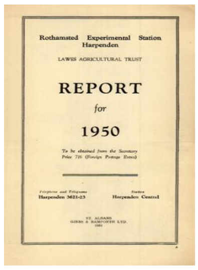
ROTHAMSTED RESEARCH

Report for 1950


Rothamsted Experimental Station
Harpenden

REPORT
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Plant Pathology Department

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PLANT PATHOLOGY DEPARTMENT

By F. C. Bawden

Two new appointments were made in August, when Mr. J. M. Hirst and Dr. F. T. Last began work on the epidemiology of potato blight and cereal mildews.

Six members of the department attended the Seventh International Botanical Congress at Stockholm in July, and papers were read by Mr. F. C. Bawden, Dr. M. D. Glynne, Dr. P. H. Gregory, Dr. R. Hull and Dr. M. A. Watson ; Mr. Bawden was Vice-President of the Phytopathology Section.

Dr. Gregory attended the Fifth International Congress of Microbiology at Rio de Janeiro in August and read a paper entitled *The efficiency of spore traps used in the study of aerobiology* ; Mr. Bawden was President (*in absentia*) of Section VII (Plant Pathogenic Micro-Organisms).

In March and April Mr. Bawden gave a course of lectures on Plant Viruses and Virus Diseases at Yale University ; he also attended a conference on viruses at the California Institute of Technology, Pasadena, and visited other Universities and Research Stations in the United States of America and in Canada.

Dr. B. Kassanis was awarded the degree of D.Sc., and Mr. R. H. E. Bradley the degree of Ph.D. of London University.

Viruses and Virus Diseases

Laboratory and glasshouse work

In previous reports the anomalous behaviour of the Rothamsted tobacco necrosis virus has been mentioned, particularly the variations in infectivity of different preparations and the occurrence in sap from infected plants of specific nucleoproteins with two different particle sizes. Further work on the purification and properties of this virus has produced preparations with greater infectivity than that of those obtained previously. The relationship between the particles of two different sizes still remains obscure, but evidence accumulates that not all the specific nucleoprotein is infective. Some particles seem to become infective only after being liberated into the sap, infectivity apparently being conferred by some mechanism which is activated when leaf cells are injured and which is destroyed by freezing undamaged leaves. Exposure to citrate destroys the infectivity of this virus without denaturing the nucleoprotein or affecting serological activity. The inactivation by citrate depends greatly on other factors, which may partially explain the variations in infectivity found with different preparations of this virus (76, 77).

Much time was spent testing various spraying techniques in attempts to produce uniform droplets suitable for counting virus particles by electron microscopy, but so far great difficulty has been encountered in getting consistent results. Isolated intracellular inclusions from plants infected with several different viruses were examined in the electron microscope. Those from plants infected with tobacco mosaic, tomato aucuba mosaic, cabbage blackring and henbane mosaic viruses appeared to be composed largely of bundles of rod-shaped particles similar to those earlier demonstrated in mounts of clarified infective sap (62). Rod-shaped particles were also detected in inclusion bodies formed by tobacco etch virus, but these were over-lain by other material, suggesting that the bodies may have a membrane. The inclusions formed by cauliflower mosaic virus were so stable that they could not be broken into fragments small enough for electron microscopy, and, as with examinations of infective sap, no particles could be identified as likely to be virus particles.

Previous attempts to identify any specific particles in sap from sugar beet with yellows have failed, but electron micrographs of the precipitate produced by mixing infective sap with virus-antiserum showed clusters of rods adhering to larger masses of indeterminate shape. The rods appeared to be destroyed when the sap was frozen, though the sap was still serologically active. Similar rods were also seen occasionally in sap from infected beet without precipitation with antiserum. Their relationship with the virus is uncertain and they would seem to be too few to form more than a minor component of the antigens specific to yellows-infected plants ; also, the somatic type of precipitin reaction suggests that most of the antigen particles are not rod-shaped.

