ROTHAMSTED RESEARCH

# Rothamsted Report for 1947

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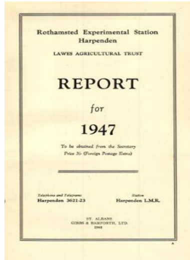


## Special Reviews

### Rothamsted Research

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# THE ELECTRIC CHARGE ON SOIL PARTICLES

By R. K. Schofield

Experimenting both in his laboratory and in his garden near Moscow in 1808, Reuss found that water in contact with soil carries a positive electric charge in consequence of which it is transported towards a cathode. In this way he discovered the phenomenon now known as electro-osmosis. Nearly half a century later, Thompson and Way discovered the phenomenon of base exchange in soil. For many years these two phenomena were separately investigated: the first by physicists, and the second by chemists. The artificial division between these investigations retarded progress, and the realisation that both phenomena have the same root cause is a comparatively recent development. One object of the physico-chemical studies conducted in the Physics Department has been to establish the nature of the electric separation in soil. For while electro-osmosis and base exchange provide the clearest evidence for electric separation it influences both the physical and the chemical behaviour of soil in other ways.

The fact that clay soils shrink when dried, and swell again when rewetted, leads to the conclusion that the particles are not in solid contact but are separated by water films. It is now clear that the exchangeable cations play a dominant part in maintaining these water films and regulating their thickness. In this phenomenon the chemical nature of the exchangeable ions profoundly influences the physical effects they produce.

In connection with the availability of exchangeable cations as plant nutrients the fact that they are held by electrostatic attraction to negatively charged soil particles is of great significance, and it is not surprising that investigations with a purely chemical outlook, which take no account of the powerful electric fields close to soil particles, have achieved only a limited success.

It has become increasingly clear that as far as possible all the consequences of electric separation must be considered in relation to one another, and that the artificial distinction between physics and chemistry must be completely broken down. The undertaking is formidable, and much groundwork is needed before results can be obtained that bear directly on the very complex conditions actually existing in field soil.

## Measurement of the electric charges on soil particles

Ionic exchange provides the only reliable method for measuring the net electric charge carried by a particular sample of soil. Since the charge depends to some extent upon the nature and concentrations of the ions in the solution surrounding the soil particles these must be controlled or determined at the same time. Hitherto most methods used for determining exchangeable cations have been designed for the routine examination of large numbers of soil samples, and have been considered satisfactory so long as they were reasonably rapid and furnished reproducible results. For precise

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measurement of net charge no existing method was found to be entirely satisfactory. Control of aluminium ions has been the main problem.

A technique has now been worked out which effectively prevents disturbance from aluminium ions from pH 2·5 to pH 8 (1). The belief generally held that clays lose their negative charge when in contact with solutions of low pH is ill-founded. The methods usually employed fail to detect the presence of exchangeable aluminium. When sufficient washings are given to remove the exchangeable aluminium it is found that the negative charge falls off much less with fall in pH than earlier work had indicated. For example, a sample of Rothamsted subsoil clay, which has a net negative charge of 27 milliequivalents per 100 g. when in equilibrium with a N/5 ammonium chloride solution at pH 7, has a net negative charge of 22 milliequivalents when the pH of the solution is reduced to 2·5.

By simultaneously measuring the retention of ammonium and chloride ions it has been found that only ammonium ions are concentrated close to the surfaces of the clay particles in the solution at pH 7. Chloride ions are actually repelled from the surfaces, which indicates that all the electric charges on the clay particles are of negative sign. In the solution of pH 2·5, however, chloride ions are slightly attracted. Compared with the condition at pH 7 about 2 milliequivalents of chloride ions are attracted to the surfaces of the particles. It thus appears that the 22 milliequivalents of *net* negative charge is made up of 24 milliequivalents of negative and 2 milliequivalents of positive charge.

An independent test fully supports this conclusion. It has been found that if the clay is repeatedly washed with acid ammonium oxalate in sunlight a photo-chemical action occurs resulting in the solution of iron and aluminium amounting to about 7 per cent. of the original weight. The residue is nearly white, and has a charge at pH 2·5 of close on 24 milliequivalents computed on the original weight. There can be no doubt that the positive charges present on the original clay when in the solution of pH 2·5 were on the hydrous oxides of iron and aluminium (which the oxalate washing removed), leaving the negative charges carried on the clay mineral proper. It was also observed that the residue repels chloride ions in the solution of pH 2·5, thus confirming that only negative charges are present.

