549	2,753	1,401	7
8. Epicure . .	13,881	7,172	349	183	14,230	7,355	17,048	15,206	8
9. May Queen .	880	516	17	14	897	530	56	93	9
10. Ninetyfold .	7,817	5,779	499	73	8,316	5,852	179	126	10
11. Sharpe's Express	2,773	2,389	772	601	3,545	2,990	1,675	1,153	11
12. Other Varieties .	1,616	1,768	204	304	1,820	2,072	564	526	12
A. Total First Early	196,860	167,245	13,355	11,940	210,215	179,188	48,635	36,074	A
Second Early—									
21. Catriona . .	227	246	26	31	253	277	234	246	21
22. Dunbar Rover .	1,311	1,233	23	27	1,334	1,260	656	600	22
23. Great Scot .	8,930	8,441	363	366	9,293	8,807	6,471	5,374	23
24. British Queen .	626	510	65	64	691	574	1,376	1,277	24
25. Royal Kidney .	432	404	17	6	449	410	187	397	25
26. Other Varieties .	1,686	1,861	165	168	1,851	2,029	759	733	26
B. Total Second Early	13,212	12,695	659	662	13,871	13,357	9,683	8,627	B
Maincrop—									
31. Arran Banner .	60,033	51,227	5,211	5,139	65,244	56,366	5,331	5,446	31
32. Arran Consul .	10,596	6,798	553	380	11,149	7,178	943	806	32
33. Arran Peak .	64,068	71,218	836	951	64,904	72,169	2,199	3,077	33
34. Arran Victory .	2,292	1,355	913	658	3,205	2,013	447	457	34
35. Craigs Defiance	3,254	5,589	70	64	3,324	5,653	670	611	35
36. Doon Star .	10,565	9,354	80	59	10,645	9,413	1,655	1,432	36
37. Dr McIntosh .	(i)	1,835	(i)	43	(i)	1,878	(i)	435	37
38. Dunbar Standard	4,570	3,969	402	298	4,972	4,267	818	575	38
39. Gladstone . .	52,702	49,679	8,394	7,132	61,096	56,811	6,811	5,903	39
40. Golden Wonder .	306	293	74	65	380	358	3,952	4,713	40
41. Kerr's Pink .	4,235	3,614	1,560	1,241	5,795	4,855	45,878	44,232	41
42. Majestic . .	249,970	242 732	9,304	9,113	259,274	251,845	30,148	36,794	42
43. Record . .	1,923	2,813	73	64	1,996	2,877	556	900	43
44. Redskin . .	21,521	20,994	329	230	21,850	21,224	16,753	16,286	44
45. Stormont Dawn .	9,400	8,526	112	82	9,512	8,608	232	199	45
46. Ulster Supreme .	(i)	225	(i)	3	(i)	228	(i)	11	46
47. Arran Chief .	3,421	3,204	160	154	3,581	3,358	1,312	1,210	47
48. Bintje (Muizen) .	482	1,095	7	9	489	1,104	(i)	(i)	48
49. King Edward VII	79,327	78,975	1,279	1,089	80,606	80,064	6,979	9,300	49
50. Red King . .	10,948	10,853	666	591	11,614	11,444	1,287	1,709	50
51. Up-to-Date .	1,599	1,343	115	90	1,714	1,433	1,431	1,863	51
52. Other Varieties .	5,789	4,700	1,947	1,607	7,736	6,307	2,294	2,019	52
C. Total Maincrop .	597,001	580,391	32,085	29,062	629,086	609,453	129,696	137,978	C
D. Total All Varieties	807,073	760,331	46,099	41,664	853,172	801,998	188,014	182,679	D
E. Other Acreage Grown (iii)	63,850	54,346	12,287	10,410	76,137	64,756	4,185	11,321	E
F. Total Acreage Grown (iv)	870,923	814,680	58,386	52,074	929,309	866,754	192,199	194,000	F

[1] Reproduced by kind permission of the Ministry of Food.