At the request of workers in the Gold Coast and in East Africa, attempts were made to identify the particles of cacao swollen shoot and groundnut rosette viruses. Electron micrographs were made of extracts from various organs of infected plants but these showed nothing that was not also present in comparable extracts from healthy plants. Groundnut rosette virus, which hitherto had been transmitted only by grafting and aphids, was transmitted mechanically, though only with difficulty; about 10 per cent of healthy seedlings inoculated with sap from diseased plants became infected if they were placed in darkness for a few days immediately before inoculation and an abrasive was incorporated in the inoculum. Similar methods failed to transmit cacao swollen shoot virus ; the Rothamsted tobacco necrosis virus, however was readily transmitted by inoculation to and from leaves of cacao.

Previous studies on the effect of dilution on the numbers of local lesions produced by plant viruses have shown that results are incompatible with the generally held idea that infection occurs because of chance encounters between single virus particles and uniformly susceptible sites. To gain further information on this problem, experiments were made with a virus that attacks clover-nodule bacteria. These showed that single particles can infect bacteria, but that not every particle succeeds in doing so, and the chance of one doing so depends on the conditions in the bacterial culture. By analogy, it seems that infection of crop plants may also be produced by the action of single virus particles, but that susceptible sites in the inoculated leaves are not uniform, so that the chances of a virus particle becoming established differs at different sites (73).

Work has started on the inactivation of plant viruses by irradiation with ultra-violet light. Workers studying some bacterial viruses have found that irradiated particles that are non-infective when acting singly may cause infection when two or more enter the same bacterial cell. No evidence has been obtained that plant viruses behave in this manner, but evidence is accumulating that virus inactivated by irradiation specifically interferes with infection by active virus.

Host-plant physiology

The fact that carbohydrates accumulate in leaves of sugar beet with yellows has long been known and generally attributed to failure of normal translocation because of phloem necrosis. This is not the correct interpretation, however, for during a period of darkness yellowed and healthy leaves lost equal quantities of carbohydrate (37). Spraying infected sugar beet leaves daily with 2 per cent and 10 per cent sucrose solutions increased the severity of the symptoms in conditions of low light intensity when they normally are masked. Spraying produced no symptoms in uninfected plants, though it increased their carbohydrate content, and it was concluded that the external symptoms of yellows require a high sugar content, but they are not directly caused by it.

Reducing the light intensity under which plants are raised has previously been found to increase their susceptibility to infection by mechanically transmitted viruses. Experiments with henbane mosaic and sugar beet yellows suggest that there is no comparable increase in susceptibility when viruses are introduced by aphid vectors. Differences in susceptibility comparable with those produced by varying illumination were also produced by varying the amount of water supplied to plants before they were inoculated, those receiving abundant water giving many more local lesions than those kept drier. These differences are possibly correlated with the thinner cuticle and disorganized palisade cells that characterize plants grown in a saturated soil. The differences between plants receiving different amounts of water were reduced, but not abolished, by shading or by incorporating an abrasive in the inoculum. Differessential watering appeared to have no consistent effect on the extent to which tobacco mosaic virus multiplied in systemically infected plants.

The freeing of Majestic potato tubers from leaf roll by heating for 20 or more days at 37·5°C. was confirmed, and the effect shown to be permanent. Plants in the third generation as progeny from heated tubers were still without symptoms, and there seems little doubt that such treatment destroys the leaf roll virus in infected tubers and does not merely produce a temporary masking of symptoms (71).

Transmission by aphids

The readiness with which aphids became infective with potato leaf roll virus was found to depend greatly on the age of the plants on which they are fed. When feeding on potato plants, many more aphids became infective after feeding on emerging sprouts, which were symptomless, than after feeding for similar lengths of time on older plants which showed pronounced symptoms. Similarly, with *Datura tatula*, plants infected for only a fortnight and showing slight symptoms were a better source of virus for aphids than were more severely diseased plants that had been infected for longer periods. It seems likely that the concentration of infective virus reaches its highest level early in the course of infection and then declines as the leaf symptoms develop. This may help to explain the fact that, in most years, the main spread of leaf roll in crops at Rothamsted occurs early in the season.