These and parallel results with several other clays compel us to abandon the view hitherto widely held that between pH 3 and pH 7 clays greatly increase their negative charge by dissociation of hydrogen ions. No clay mineral so far examined has been observed to dissociate any hydrogen ions between pH 2·5 and pH 5 in N/5 ammonium chloride solutions. From pH 5 and pH 6 dissociation is just detectable, and it becomes progressively greater to pH 8—the limit of the present measurements.

The crystallographic study of the clay minerals has led to the view that isomorphous replacement should give rise to negative charges that are permanent in the sense that they cannot be increased and decreased reversibly by altering the pH, but can only be changed by processes that disturb the atomic arrangement within the crystals. Below pH 2·5 the charge diminishes but is not

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restored again on raising the pH. There is other evidence that the clay mineral has suffered destructive attack.

It is entirely reasonable to suppose that the constant charge found between pH 2·5 and pH 5 is the "permanent" charge due to isomorphous replacement. It would be very desirable to check this conclusion by direct chemical analyses, but until the process for freeing clay minerals from contamination has been further refined this cannot be done.

It is also reasonable to attribute the progressive rise in the negative charge above pH 6 mainly to the dissociation of hydrions from hydroxyls attached to silicon atoms. Such hydroxyl groups occur round the edges of the silicon-oxygen sheets of the clay minerals and on the free silica. There is some evidence that the iron oxide removed by acid ammonium oxalate, besides carrying positive charges at low pH, may carry a few negative charges above pH 7; but this matter requires further study.

## Negative adsorption and surface areas

Parallel with measurements of the electric charges on soil and clay, investigations have been made to elucidate the way in which electric separation influences soil properties. Mention has already been made of the repulsion exerted by the negative charges on the soil particles upon the free negative ions in the soil solution. By extending Gouy's theory of the diffuse electric double layer the relationship

$$\frac{\Gamma_-}{n} = \frac{q}{\sqrt{\nu\beta n}} - \frac{4}{\nu\beta\Gamma}$$

has been obtained (2). Here $\Gamma_-$ is the "negative adsorption" of the repelled ion, $n$ is the normality of the solution and $\Gamma_-/n$ is a distance that conveniently expresses the extent of the repulsion. $q$ is a factor depending on the valency ratio, $\nu$ is the valency of the repelled ion, $\beta$ is a constant depending on the temperature and dielectric constant of the solvent, and $\Gamma$ is the electric charge on the surface expressed in milliequivalents per square centimetre. This simple equation is valid so long as $\Gamma$ is large enough for the first term to be several times the second, otherwise a more complex expression must be used.

This equation was first applied to existing data of Mattson for the negative adsorption of the chloride, nitrate, sulphate, and ferrocyanide ions by sodium bentonite. Dividing the negative adsorption per 100 g. of bentonite by the normality, and plotting this quotient against $q\sqrt{\nu\beta n}$, the points fall very well on a single straight line from the slope of which an area of 450 square metres per gram is obtained. From crystallographic data we find that pure montmorillonite completely dispersed into its constituent sheets would expose an area of 800 m.$^2$ per gram. Measurements of negative adsorption were, therefore, made using a very fine fraction of bentonite separated with the aid of the supercentifruge. As it is difficult to handle this material except in a flocculated state, calcium chloride was used. Even so, the material could not be concentrated by centrifuging to more than 2 per cent. compared

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with 10 per cent. used by Mattson. The measurement of negative adsorption in these circumstances requires high precision in the chloride determinations, and it was considered very satisfactory that none of the points deviated from a line for 800 m.$^2$ per gram by more than the possible experimental error.

Measurements were also made of negative adsorption by jute (3) in solutions of lithium, sodium, potassium and calcium chlorides. With this material a small negative adsorption was found even in N/20 hydrochloric acid, in which case there would be scarcely any negatively charged carboxyl groups. It appears that about 11 per cent. of water is taken up by the solid matter, the chloride ions being too large to be admitted. In neutral solutions a large additional negative adsorption is found which clearly must be due to the repulsive action of the negative charges resulting from the dissociation of hydrions from the carboxyl groups.

Values ranging from 6 to 22 milliequivalents per 100 g., by means of cation exchange, were obtained for the carboxyl content of different samples of jute. It was found that the negative adsorption observed in the sample of lowest carboxyl content scarcely differed from the amount calculated by the use of Donnan's equation for the membrane equilibrium. Examination of the theory showed that this result is to be expected when the surface density of charge is low in relation to the distances separating opposing surfaces.

The sample with the greatest carboxyl content gave values considerably below the value given by the Donnan equation. The results obtained for solutions above N/20 indicated that in this jute the charges were spread over an area of 160 m.$^2$ per gram. This is roughly a thousand times the external area of the fibres. At the same time an extrapolation of the values obtained in more dilute solutions shows that, in the limit, the chloride ions are completely expelled from 70 c.c. per 100 g. of jute. This is evidently the volume of internal passages within the jute fibres. The area of the walls of the passages being 160 m.$^2$, it follows that the average width of the passages is of the order of 100 Angstrom units.

