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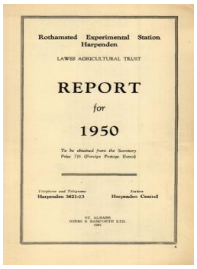
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Review of Work on Potato Root Eelworm

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REVIEW OF WORK ON POTATO ROOT EELWORM

By B. G. Peters

Before summarizing the work of the Nematology department on this subject, a brief account of the nematode itself may be useful. The potato root eelworm, *Heterodera rostochiensis* Wollenweber, 1923, was first found causing damage to potatoes in 1913, simultaneously in Scotland (by Massee) and Germany (by Zimmermann), though there had been a doubtful report of it in Germany as early as 1881 (by Kühn). Its origin is quite unknown and there is no evidence to suggest that it came, with the potato, from South America. Today it is known as a serious parasite of only potatoes and tomatoes, and as mildly attacking a few solanaceous weeds. It was found in Yorkshire by 1917, and in Lincolnshire by 1924. Since then it has spread to most of the potato areas of Britain and Ireland. On the Continent it was early recorded from Denmark and Sweden, as well as Germany, and since 1940 has been found in Holland, Finland, France and Belgium. Outside Europe it is known only from Long Island. It thus appears to be limited to temperate regions, unlike the root-knot eelworm, *H. marioni*, which extends from the temperate zones throughout the tropics.

Like the other cyst-forming species of *Heterodera*, the potato root eelworm enters the finer roots of the growing plant in spring, as a slender larva about 0·5 mm. long. Entrance is assisted by the protrusible mouth-spear (present in all plant eelworms) and it is probable that histolytic enzymes are also involved. The larvae lie within the root cortex, some cells of which are destroyed. The head is closely applied to cells in the developing stele which become changed into giant cells. These in turn serve as sources of food, and the general result is to impede the free circulation of sap. The female worms swell considerably and, the head remaining within the root cortex, the sac-like body bursts out to the exterior some five to eight weeks after larval penetration. At this stage the worm-like males leave the root, fertilize the females, and are found no more. Most female nematodes lay their eggs as they are produced, but the potato root eelworm retains hers within the body, which swells until it is almost spherical, apart from the projecting neck and head. At first white, the colour of the female changes through yellow to brown, this being the outward sign of a chemical change in the nature of the cuticle, which becomes tanned to a tough leathery coating. At some indeterminate time the female releases her hold on the root cortex, falls off into the soil and dies. This stage, a tough, brown, inanimate, spherical sac containing living eggs, and measuring about 0·5 mm. in diameter, is the "cyst." Each egg is an oval, thin, chitinous membrane, about 100μ by 47μ, having a larva coiled within it when mature.

Cysts vary considerably in size. The largest, nearly 1 mm. in diameter, may contain upwards of 600 eggs. It is a feature of this and the other cyst-forming Heteroderas that eggs may remain alive within the cyst for many years—about 10 years but depending on conditions. Each year a few larvae hatch from their eggs and leave

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the cyst, so that an old cyst may be almost or quite empty. The hatching and emergence of larvae is greatly stimulated by a chemical substance diffusing from the roots of growing potatoes or tomatoes. If a root is in the vicinity of a cyst, a large proportion of the contained larvae emerge from the cyst and enter the root, thus completing the life cycle.

A healthy potato may support many thousands of eelworms on its roots without obvious signs of distress. Usually, however, a heavily attacked plant is very stunted in growth. The foliage readily withers and turns brown and the tubers produced are both scanty and small, though not otherwise abnormal. In the field, an infestation first shows itself as one or more small patches of unthrifty plants, the patches extending with each potato crop. Eelworm disease makes itself felt, therefore, as a reduction in yield, especially of ware tubers. The position has been exacerbated in Britain by two world wars involving a great extension of areas under potatoes, with potatoes too frequently in the rotation. The annual economic loss in Britain has recently been officially estimated at £2 million, which makes this one of the worst of our potato pests. It is also a source of serious loss in tomato glasshouses.