Using *D. tatula*, which reacts more quickly than potato, shows more definite symptoms, is more easily infected and is a better source of the virus for aphids than potato, some of the factors influencing the transmission of the leaf roll virus by *Myzus persicae* were studied. The results confirmed that leaf roll virus persists for many days in the aphids and that aphids cannot infect healthy plants immediately they have acquired the virus. Aphids that had fed for two hours on infected plants became infective, but they did not transmit the virus to healthy plants within the next day. The delay period could be passed while feeding on diseased plants, and aphids which had fed on these for several days could infect healthy plants within the first fifteen minutes of feeding on them.

A virus isolated from a sugar beet found naturally infected at Lincoln seems to be similar to one previously described in the United States of America with the name yellow net. It is not related to beet yellows or mosaic. It is aphid-transmitted and persists in the vector for some time; preliminary results suggest that aphids do not become infective until about two days after they first start to feed on infected plants.

Other viruses whose insect transmission was studied were henbane mosaic, cauliflower mosaic and cabbage black ringspot. None of these persists for more than a few hours in the aphid vectors, and the whole process of acquiring the virus and infecting a healthy plant can occur in less than two minutes. Before settling down to feed continuously, aphids were found to make several preliminary probes into leaves, and these first punctures seem to be the important part of the aphids' feeding habits in transmitting these non-persistent viruses. It was shown that aphids could become infective by feeding on detached epidermal strippings of leaves, and it seems that they normally acquire these viruses from, and transmit them to, the epidermis. When infective aphids were disturbed at intervals and prevented from feeding continuously, they caused more infections than when they were left undisturbed. The probability that a puncture of a leaf by an infective aphid would result in an infection reached a maximum in punctures maintained for about half a minute. The mechanism responsible for such speedy transmission is unknown, but it would seem that only virus which is carried somewhere in the mouthparts of the aphids could be concerned. The process does not seem to be wholly mechanical, for there is considerable specificity between non-persistent viruses and the insects that act as vectors; also, when the stylets of aphids were smeared with infective sap, the aphids did not infect healthy plants on which they subsequently fed.

In attempts to gain further information on the feeding behaviour of aphids, experiments were made with *M. persicae* colonizing turnip and sugar beet plants raised in nutrient solution containing radioactive phosphorus (P^{32}). The results suggest that the method will not help to elucidate the transmission of the non-persistent viruses but may help with the persistent viruses, the vectors of which need

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to feed for long periods to become highly infective. When aphids were fed on plants containing the optimum concentration of the tracer, they showed their first detectable radio-activity after 15 minutes. Autoradiographs made of various organs, dissected from aphids that had fed on such plants for different periods, showed slight activity in the stomach after about 10 minutes' feeding; after 1 to 2 days, activity was detectable in all organs except the nervous tissue, but was most concentrated in the stomach of the adult and in the developing ova and nymphs. The activity increased during periods of 24 hours' feeding in a manner suggesting that aphids feed at the same rate during the hours of daylight and darkness.

This suggestion was confirmed by studies on excretion, for aphids excrete honeydew only while feeding, and they excreted at equal rates during periods of light and darkness. The effect of evaporation on excretion was studied in the wind-tunnel and it was found that the rate at which honeydew was deposited was not a reliable indication of feeding rate when external conditions varied. The method of excreting honeydew was studied in 22 aphid species, and was found to be similar in all those that infect aerial parts of plants. Methods were modified in gall-inhabiting and root-feeding species, and it seems that the production of wax by many gall-inhabiting species may be correlated with the need to cover the sticky excretion.

Experiments were made on the effects of high temperatures on the survival of aphids in different conditions. When removed from their host plants and kept for an hour at relative humidity of 50 per cent, the thermal death point of five species lay between 38° and 41°C. Many individual aphids alive at the end of the tests, died within the next day. Increasing the relative humidity during the period of heating increased the number of aphids killed. Fewer were killed when the aphids were kept for the previous four hours at high humidities than when they were kept at low humidities. Aphids on plants withstood temperatures higher than those which killed when they were not on plants, presumably because water lost by evaporation could be replenished.