Thus, by applying physical reasoning to chemical measurements, a new way has been opened up for the exploration of minute structures which are not regular enough to be investigated by X-ray diffraction, and could not be preserved in the high vacuum conditions needed for examination by the electron microscope. It can only be applied when the surface area is very large and when it carries a sufficient density of electric charge, but even with these limitations it should have a wide scope.

### Film thickness

The same basic theory that yielded the equation for negative adsorption has been used to obtain the equation (4)

$$X = \frac{\pi}{\nu\sqrt{\beta c_0}} - \frac{4}{\nu\beta\Gamma}$$

for the thickness, $X$, of the water film on a surface carrying a surface charge $\Gamma$ balanced by exchangeable ions of valency $\nu$, which have a concentration $c_0$ at the outer surface of the film.

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The theory shows that for equilibrium between the film and water in bulk there must be a pressure difference given by the Van t'Hoff equation

$$p_0 = RTc_0.$$

Deryaguin and Kussakov's determinations by optical interference of the thickness of water films between hydrogen bubbles and surfaces of mica and glass are in excellent agreement with the relationship to be expected between $X$ and $p_0$. There is no adjustable constant in the theory so the test is a searching one. The results of their experiments with solutions of sodium chloride are not in satisfactory agreement with the theory. This is puzzling since over the same range of concentration the equation for negative adsorption seems to be entirely reliable. New optical measurements are being carried out with the help of Prof. L. C. Martin.

The theory indicates that $p_0$ is the repulsive pressure between two parallel opposing surfaces separated by a water film of thickness $2X$. We have here a basic concept upon which to build the theory of swelling and shrinking of clay. By itself the concept is too simple because it does not explain flocculation. In its simple form it may, however, be expected to give a fairly good account of the swelling of bentonite containing only monovalent cations.

### Ionic equilibria

When a dilute solution is in equilibrium with a soil having sufficiently high density of surface charge, theory leads us to expect that the following "ratio law" will be obeyed (5):—

> When cations in a dilute solution are in equilibrium with a larger number of exchangeable cations, a change in the concentration of the solution will not disturb the equilibrium if the concentrations of all the monovalent cations are changed in one ratio, those of all the divalent cations in the square of that ratio, and those of all the trivalent cations in the cube of that ratio.

This ratio law has been tested for a number of ion combinations. Using soil from Park Grass Plot 7, that has received dressings of potassium and magnesium salts, a solution containing the chlorides of potassium, magnesium and calcium at a total concentration of N/100 was found, by trial, that would percolate unchanged through the soil. Another solution containing half the concentration of potassium and one quarter the concentrations of magnesium and calcium was then made up, and it was verified that this solution also would percolate unchanged through the same soil sample. The concentrations in these experiments were measured spectrographically in the Chemistry Department. In the majority of soils, calcium is the most abundant ion in the soil solution. These experiments and the theory they support indicate that the potash "status" of the soil should be judged by the ratio of the potassium ion concentration to the square root of the calcium ion concentration in a solution in equilibrium with it.

A further support to the "ratio law" was obtained in experiments with soil from Plot 9 (unlimed), which has become very acid after repeated application of ammonium sulphate. It was found that appreciable concentrations of aluminium ions and hydrogen ions must be present in the solutions in equilibrium with this soil.

Moreover, the aluminium behaved in the way expected of a trivalent ion, while the hydrogen behaved as a monovalent ion.

The behaviour of hydrogen ions has been the subject of special study. Experiments with soil from the unmanured Plot 3 (unlimed) show a nearly constant ratio of hydrogen ion concentration to the square root, the calcium ion concentrations ranging from 40 millinormal to 0·1 millinormal. In the course of these experiments several factors that disturb pH measurements on soil and similar materials have been recognised and brought under control.

When a sufficient degree of control can be secured it will be possible to determine the concentration at which the ratio law begins to fail. This should be higher the higher the density of electric charges on the soil. We already have general evidence to support this expectation, but more work is needed to establish the matter beyond doubt.

## Conclusion

The presence of electric charges on soil particles could be inferred from the early observations mentioned at the beginning of this review. Yet it was only through the work recently carried out in this laboratory that the net amount of charge on soil particles has been measured with reasonable precision over an extended range of pH. The study of the effects produced by these charges has been facilitated by an extension of Gouy's theory which has been checked experimentally in several ways. In this way a number of new lines of investigation have been opened up.

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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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