The Nematology department came under Rothamsted's administration in 1947 and has been located at Rothamsted only since the summer of 1948. Before that it formed part of the now disbanded Institute of Agricultural Parasitology at St. Albans. In order to see the work on potato root eelworm in its correct perspective it will be essential to bring under brief review the earlier work at the Institute—work carried out successively by some who have never been on the Rothamsted staff : D. O. Morgan, Marjorie J. Triffitt, R. H. Hurst, Enid M. Smedley, and C. T. Calam.

The Institute's work started when Morgan investigated the Lincolnshire outbreak in 1924 and was joined a year later by Peters. After 1926 the biological problems were taken over successively by Triffitt, Franklin and Fenwick, Peters returning to them in 1945. Chemical aspects were dealt with by Hurst, Smedley and Calam.

Morphology and Systematics

At first all the cyst-forming species of *Heterodera* were regarded as biological strains of the one species *H. schachtii*, now the sugar beet eelworm. Misled partly by a German report that the potato root eelworm could slowly become adapted to living on beet, Triffitt (1928) concluded that Wollenweber's species, *H. rostochiensis*, could not be defended. She also found that the Lincolnshire strain produced smaller cysts when transferred to Hertfordshire clay. She noted that these cysts, and others from Ormskirk (1929b), were always of the round type, unlike the lemon-shaped cysts from most other hosts. Franklin (1939b) found that the latter bore minute superficial punctations, randomly scattered, whereas the potato strain resembled another round-cysted species (described from wheat in the United States of America) in having these punctations arranged in rows. Later (1940a) Franklin showed that at least some strains could be distinguished by measuring the lengths of larvae newly hatched or dissected from cysts. In the same year (1940b), on the basis of cyst char-

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acters, lengths of males, length and digitation of spicules, and length of larvae, she split up the species *H. schachtii*, reinstating *H. rostochiensis* as the name of the potato root eelworm, and establishing two others. In addition, Fenwick and Franklin (1942) specified standard conditions for the measurement of larval lengths.

In 1935 Triffitt called attention to "microcysts," spherical bodies with a neck, found in soil, and closely resembling small cysts of the potato root eelworm. While the largest of these is larger than a small eelworm cyst, the smallest is actually smaller than an eelworm egg. If not empty, they contain an undifferentiated cytoplasm, and the wall is rigid and laminated. They are not of nematode origin, but no mycologist or zoologist will yet claim them.

Life-history and Biology

Triffitt (1930b) showed that the potato root eelworm tends to pass through only one generation in a year, although there would seem ample time for at least two during the potato's growing season. She found that cysts attached to potato roots did not turn brown until more than nine weeks after infestation in the spring. Later in the season some started browning before seven weeks, and by August all white cysts visible to the naked eye turned brown within 24 hours on exposure to the air. Eggs from white cysts were found to be immature.

Franklin (1938) showed that one-year-old cysts contained more eggs, and the hatching larvae invaded potato roots more rapidly, than was the case with older cysts. She had earlier shown (1937b) that hatched larvae survive in soil outdoors for 9 months, and in the laboratory for at least 16 months. Both these points have a bearing on the formerly frequent practice of growing potatoes year after year on the same land. The delayed hatching from older cysts might enable potatoes, in a rotation, to establish themselves before the invasion of their roots became heavy. In such a case the crop would be less likely to fail, though it might carry a large population of cysts later in the season.

In a pot experiment in 1925, Morgan had found potato eelworm cysts on tomato and *Solanum dulcamara* but none on sugar beet or mustard, or any other crop commonly grown in South Lincolnshire. Triffitt (1929c) could find none on ten solanaceous species tested. Franklin (1940a) carried out numerous infestation tests but, of cultivated crops, only tomato and potato were susceptible, and of other solanaceous species only *S. dulcamara*, *S. utile* and *Atropa belladonna*.

Triffitt showed (1930a) that oxygen was essential to the hatching of larvae in the laboratory. She and Hurst (1935) studied the thermal death point and found that the following exposures of cysts to hot water were lethal: 45 minutes at 116°F, 30 minutes at 120°F and 5 minutes at 130°F, shorter exposures at these temperatures retarded subsequent hatching. Exposures up to 1 hour at 110°F were without effect. Cyst contents are less susceptible to dry heat, judging from results found elsewhere.

