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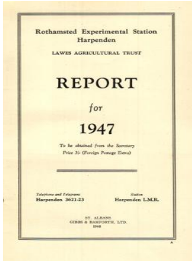

Review of Work on Potato Virus Diseases

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REVIEW OF WORK ON POTATO VIRUS DISEASES

Work on potato virus diseases was started in 1940 with the appointment to the department of Mr. J. P. Doncaster and Dr. P. H. Gregory, as Officers of the Agricultural Research Council, to study the spread of potato virus diseases in the ware-growing districts of eastern England. It was known that the rapid degeneration of potato stocks in such districts occurs because of increasing infection with the aphis-transmitted viruses that cause leaf roll and rugose mosaic, but there was no information on factors affecting the rate at which these spread.

In seed-producing districts correlations have been found between aphis infestations and the spread of leaf roll, and the usefulness of such practices as roguing and early lifting in maintaining the health of stocks is well established. In ware-growing districts, however, there have been few tests of the practicability of such control measures, and there was no information about the relative importance of different sources of infection, the distance over which spread takes place, or the time at which it occurs. The peach aphis, *Myzus persicae*, was generally assumed to be the most important vector, but the relative importance of different aphides was uncertain and knowledge of their life histories was incomplete. There was little or no information about the course of aphis infestations, the time at which they occur and the populations reached, or about the variations in infestation from field to field, district to district, and season to season, and whether such variations are directly correlated with spread of virus diseases. The relative importance of leaf roll and rugose mosaic was uncertain, and few data existed to show whether roguing or isolation from diseased stocks would suffice to prolong the useful life of seed stocks.

An epidemiological study of the two diseases was started in an attempt to remedy such defects in our knowledge. Experiments on a standard plan were made annually in different parts of the country and repeated records were made on selected crops in East Anglia to provide information on the activities of aphides and the spread of viruses. The work also had an immediately practical aim; in 1940 there was need to increase the potato acreage and it seemed likely that to do this seed-sized tubers from ware crops would have to be planted. Hence information was urgently needed on any factors that might be useful in assessing the suitability of stocks for seed. Actually the recognised seed-growing districts increased production enough to supply the need, and there is little doubt that, in spite of the cost of new seed to the ware grower. the separation of potato crops for seed and ware is the most effective and economic method of controlling virus diseases.

During the course of the field work many problems arose that required detailed study in the glasshouse and laboratory. Many of these came from difficulties encountered in attempting to diagnose causative viruses from symptoms. This work disclosed many new strains of virus X, some of which produced symptoms in potatoes readily confused with rugose mosaic; it also showed that some viruses previously regarded as distinct are strains of the almost ubiquitous virus X (Bawden and Sheffield, 1944). Other variations in the severity of symptoms of plants with rugose mosaic led to the discovery that potato virus Y is not a single, stable virus as generally believed, but occurs in the field in many strains of different virulence causing first-year symptoms in the variety Majestic that vary from a faint mosaic to severe leaf-drop streak. The common strains are all aphis-transmitted, but one strain, previously thought to be a separate virus and called virus C, was not transmitted by any of the tested aphides. Several new aphides were identified as vectors of virus Y; some of these, e.g., *Aphis rhamni*, are in glasshouse experiments as effective vectors as *M. persicae*, but field observations suggest that they are of little importance as natural vectors (Kassanis, 1942; Bawden and Kassanis, 1947). Experiments with different potato varieties showed that these not only differ in the symptoms produced by virus Y, but also in their susceptibility to infection, in the concentration of virus reached in their sap, and in their efficiency as sources of infection for aphides. It was shown that glasshouse tests needing few tubers could reliably be used for assessing performance in the field. Resistance to infection with virus Y was independent of resistance to leaf roll, and the differences found between different varieties were amply sufficient to account for the facts that different varieties degenerate at different rates and because of infection with different viruses (Bawden and Kassanis, 1946).

The diagnosis of leaf roll is also far from easy, for individual plants are dwarfed to varying extents and causes other than virus infection may make the leaves roll. Part of the differences in the severity of reaction of individual plants to leaf roll virus undoubtedly arise because the plants contain strains of virus X of different virulence, but there is evidence, though as yet inconclusive, that leaf roll virus, like virus Y, occurs in a range of strains differing from one another in virulence. Phloem necrosis was found useful for differentiating between true leaf roll from leaf rolling produced by other causes; with the virus disease, necrosis was invariably present at the base of the stem but was not found in other plants (Sheffield, 1943).