TABLE XXXVI—*Continued*

Varieties	Great Britain		Northern Ireland		United Kingdom		Variety No.
	1949.	1950.	1949.	1950.	1949.	1950.	
First Early—	Acres.	Acres.	Acres.	Acres.	Acres.	Acres.	
1. Arran Pilot	90,350	81,547	3,718	1,965	94,068	83,512	1
2. Ballydoon	1,270	582	2,913	2,534	4,183	3,116	2
3. Home Guard	71,091	61,185	(ii)	(ii)	71,091	61,185	3
4. Ulster Chieftain	24,913	17,503	2,675	932	27,588	18,435	4
5. Vanguard	1,463	1,037	(ii)	(ii)	1,463	1,037	5
6. Duke of York	7,303	6,555	(ii)	(ii)	7,303	6,555	6
7. Eclipse	14,130	10,950	(ii)	(ii)	14,130	10,950	7
8. Epicure	31,278	22,561	1,126	1,080	32,404	23,641	8
9. May Queen	953	623	(ii)	(ii)	953	623	9
10. Ninetyfold	8,495	5,978	(ii)	(ii)	8,495	5,978	10
11. Sharpe's Express	5,220	4,143	(ii)	(ii)	5,220	4,143	11
12. Other Varieties	2,384	2,598	624	...	3,008	2,598	12
A. Total First Early	258,850	215,262	11,056	6,511	269,906	221,773	A
Second Early—							
21. Catriona	487	523	(ii)	(ii)	487	523	21
22. Dunbar Rover	1,990	1,860	(ii)	(ii)	1,990	1,860	22
23. Great Scot	15,746	14,181	(ii)	(ii)	15,746	14,181	23
24. British Queen	2,067	1,851	3,377	2,937	5,444	4,788	24
25. Royal Kidney	636	807	(ii)	(ii)	636	807	25
26. Other Varieties	2,610	2,762	883	337	3,493	3,099	26
B. Total Second Early	23,546	21,984	4,260	3,274	27,796	25,258	B
Maincrop—							
31. Arran Banner	70,575	61,812	29,732	31,189	100,307	93,001	31
32. Arran Consul	12,092	7,984	6,485	5,951	18,577	13,935	32
33. Arran Peak	67,103	75,246	13,931	14,202	81,034	89,448	33
34. Arran Victory	3,652	2,470	69,180	67,301	72,832	69,771	34
35. Craigs Defiance	3,994	6,264	(ii)	(ii)	3,994	6,264	35
36. Doon Star	12,300	10,845	(ii)	(ii)	12,300	10,845	36
37. Dr McIntosh	(i)	2,313	(ii)	(ii)	(i)	2,313	37
38. Dunbar Standard	5,790	4,842	701	664	6,491	5,506	38
39. Gladstone	67,907	62,714	8,722	5,716	76,629	68,430	39
40. Golden Wonder	4,332	5,071	(ii)	(ii)	4,332	5,071	40
41. Kerr's Pink	51,673	49,087	34,527	33,868	86,200	82,955	41
42. Majestic	289,422	288,639	1,877	2,326	291,299	290,965	42
43. Record	2,552	3,777	(ii)	(ii)	2,552	3,777	43
44. Redskin	38,603	37,510	(ii)	(ii)	38,603	37,510	44
45. Stormont Dawn	9,744	8,807	3,474	3,350	13,218	12,157	45
46. Ulster Supreme	(i)	239	(i)	189	(i)	428	46
47. Arran Chief	4,893	4,568	(ii)	(ii)	4,893	4,568	47
48. Bintje (Muizen)	489	1,104	(ii)	(ii)	489	1,105	48
49. King Edward VII	87,585	89,364	906	1,172	88,491	90,536	49
50. Red King	12,901	13,153	(ii)	(ii)	12,901	13,153	50
51. Up-to-Date	3,145	3,296	1,162	1,084	4,307	4,380	51
52. Other Varieties	10,030	8,326	1,499	2,211	11,529	10,536	52
C. Total Maincrop	758,782	747,431	172,196	169,223	930,978	916,654	C
D. Total all Varieties	1,041,178	984,677	187,512	179,008	1,228,680	1,163,685	D
E. Other Acreage Grown (iii)	80,322	76,077	...	...	80,322	76,077	E
F. Total Acreage Grown (iv)	1,121,508	1,060,754	187,512	179,008	1,309,020	1,239,762	F

(i) These varieties not asked for as indicated.

(ii) A comprehensive figure for the varieties not listed was supplied for Northern Ireland. This was divided on a proportionate basis according to the figures supplied the previous year, between First Earlies, Second Earlies and Maincrop and entered as "Other Varieties" for each group.

(iii) The recorded figures for 1950 under (D) were taken from returns representing approximately 89 per cent. of all growers in Great Britain; the "Other Acreage" shown here is the difference between the recorded totals and the total 4th June Acreage under (F).

(iv) Total 4th June Acreage (provisional), as published by the Agricultural Departments.

The Agricultural Departments' figures for First Earlies and Second Earlies and Maincrop varieties unspecified are :—

	England		Wales		Scotland	
	1949	1950	1949	1950	1949	1950
First Earlies . .	200,941	168,986	16,068	14,293	53,351	34,000
Second Earlies and Main crop	669,982	645,694	42,318	37,781	168,167	160,000
Total	870,923	814,680	58,386	52,074	221,518	194,000

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