In 1929b Triffitt reported feeding cysts to pigs. After passage through their alimentary canal the cysts were no longer viable, though it is unlikely that temperature is the lethal factor.

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ROOT DIFFUSATES

Early German work with the beet eelworm had shown that larvae were stimulated to hatch by a substance diffusing from the roots of the host plant. Morgan (1925) had failed to stimulate potato eelworms with diffusate from mustard (a host of the beet eelworm, then thought co-specific with the potato root eelworm) and had found that, when mustard was grown in the same pot as a potato, even the latter was only lightly infested. Triffitt (1930a) went thoroughly into this question, which has two main aspects: (a) the nature of the stimulating substance, and (b) the reason for the inhibitory effect of mustard. She found that the diffusate is produced only during the growing season but is not confined to the root tips. Though rapidly destroyed under non-sterile conditions, the substance is heat resistant, leachings retaining full activity after being reduced to half their volume by boiling. It remains active at high dilution (3 drops of leachings to 25 c.c. distilled water). The diffusate from mustard is present in shoots as well as roots, is less readily inactivated under non-sterile conditions, and has the effect of antagonizing the potato diffusate. This links up with later work by Smedley (1939) who found that sub-lethal dilutions of certain isothiocyanates delayed the onset of hatching. Triffitt also found that there is a dormancy period in winter during which larvae hatch very sparsely. In 1931 she showed that excess of diffusates did not check potato growth.

In 1932 Triffitt showed that root diffusates from certain grasses stimulated the hatching of potato root eelworm larvae, though these did not infest the grass roots. This was confirmed in a field experiment. In a later report (1934) she had good results from the meadow grasses (*Poa trivialis* and *P. pratensis*), moderate from rye grass (*Lolium perenne*) and slight from cocksfoot (*Dactylis glomerata*). Seven other grass species had no effect. This work was followed up by Franklin (1937a) who showed that white and yellow maize stimulated hatching; the effect was less than that of the *Poa* species, but maize is a more practicable field crop. She also found a slight response from *Alopecurus pratensis*.

The chemical nature of potato root diffusate is not only of theoretical interest: if known, it might point the way to effective control measures. Thus, if it could be cheaply synthesized, it might be applied to infested soil in the absence of a potato crop and so cause the larvae to hatch and then die of starvation; alternatively, the hatched larvae might be more vulnerable to attack by nematicides. The first step, concentration of the diffusate, was undertaken at the Institute by Hurst (1935, 1937) who produced an active powder by evaporation and ethanol precipitation of leachings from potted potatoes. In 1939 Calam, from Professor Raistrick's department, used leachings from potted tomatoes, adsorbed the active substance on charcoal, and then eluted it with aqueous acetone. The later, purely chemical work was done by Calam and others under Professor Todd, at Manchester, and latterly at Cambridge.

PATHOGENICITY

From the start there has been doubt as to how far the potato root eelworm was really implicated in the causation of "potato

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sickness." Morgan (1926) was struck by the contrast between healthy-looking potatoes on the Kirton Institue farm, producing a reasonable crop, yet with their roots smothered in eelworm cysts and, on the other hand, poor diseased plants on neighbouring farms with relatively few cysts on the roots or even in the surrounding soil. The fungus *Rhizoctonia solani* was rife on these farms and he thought this might be a contributing factor. Triffitt (1929b) also found *Rhizoctonia* on potato-sick plots at Ormskirk, whereas both fungus and sickness were absent from another plot where eelworm was present. Nevertheless, *Rhizoctonia* was not always present on potato-sick land and, down to 1931 (Triffitt) and later, there is talk of some " unknown factor."

In 1929 Morgan and Peters found a positive correlation between cyst content of soil and pathological appearance of potatoes, classified as poor, fair and good, on a number of Lincolnshire farms. Series of soil samples were taken across typical potato-sick patches and in general the cyst count was highest near the centre of each patch. Attention was drawn to the fact that Morgan's (1926) healthy-but-infested potatoes grew on a farm where scientific manuring and crop rotation were practised. There now seems little doubt that potato sickness is primarily due to *Heterodera rostochiensis*. Where potatoes are poorly fed, relatively few cysts can lead to a crop failure ; where they are well cared for they may support a large eelworm population without obvious signs of disease.