Field Work

Potato virus diseases

Experiments on the effect of roguing potato crops in south-east England were ended and summarized; the results showed that, although the practice sometimes reduces the spread of virus diseases, the effect is too small to be economically worth-while (65).

The experiment to test the effects of varying planting dates and manurial treatments on the spread of leaf roll and rugose mosaic was done for the sixth and last time in 1950. Tuber samples from the 1949 experiment were planted in 1950 and showed that fertilizer differences did not affect spread significantly; leaf roll spread more in the first-planted than in later-planted plots, but rugose mosaic spread equally in all.

Varying the spacing between potato plants also had no effect on the spread of rugose mosaic, although it had with leaf roll; 18 per cent of the plants adjacent to infected plants became infected at a spacing of 9 in., 8 per cent at 18 in. and 2 per cent at 36 in. Irrigating plots by over-head watering did not affect aphid populations or virus-spread.

The progeny from a small-scale trial in 1949, when potato plants were sprayed at weekly intervals with DDT, Parathion and Pestox III, showed that spread of leaf roll was reduced from 15 per cent in unsprayed plots to 1 per cent, but rugose mosaic was unaffected, averaging 76 per cent in control plots and 77 per cent in the sprayed. Further experiments to test the effects of five of the newer insecticides on aphid populations and virus spread in potato crops were made in 1950.

A technique for marking aphids with a radio-active tracer was developed ; it was hoped to use this to study the distance to which aphids move in potato crops, but there were too few aphids during the summer for it to be applied. Many winged *M. persicae* entered the crops during May and June, but the activity of predators prevented heavy infestations from developing.

Further evidence that most of the spread of potato viruses is occasioned by winged aphids was obtained from experiments in which some plants were surrounded by sticky boards to prevent wingless aphids from colonizing them (66).

Sugar beet virus diseases

As in previous years much work was done in attempts to devise methods whereby beet yellows could be controlled in steckling beds. The most beneficial measure again found was to raise stecklings in districts remote from other crops of beet and mangolds, but considerable benefit was also derived from other treatments such as growing stecklings under cover crops or spraying with systemic insecticides. These control measures were extensively practised in 1950, when a certification scheme for stecklings was introduced. More than half the total stecklings needed for the British seed crop were grown in isolation and the remainder were raised under cover crops or sprayed. Methods were devised for making inspections of crops and courses of instruction arranged for inspectors. Samples of inspected beds and of all crops raised in isolated districts are being obtained for planting at Dunholme, so that the state of the crops in autumn can be compared with that in the next spring.

Producing stecklings in isolation raises problems of storage and transport, and some unexplained anomalies have arisen. A crop of virus-free stecklings grown in Perthshire, for example, gave an excellent stand when out-wintered in the field or lifted and clamped there but plants sent to Suffolk and clamped there in the autumn failed completely, although the roots looked satisfactory when taken from the clamp. Experiments to determine the best sowing date, cultural practices and storage conditions, for stecklings of sugar beet, red beet, and mangolds, therefore, were started in Scotland.

In attempts to find sugar beet that resist or tolerate yellows, further selections were made from plants that showed relatively little yellowing in the field. There was no evidence from glasshouse tests that the progeny of these were more difficult to infect by aphids than the progeny of other lines, but in the field some of them remained greener when infected. The results of yield trials to see whether the extent of yellowing is correlated with loss of yield, are not yet complete.

In a field trial on the root crop, late singling was found to reduce the incidence of yellows by enough to increase yield by about two tons of roots to the acre. Late singling had little effect on late sown crops, but on those sown in March it reduced yellows because at the time of the first migration of aphids there were more aphids per plant on the unsingled than on the singled crops, and many of the plants infected in the unsingled crops were eliminated at singling.

To test the influence of mangold clamps in initiating outbreaks of yellows, a scheme was arranged in conjunction with a Farmer's Committee at Bury St. Edmunds, for clearing all clamps by the end of March from an area of 70 sq. miles. The population of winged aphids in this area was compared with that in a neighbouring untreated area by trapping methods, but the catches have not yet been analyzed. Counts in 160 beet crops in and around the cleared area showed less yellows in the area than outside it, but it is not yet known whether the differences are significant.