Aphis investigations

Four species of aphides occur regularly in potatoes in eastern England, *Myzus persicae* (Sulz.), *Aphis rhamni* Fonsc., *Macrosiphum solanifolii* (Ashm.), and *Aulacorthum solani* (Kalt.). The infestations of these aphides vary widely from season to season; *M. solanifolii* and *A. solani* occurred in large numbers only in 1945 and there is no reason to believe these two species are important in spreading rugose mosaic and leaf roll. *A. rhamni* also seems to be unimportant compared with *M. persicae*, possibly because it is less active and moves less freely from plant to plant. Heavy infestations of *A. rhamni* occurred in 1940, 1941 and 1942; the species was rare between 1943 and 1946, but became abundant again in 1947. Its only method of overwintering seems to be in the egg stage on species of *Rhamnus* from which migrants pass to potatoes in June

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or early July; infestation on potatoes are usually maximal in August (Doncaster, 1943).

Fruiting peaches out of doors and in unheated glasshouses were the most important hosts on which *M. persicae* overwintered as eggs. This species, however, has alternative methods of overwintering, though the success of these depends greatly on the weather. During mild winters the aphid can continue to survive on brassica crops, sugar beet stecklings and other winter-hardy herbaceous plants. After the severe winters of 1940–1, 1941–2, 1944–5 and 1945–6, few *M. persicae* survived by this manner, and migrations from peach were also smaller and later than usual, so that infestations on potatoes developed later than in other years. Another overwintering site for *M. persicae* was discovered in mangold clamps. Aphides introduced on the leaves survive and multiply provided the clamp covering is adequate to prevent damage to the roots by frost (Broadbent, 1947).

The spring migration of *M. persicae* from overwintering sites to potatoes took place each year during May, and sometimes continued into June, a period when early potatoes are well advanced and main crops just above ground. The maximum population on the foliage was usually reached towards the end of July. The numbers then declined (because of migration to other hosts and the activities of parasites and predators), reached a minimum during the first half of August, and sometimes showed a second but smaller rise in September. In 1941 the population did not reach its maximum until about the end of August, and this was associated with unusually late spread of leaf-roll in potato crops.

There was more spread of both leaf roll and rugose mosaic in years of heavy infestations of *M. persicae* than in others, but there was no simple quantitative relationship between aphis numbers on different crops and the spread of virus diseases. Often there was a greater spread in crops with light than with heavy infestations, suggesting that the activities of individual aphides are more important than the populations achieved. Only aphides that move from plant to plant can transmit viruses, and it seems that conditions within the crop that influence their movement, particularly in early stages of crop growth, are more important than the size of the population reached later in the season. Apterae may do some transmission at or near the peak of infestation, especially in dense crops where interlacing of the foliage facilitates movement from plant to plant, but the winged spring migrants seem to cause much of the total spread (Gregory, 1943). The winged migrants bred on potatoes seem to be relatively unimportant, perhaps because they are no longer attracted by potatoes or because the plants are now more resistant to infection.

The aphis populations were estimated by counts at regular intervals of the numbers occurring on 100 leaves taken from plants selected at random. Information on the number and movement of winged migrants was obtained by catches on specially designed sticky traps. The lack of any quantitative agreement between trap catches or counts of aphis populations on the plants and the amount of spread of virus diseases suggested that the method might be unreliable. The efficiency of the counting method and of the sticky traps was therefore tested thoroughly. It was concluded that an estimate of the aphides per plant is more useful in virus work than one per 100 leaves, for the number of leaves per plant varies greatly during the season and from crop to crop, and the individual plant is the unit concerned in infection. A rapid and reasonably accurate method of estimating the aphis population per plant was devised based on the percentage of leaves infested and not calling for counts of individual aphides.

Sticky traps were found to give reproducible results when placed at the same height in different parts of the same potato crop. Hence the catch of a single species or total catches in different localities or in different seasons can be legitimately compared. Yellow traps caught more aphides than did white ones. Different species fly at different heights during the summer migration, so that traps at one height only are unsuitable for estimating the relative abundance of different species.

The conditions influencing flight of winged aphides are still far from understood. Field observations and preliminary laboratory experiments suggested that high humidity is less effective in preventing flight than was generally believed. Also, records of wind speeds taken within and above potato crops showed that wind speeds within the crop are often suitable for flight when meteorological instruments in more normal positions would suggest a too strong wind.

The spread and control of leaf roll and rugose mosaic

Periodical sampling of 63 crops of Majestic showed that on the average three-quarters of the final yield of tubers was obtained by the middle of August. In the wet summers of 1941 and 1944, however, about a quarter of the final yield was added in September. The weight of "seed" size tubers averaged 4·1 tons per acre at its maximum in July or August, and declined to 3·2 tons at the end of the season. Tubers are formed during July and subsequent differences in the rate of growth of individual tubers leads to their differentiation into "ware", "seed" and "chats". The yield of seed sized tubers per acre can be increased by close spacing and by planting large setts, but the total increased yield of all tubers obtained by these practices does not usually exceed the increased weight planted. Wide spacing of small setts gives the highest yields of seed and of total tubers per ton of potatoes planted, but close spacing of large setts gives the highest yields per acre. Under present conditions in the ware-producing districts it is more profitable to allow a crop to mature at normal spacing than to attempt by early lifting, or by close spacing, to increase the proportion of seed.