Triffitt (1931) showed that, after an early set-back due to the eelworm, a healthy plant responds by forming new lateral roots. She found that such a plant maintains a normal transpiration rate. From a study of transverse and longitudinal root sections she showed that giant cells are formed and extend inwards towards the centre of the stele. In any one transverse section the area of vascular tissue might be reduced by one half, but longitudinal sections revealed that most vessels were plugged by the intrusion of giant cells, thus destroying the efficiency of the water-carrying system.

Soil Conditions

Morgan (1925) emphasized the importance of plant nutrients in soil in combating potato sickness. From a detailed study of a large potato field at the Kirton Institute, Peters (1926) found a negative correlation between soil pH and cyst content, later (1929) shown to be highly significant. There was no such correlation, however, in soil samples from several scattered fields in the locality (Morgan and Peters, 1929). Triffitt (1930a) drew attention to the effect of soil type, the heavier Hertfordshire clays giving not only fewer cysts, but also considerably *smaller* cysts ; she associated this with poor aeration in connection with hatching of the larvae. Experiments on the effects of soil type on an eelworm population are in progress at present.

Disinfestation of Tubers

One of the obvious ways in which cysts of the potato root eelworm can be spread is in the soil adhering to seed potatoes. Triffitt and Hurst (1935) sought to use hot water for disinfesting tubers, but the temperatures lethal to the eelworm (118°F for 30 minutes) were considered too high for the health of the tubers.

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This was confirmed by Franklin (1939a) who tried also 5 per cent phenol, 0·2 per cent mercuric chloride, iodine (5 per cent of a N/10 solution in potassium iodide), and formalin. Phenol was lethal to the potatoes and mercuric chloride and iodine failed to kill the eelworms. Various formalin treatments, between 1 per cent and 5 per cent of commercial formaldehyde, were reasonably effective. In 1940b Franklin showed that the yield from Majestic tubers treated with 5 per cent formaldehyde in February was not affected, but tubers of Arran Pilot and Ally treated in December showed a 9 per cent loss. Fenwick (1942a) showed that sulphur dioxide was lethal to moist eelworm cysts and, while it killed chits already formed, treated tubers readily grew new chits; he suggested that fumigation should be done prior to chitting. The rate was 1 and 2 sulphur candles per 860 cubic feet for 24 hours, in a thoroughly moist atmosphere.

Disinfestation of Soil

The work of members of the department in this field is reported in 16 published papers. Since none of the chemical agents used has been wholly satisfactory, it will be sufficient to summarize very briefly. Morgan (1925) tested a number of compounds and claimed a slight reduction in cysts on the roots from calcium cyanide and carbon disulphide, in pot tests. Hurst (with others) carried out numerous pot and field experiments mainly with calcium cyanamide and metallic oxides. Hurst and Triffitt (1935a) found nematicidal effects and increased potato yields from potassium ethyl xanthate and chinosol (both at economically prohibitive rates), and from ferrous sulphate, ferric chloride and ferric oxide; the latter, which gave the best yield, was aimed at antagonizing the root diffusate. They then (1935b) tested sulphur, naphthalene, and a series of artificial fertilizers at high rates, calcium cyanamide being the only one with promise on a field scale. It was better than its probable break-down products (urea, ammonium salts, nitrates), but rates above 50 cwt. per acre were necessary to prevent eelworm multiplication. In 1937 Hurst and Triffitt reported on further small-scale tests with ferric oxide and calcium cyanamide; both gave yield increases, but eelworm control was inferior to that in previous pot tests. In field trials, Hurst and Franklin (1937) got increased yields from calcium cyanamide at 30 cwt. per acre, sufficient to pay for the treatment and a reduced increase in eelworm population, but the ferric oxide results were negative. They used the same plots the following year, leaving the cyanamide plots untreated and treating the ferric oxide plots with cyanamide; they found (Hurst and Franklin, 1938a) a yield response in the latter but no residual effect in the former. Field trials with various forms of ferric oxide, iron powder and zinc oxide gave disappointing results (Hurst and Franklin, 1938b), while a further cyanamide trial showed that cyanamide gave better yields than an equivalent of ammonium sulphate and lime, without killing all eelworms even at 40 cwt. per acre. Hurst (1938a) discussed the depth distribution in soil of cysts and of added cyanamide, showing that only in the top 4½ inches was there any kill of eelworm. He also showed (1938b) that acetic acid, in the form of pyroligneous acid, increased the killing power of cyanamide, and the latter was more effective in powdered than in

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granular form. Throughout all these experiments Hurst was impressed with the difficulty of getting a sufficiently intimate mixture when solids are applied to soil.