The species and numbers of aphids infesting clamped mangolds, and the times at which they migrated, were studied in the spring; species other than *Myzus persicae* are being tested to see whether they are vectors. The control of aphids in mangold clamps, by spraying crops before lifting, and by treatments applied to the clamp, was tested by experiments made in the autumn, but the results will not be known until 1951.

A yellowing disease of sugar beet which was first found in an Irish line (Variety 41) and is seed-transmitted has been mentioned in earlier reports. Further work has shown that the cause is not related to beet yellows virus and that the condition can be seed-transmitted in other lines of beet such as Kleinwanzleben E. It does not seem to be transmitted through the pollen, and infected seedlings were obtained from crosses only when the female parent was infected.

Lettuce mosaic

Epidemiological studies on lettuce mosaic were continued for the third year in the Thames Valley. These studies have shown that, in addition to disease outbreaks initiated by seed-borne infection, many occur because crops are sown or transplanted near to those already infected. Although aphid vectors were numerous during the spring of 1950, serious outbreaks of mosaic were avoided by omitting a crop of winter lettuce, and separating early-transplanted and later-drilled crops into large single blocks at a distance from one another. *Macrosiphum euphorbiae* Thomas, which occurs frequently on lettuce, more particularly during winter, was shown to be a vector of the mosaic virus, but its importance in the field is unknown.

Diseases of cruciferous crops

Virus diseases seemed unusually prevalent in brassicae during 1950 and caused extensive losses, particularly in broccoli. Of the two viruses mainly concerned, cauliflower mosaic was much more prevalent than cabbage black ringspot. Both viruses were trans-

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mitted by *Myzus persicae* and *Brevicoryne brassicae* ; in glasshouse experiments, both behaved as typical non-persistent viruses and cabbage black ringspot was the easier to transmit to broccoli, cauliflower or cabbage. Cabbage black ringspot was also found to have a wider host range than cauliflower mosaic virus, so that more sources of infection in wild hosts might be expected. The greater prevalence of cauliflower mosaic virus suggests that it has other insect vectors which do not transmit cabbage black ringspot virus. Surveys were made of the aphid infestation and occurrence of infected plants in commercial crops, as a preliminary to starting extensive field investigations on the spread and control of these viruses.

Mycology

Studies were made with the wind tunnel on the deposition of spores on plane surfaces inclined at various angles to the wind, and the results are being used to improve the design of spore traps and help the interpretation of catches in the field. The total catches and the catches on the different surfaces of horizontal microscope slides varied greatly with wind speed. At speeds around 10 metres per second, catches were high and spores were deposited almost equally on upper and lower surfaces. As the wind speed decreased to 3 metres per second, catches also decreased ; below 3 metres per second, few or none were caught on the lower surface, but catches increased on the upper surface because the effects of gravity become pronounced (69). Spore trapping in the open showed that the main deposition of *Erysiphe graminis* occurred between 15th June and 15th July, and was later and smaller than in 1948 and 1949. There was no heavy deposition of *Alternaria* spores in 1950. In a potato crop, sporangia of *Phytophthora infestans* were caught in large numbers after blight had developed.

Observations in collaboration with Mr. S. Waller were continued on the life history and distribution of the fungus associated with the lethal disease of sycamore trees at Wanstead. The fungus, which presents many novel features, has now been found to resemble *Coniosporium corticale*, previously reported as a saprophyte on maple in Canada and the United States of America.

