ROTHAMSTED RESEARCH

Report for 1982 - Part 1

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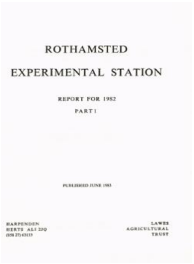

Nematology Department

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Introduction

As in the *Report* for 1981 a general account of the Department's work is given, without inclusion of substantial quantities of data which will be published elsewhere.

The main emphasis of the work of the Department is on the significant nematode pests of British crops but, by common experience, extends to species of importance in Western European agriculture. Through support by the ODA and other bodies some work is also done with nematodes of subtropical and tropical crops. Those nematodes which command most attention are cyst-nematodes (particularly potato and sugar-beet cyst-nematodes), the stem nematode and, chiefly from the tropics and subtropics, root-knot nematodes. These forms are all specialized parasites which induce specific changes in their hosts so as to produce feeding and living sites at which they complete much of their life histories. The symptoms which they induce, and the resulting crop losses, can be spectacular in the absence of control measures. More insidious are the effects of the

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numerous migratory nematodes which occur in agricultural soils. These rarely produce specific symptoms and consequently the problems they cause are much harder to define and study. The nematology components of the multidisciplinary investigations (see Report of Multidisciplinary Activities) provide examples.

The vertical band applicator, developed in the Department by A. G. Whitehead and D. J. Tite, is now being manufactured under licence from the British Technology Group by M and C (Agricultural) Ltd., Swaffham, Norfolk. This equipment permits the safe and efficient incorporation of granular pesticides, especially nematicides, into field soils (see previous *Rothamsted Reports*). The Department has this year received support from BTG for work on fungal pathogens as control agents for cyst nematodes.

Control measures

Potato cyst-nematodes

New nematicides. At Woburn, in sandy loam heavily infested with *Globodera rostochiensis*, as little as 1·5 kg a.i. ha^{-1} of two new carbamates ('DS 46995' and 'DS 47187') incorporated in the seedbed increased yields of ware-sized Pentland Crown tubers by over 20 t ha^{-1} and decreased nematode numbers in the soil by two-thirds. At Woodwalton, Huntingdonshire, in peaty loam infested with *G. pallida*, the same compounds controlled the nematodes on Pentland Crown potatoes better than did oxamyl or a new organophosphorus compound ('Hoe 00752'). These experiments, following the preliminary pot experiment reported last year (*Rothamsted Report for 1981*, Part 1, 158) show that 'DS 46995' and 'DS 47187' are powerful new nematicides. (Whitehead, Tite, Fraser and Nichols)

Cultivar responses. In Lansome field at Woburn, yield loss due to potato cyst-nematode attack was measured in Désirée potatoes. The yield of total tubers decreased from about 58 t ha^{-1} at 2 eggs g^{-1} to 21 t ha^{-1} at 95 eggs g^{-1} soil. This is much greater than the greatest yield loss attributed by Brown (*Annals of Applied Biology* (1969) **63,** 493–502) to potato cyst-nematode attack and nearly four times greater than the average losses of 2·1 t ha^{-1} per 20 eggs g^{-1} soil which he obtained. Yield of total tubers (Y) in Lansome followed a negative linear regression on numbers of nematode eggs in soil before planting (X):

$$Y = 71 - 10{\cdot}8 \log_e (X + 1)$$

Oxamyl, incorporated in the seedbed before planting, controlled the nematodes well and prevented significant yield loss over the same range of nematode infestations in soil. The slope of the regression of total yield on nematode number in oxamyl-treated plots was about zero and met the extrapolated regression line for untreated plots at 1 egg g^{-1} soil. This shows that yield response to oxamyl in Désirée potatoes in this experiment can be attributed to control of potato cyst-nematode alone.

As in 1980 and 1981, yield responses and nematode control were measured in a range of potato cultivars grown in soil treated with oxamyl. At Woburn, in soil lightly infested with *G. rostochiensis*, oxamyl prevented or minimized nematode increase on susceptible cultivars and increased yields of ware-sized tubers in cv. Record by 138% and in cvs. Maris Piper, Pentland Crown and Croft by over 50%. Yield increases in cvs. Maris Anchor, Arran Banner, Cara, Pentland Dell, Désirée and Maris Peer were smaller and not statistically significant. At Woodwalton, in peat moderately infested with *G. pallida*, oxamyl increased yields of ware-sized tubers by 76% in cv. Croft and by 35% in cv. Pentland Crown. In seven other cultivars, yields were not significantly increased. The Dutch ex *Solanum vernei* cultivar Klondyke, bred for resistance to both *G. rostochiensis*

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and *G. pallida*, was susceptible to the Woodwalton population of *G. pallida*. Oxamyl reduced nematode increase in this experiment by only 30%, on average, which is unsatisfactory. Reasons are being sought for the inadequate nematode control in this and two earlier field experiments, all of them on irrigated, peaty loam soils infested with *G. pallida*.