Smedley (1936) showed that sodium hypochlorite solutions of 1 per cent available chlorine would dissolve eelworm cysts in half an hour ; they also dissolved larvae within the egg shell but not the shell itself which, however, was rapidly dissolved by calcium hypochlorite. The latter at 1 in 7,500 of available chlorine greatly increased the hatching of larvae. In 1938 Smedley showed that various chloro-acetates, and particularly the ammonium salt, were toxic to eelworms in soil, no larvae hatching from cysts treated at a rate corresponding to 15 cwt. per acre. In 1939 she reported on the good nematicidal effects of phenyl, ethyl, and n-butyl isothiocyanates. P–hydroxyphenyl isothiocyanate had no effect, and o– and p– tolyl isothiocyanates (like high dilutions of the first three) merely delayed hatching. The best was the phenyl compound, which was fully lethal to cyst contents as a vapour in 24 hours and also as a solution at 10 parts per million. Adsorbed on talc dust, it was used in a field trial at rates up to 2 cwt. per acre, giving increased yields and reduced eelworm multiplication. As before, the difficulty with field trials was the thorough incorporation of chemicals with soil.

During the last war, preliminary work was carried out on the dichloropropylene–dichloropropane mixture known as D–D. The results (unpublished) were sufficiently promising to justify a full-scale field trial under the auspices of the Agricultural Research Council. Seven 2-acre sites were used and many co-operated in the experiment, which was reported on by Peters and Fenwick (1949). Results were disappointing. At some sites (but not on fen soils) the highest rate of D-D used, 800 lb. per acre, gave a 50 per cent increase in yield and a 50 per cent kill of eelworm as measured four weeks after injection. After a following potato crop, however, the eelworm population was as high (or higher) on these plots as on untreated control plots. Peters (1948 a and b) has shown that D–D leads to an increase in yield of tubers even in the absence of eelworm, but that (1949) this effect is not carried over into a second year. The same pot experiment gave evidence that part of the food value of artificial fertilizers is diverted from production of tubers to production of eelworm cysts. Work on D–D and other nematicides continues.

Techniques

The establishing of various technical procedures should not go unnoticed. Morgan (1925) devised the method of recovering cysts from soil by flotation in water, Morgan and Peters (1929) showing that cyst counts from air-dried soil measured by weight were the least variable. Fenwick (1940) extended the method with an apparatus to take 200 gm. soil samples and another to take up to 1 cwt. : these are now in routine use. Triffitt (1929a) used a method for counting white cysts exposed on the roots of a potted plant when carefully turned out of its pot.

Fenwick (1943a) also devised a plate for isolating the progeny of 50 single eelworm cysts : individual receptacles were moulded from round coverslips. He has described methods for counting

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eelworm larvae artificially "hatched" from cysts by the use of calcium hypochlorite solution (1942b), and stimulated to hatch by dilute picric acid (1943b). Latterly, Fenwick has dealt with the whole process of hatching in root diffusate. He has shown (1949) that the numbers of larvae hatching from individual cysts are so variable that it is desirable to use a batch of 100 cysts in any one test ; transformation of larval counts to a form suitable for statistical analysis is discussed here and in Peters (1948a). Later, Fenwick (1950a) has investigated the numbers of larvae hatching in successive time intervals : he has shown that a plot of the probit (corresponding to the percentage hatched) against log time is a straight line, both for single cysts and for batches of 100. Lastly, he has shown that, when potato diffusate is leached from potted plants into pots of infested soil, both the variety of potato and the type of infested soil (or of the contained cysts) have a significant effect on the proportion of larvae hatching. On the average 84 per cent of larvae hatched in the one season of the experiment. Surprisingly, about 50 per cent of larvae hatched in control pots receiving the leachings of pots in which no potato was growing, i.e. without the stimulus of root diffusate.