A rotation experiment to compare the effects of different crops in freeing land from infestation by eyespot, caused by *Cercosporella herpotrichoides* Fron., from take-all, caused by *Ophiobolus graminis* Sacc., and from weeds, was begun after harvesting the 1948 wheat crop in which all three were abundant. Some effects of wheat, winter beans, potatoes and fallow in 1949 on the following wheat crop were recorded in May, 1950 ; 37 per cent of the wheat plants following wheat were infected by eyespot, 27 per cent by take-all ; wheat following beans, potatoes and fallow had respectively 20, 20 and 6 per cent plants infected by eyespot, none by take-all. Wheat after fallow was heavily infested by wheat bulb fly *Hylemya coarctata*, 85 per cent of the plants being affected in March, about two-thirds of them dying later (only 4-8 per cent were affected in wheat after crops). The resulting bare patches became colonized by weeds, which at harvest were almost as abundant after fallow as after wheat ; weeds were much less abundant after beans and potatoes where a good plant was maintained. Barley had slightly less eyespot than wheat, and oats had very little. Take-all occurred on the barley after wheat, but there was none in any other crops. The eelworm causing tulip root, *Ditylenchus dipsaci*, was found on oats and on some weeds in this experiment, the only record of this pest at Rothamsted since the severe attack on Pastures field in 1934.

A field experiment on the effects of spraying with H_2SO_4, varying seed rates and dates of application of nitrogenous fertilizer, on wheat gave few significant effects of treatments because the crop was heavily and unevenly infested by wireworms which killed many plants. There was also a heavy infestation by the root eelworm *Heterodera major* and a moderate one by wheat bulb fly. In this poor crop, spraying with H_2SO_4, though it reduced the proportion of straws severely infected by eyespot at harvest, did not increase yield of grain.

The effect of applying nitrogenous fertilizer at different dates in a pot experiment showed that the per cent straws severely infected at harvest was reduced (from 77 per cent) by applying the fertilizer in autumn or in early spring (to a mean of 15 per cent) but that application in May did not reduce the disease appreciably.

Eyespot is most severe in wet seasons and spores are probably dispersed by rain, but little is known about the importance of rain falling at different times. To gain information on the point an experiment was made in which rain was excluded and pots were watered either overhead or from below. Overhead watering in December and January had the greatest effect in increasing the incidence of eyespot and the number of plants killed by the disease.

The manner in which host-plant nutrition affects the susceptibility of different cereals to eyespot was examined using plants grown in water cultures. Susceptibility was expressed as the proportion of total leaf sheaths per plant that were penetrated by the fungus before the plants tillered, a method that seems to be more precise than any previously employed. When grown in water, susceptibilities of wheat, barley, oats and rye were 96, 83, 75 and 60 per cent respectively, whereas in nutrient solution the values fell to 72, 25, 10 and 3 per cent.

Corticium (*Rhizoctonia*) *solani*, the cause of sharp eyespot in wheat, was found for the first time causing a severe disease in oats. Some evidence was obtained that the fungus occurs in strains that affect different plants differentially (68).

Further work on the relation between the concentration of spores of *Plasmodiophora brassicae*, the cause of club root, and the number of root-hair infections, showed that logarithms of the two variables are linearly related. Comparisons of results from experiments using new and mature spores suggested that differences were correlated with different proportions of viable spores. Host-plant nutrition was found to affect the proportion of plants that became clubbed when exposed to given spore concentrations. Clubbing was increased by high nutrient levels and early application of nutrients. The proportion of clubbed plants can be used quantitatively for assessing infestation of soil by *P. brassicae*, but only at lower levels of infestation than can counts of root-hair infections and only when the nutrient status is known. New techniques were developed for studying the factors involved in spore germination and the early stages of infection and it is expected that these will provide more precise information than has been possible previously.

The unusually wet summer led to the earliest and most severe outbreak of potato blight (*Phytopthora infestans*) experienced at Rothamsted for many years. Observations on the time of appearance of new lesions in the crops and the time at which potted plants became infected suggested that night temperatures and humidities were important factors in determining spread. Two applications of copper-containing sprays increased the yield of tubers by 1·5 tons per acre. Of five materials compared for haulm destruction, sulphuric acid was the most effective : *P. infestans* was sometimes still active on stems that appeared dead.

As a preliminary to starting experiments to determine the effects of powdery mildew (*Erysiphe graminis*) on the yield of cereals, the protective actions of various fungicides were studied, and lime sulphur was found to have a beneficial effect lasting for a fortnight.

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