Information on the times and distances of spread of rugose mosaic and leaf roll was obtained by standardised trials made each year at a number of centres. In high-land seed-growing districts, such as North Wales, Dartmoor and Northumberland, the diseases increased little in any year, but the amount of spread in lowland districts varied greatly. It was least in 1942 when *M. persicae* was scarce on all hosts. The two diseases spread at different rates in different districts, the increase of rugose mosaic varying from one-quarter to nearly six times that of leaf roll. Most infections occurred early in the season; about half the season's spread of both viruses normally occurred by the time the aphis population reached its peak. Rugose mosaic increased after the first week in August in only 10 per cent. of the crops and leaf roll in 30 per cent. Burning of haulm, or lifting early enough to avoid virus infection of the tubers, would therefore involve very substantial losses of crop. Spread of virus is mainly local, and distant stocks of infected potatoes are relatively harmless to healthy stocks, except perhaps to the edge rows. The most important sources of virus are infected plants scattered within the crop, that is infected tubers in the stock planted or volunteer plants surviving from previous crops. Volunteer plants were found to be unexpectedly numerous and their existence points to the value of a good rotation in safeguarding the health of stocks. In the years 1944–46, from 2,000 to 7,000 volunteer plants to the acre were found in the first crop after potatoes. In the third year, the average interval before another potato crop was taken on the same land, there was an average population of 700 volunteers. The health of these volunteers was roughly the same as that of the crop from which they came, for leaf roll and rugose mosaic do not appear to spread between volunteer plants growing in other crops. In agreement with this, no aphides were found infesting volunteer potato plants in cereals. Volunteers from badly infected potato crops, however, are common sources of infection and are often responsible for the rapid degeneration of high quality stocks (Doncaster and Gregory, 1948).

Removing obviously infected diseased plants from Majestic stocks during July did not appreciably reduce the spread of either rugose mosaic or leaf-roll. Roguing in mid-June, tested in one season only, reduced rugose mosaic to one-third of the amount in unrogued plots, but had no effect on the spread of leaf-roll. Roguing presumably fails to control spread because of the early date at which most transmission occurs. If roguing were repeated and plants showing symptoms of current season infection were also removed, the percentage of diseased tubers could be halved; further improvement in health would result from removing the plants adjacent to those showing symptoms, but roguing on this scale is uneconomic.

The amount of transmission by early winged migrants in all probability also explains the failure of fumigating large plots with nicotine vapour to maintain the health of potato stocks. Tests in 1942, 1943 and 1944 showed that one fumigation successfully destroyed the aphis infestation but had little effect on the spread of rugose mosaic and leaf-roll.

The results of these field studies and experiments suggests that healthy potato seed could if necessary be produced in the English lowlands, but this would call for drastic roguing and such early lifting that it would be uneconomic. The most practical method of increasing the useful length of life of stocks seems to be the further improvement of health in seed-growing districts, so that fewer infected tubers are planted in the ware crops, which themselves should be grown away from infected stocks and, most important, on land free from volunteers.

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Potato virus X

Improvement of seed stocks requires more than the still further reduction of leaf roll and rugose mosaic and needs extending to the control of mild mosaic caused by potato virus X. This virus is almost universally present in commercial stocks of many varieties, and though its effects on individual plants are small compared with those of the aphis-transmitted viruses, the aggregate losses it causes probably exceed those caused by the others combined. Yield trials with Majestic and Arran Banner (Bawden, Kassanis and Roberts, 1948) showed that infection with different strains of virus X reduced the yield by from 5 to 25 per cent., so that with present potato acreage the annual loss in Majestic alone is probably the equivalent of the produce from 50,000 acres.

Control is being attempted by the establishment of new virus-free stocks of these varieties, which necessitates first the selection of individual tubers and their subsequent propagation to large quantities. Rapid and reliable methods of testing for avirulent strains, applicable to tubers as well as growing plants, have been devised, but evidence was also obtained that selection of new lines needs basing on features additional to freedom from infection. The progeny of different tubers of one variety may vary in yield and other cultural qualities, even though they are virus-free.

Field experiments showed that virus X spread slowly at Rothamsted compared with leaf roll and rugose mosaic. Spread occurred only to healthy plants in direct contact with infected ones. Some strains spread more rapidly than others, but less than 1 in 10 of the healthy plants in contact with infected ones during one growing season became infected. Spread was much more rapid in tomato plants than in potatoes, and in tomatoes spread was demonstrated between plants having only root contact with one another. Underground spread also probably occurs with potatoes, for this is the simplest explanation of the occurrence of infected tubers from plants where foliage is apparently virus-free at the end of the season (Roberts, 1946; 1948). Spread can also occur as a result of contact between the sprouts of healthy and infected tubers, but other parts of the tuber are difficult to infect.

It is concluded that the propagation of virus-free stocks on a commercial scale is possible provided strict precautions are taken to exclude sources of infection, of which the most important are likely to be volunteer plants.

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