The Present Position

This review has necessarily dealt with published work, but it may be of interest to end with a brief account of current research on this pest. Inevitably, much of the past work has proceeded on an empirical basis which is effective only up to a certain point. Beyond this, fundamental work is required before progress can be made. The field trials with D–D mixture sponsored by the Agricultural Research Council are a case in point. The criteria were eelworm kill and crop yield at seven sites ; even where kill and yield were highest the subsequent increase in the eelworm population more than compensated for the initial kill. The discrepant results of these trials have largely influenced later work in the department.

Both kill and yield were very different at different sites, reflecting variations in soil type. There is here not only the persistent physico-mechanical problem of intimately incorporating chemicals in soils of differing structure, but also the many physico-chemical problems of the diffusion of a fumigant through soils and its sorption by clay particles or by organic matter. The department is not working on these but it is understood that the diffusion and sorption problems are receiving attention elsewhere.

Further, the ratio of eelworm kill to yield increase varied widely between sites. Taking yield as a rough measure of plant health, this situation involves the complex relationship between parasite and plant, and the factors making for disease, under the influence of a soil fumigant. It seems likely that the use of such a fumigant may lead to improved yields by directly killing eelworms, or by delaying the hatching of larvae so that the plant gets a good start, or by a partial sterilization of the soil independent of the presence of eelworm, or by some combination of these factors. Data which might throw light on this complex problem are scanty, and current pot tests with various fumigants always include a measure of the immediate kill, the response of subsequently grown potato plants,

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and the final eelworm population. A co-operative 3-year field trial, with DD injections followed by potatoes each year, seems to show that this fumigant may improve the yield of the next crop without appreciably changing the final eelworm population. Laboratory tests, suggested by the Soil Microbiology Department, show that the nematicidal effects of frequently repeated soil injections with DD are cumulatively reduced, possibly due to the building up of a soil flora capable of splitting the molecules of the active ingredients The disease problem is also being explored by a histological study of plant roots under eelworm attack.

The mere assessment of kill in the D-D trials proved difficult. There is no direct way of finding what proportion of eelworm larvae within the cysts has been killed by a fumigant ; batches of 100 cysts are incubated in potato root diffusate until hatching ceases—a period varying up to 16 weeks. In a series of experiments since the trials Fenwick has investigated the conditions under which root diffusates act. As a result, not only can the hatching technique now be applied under optimal conditions but also a reasonable estimate of kill can be got in a matter of days rather than weeks, by following the early course of the hatch/time curve. Other results of this work include a method for the bio-assay of diffusates and evidence on their limited efficacy in soil : they are probably effective only in a narrow zone close to the root and (if production ceases) only for a few days, owing to their rapid breakdown in soil.

The recovery within a season of the eelworm populations on treated plots in the D-D trials has focussed attention on the rates of rise and fall of such populations. The annual rise is being followed in a pot test involving several edaphic factors, and the annual fall in crop-rotation field trials in co-operation with the National Agricultural Advisory Service at Cambridge. A highly dynamic concept of population is probably required to fit the facts. It is likely that most of the larvae hatch during one season from cysts lying close to a potato root, whereas some of those in more isolated cysts may remain quiescent for years. Even where annual determinations of larval density in soil show a fairly constant value, in the presence of potatoes each year, this situation probably conceals wide fluctuations within a season. The migration of larvae through soil, once they have hatched, is probably slight both vertically and horizontally ; the limiting effects of soil moisture and particle size on such migration are being examined in co-operation with the Physics Department.

Indirectly concerned with potato root eelworm, a rapid method for the preliminary screening of nematicides is being developed, using the free-living vinegar eelworm as a test organism. The ways in which nematicides act are largely unknown ; further work awaits fundamental studies in biochemistry and eelworm physiology.

Further progress in controlling potato root eelworm probably depends not so much on the efforts of isolated nematologists as of co-operative exploration of the frontiers with physics, chemis y, bio-chemistry and microbiology.

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