Although injury to potato is clearly related to the number of potato cyst-nematodes in the soil at planting, the degree of injury suffered and the response of the cultivar to oxamyl seem to be dependent on many factors including the speed of invasion of the roots by the juveniles, soil moisture stress and perhaps, the virulence of the nematode population. (Whitehead, Tite, Penn, Fraser and Nichols)

***Effect of wild* Solanum *spp. on* G. rostochiensis *and* G. pallida.** The study of effects of British wild *Solanum* spp. on the numbers of potato cyst-nematodes in the soil (*Rothamsted Report for 1981*, Part 1, 159) was completed. In pots of sandy loam infested with *G. rostochiensis*, nematode numbers were unaffected by two forms each of *S. nigrum nigrum*, *S. nigrum schultesii* and *S. villosum villosum* or by one form each of *S. villosum puniceum*, *S. scabrum*, *S. chenopodioides*, *S. americanum* and *S. sarrachoides*. The same range of *Solanum* spp. had no effect on the numbers of *G. pallida* in pots of peaty loam, except for one form of *S. nigrum schultesii* which apparently halved the soil infestation, and *S. americanum* which doubled the soil infestation. We conclude that there is little prospect of controlling potato cyst-nematodes by growing 'trap crops' of British weed species of *Solanum*. (Whitehead, Fraser and Nichols)

Stem nematodes. In field plots at Rothamsted, pirimiphos-methyl ('Actellic') applied at 2, 4 or 20 g a.i. t^{-1} to Minden bean seed infested with giant race of stem nematode, *Ditylenchus dipsaci*, did not affect the percentage of stems infested nor the yield of bean seed. In pots, pirimiphos-methyl, thiabendazole, triazophos and dimethoate all applied at 200 g a.i. t^{-1} seed also failed to control giant race. It is concluded that the practice of treating bean seed with pirimiphos-methyl to control insect pests in store does not protect the plants from stem nematode attack in the field and at present no seed dressing is known which will do so. Thiabendazole and thiabendazole hypophosphite applied in liquid formulations at 800 ppm to the infested stems of bean plants at the six true-leaf stage prevented development of the giant race for at least two months. Carbendazim, dimethoate, triazophos, pirimiphos-methyl, formothion, phosphamidon and vamidothion, all in liquid formulations at 800 ppm, failed to affect development of the giant race when similarly applied to bean stems.

At Rothamsted, in contrast to 1981, oat and giant races of stem nematode were not controlled on winter beans (c.v. Throws MS) by aldicarb applied to the seed furrows at sowing, whether aldicarb or thiabendazole were applied over the rows of plants in the spring. Similarly, thiabendazole applied over the rows at sowing and again in spring was also ineffective. None of these treatments significantly increased the yield of bean seed but carbofuran applied to the seed furrows and over the rows of plants in spring increased bean seed yield from 2·8 to 5·5 t ha^{-1} (85% D.M.).

Doubling the dosage of carbofuran from 1·25 to 2·5 kg ha^{-1} at each application increased yield to 5·8 t ha^{-1} and greatly improved nematode control. The poorer performance of aldicarb this year may be the result of its shorter persistence in comparison with carbofuran and the application of the top dressings to the rows of plants later in the spring in 1982 than in 1981. In a similar experiment at Rothamsted on land well infested with oat race, stem nematode attack was slight in the untreated plots of spring beans (cv. Minden) and yields were small and unaffected by treatment. Although the beans grew well they were defoliated early by rust. The failure of the stem nematode

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attack was probably due to the very dry conditions in May, which also affected experiments on control of stem nematode in spring sown oats and lucerne.

Although lucerne (cv. Europe) sown in spring on land infested with lucerne race of stem nematode at Rothamsted was not attacked in 1982, carbofuran at 1·5 kg a.i. ha^{-1} applied to the seed furrows significantly increased the yield of dry matter (2 cuts only) from 6·1 t ha^{-1} by about 1 t ha^{-1}. The same result was obtained in an identical experiment on uninfested land. Aldicarb and thiabendazole applied to the seed furrows had no effect on lucerne yields, nor did aldicarb or thiabendazole applied over the rows of plants after the first cut. On both sites, the resistant cv. Vertus yielded about 1·4 t ha^{-1} less than cv. Europe and was injured by aldicarb. The beneficial effect of carbofuran to lucerne in these experiments may have been due to control of the pea and bean weevil, *Sitona*, which was damaging to the young plants in all the other plots. (Whitehead, Tite, Penn, Fraser and Nichols)

The effects on control of stem nematode of different distributions of nematicides in soil in winter field beans have been compared. Beans cv. Throws M.S. were sown in 25 cm diameter pots in November 1981, the soil being treated with granules of aldicarb or carbofuran (10% a.i., 15 mg a.i. per pot ≡4 kg ha^{-1}) in one of three ways: with the seed, simulating row treatment; uniformly incorporated into the soil; incorporated into the 7.5 cm layer of soil above the bean seeds. Each pot was inoculated with 70 000 giant-race juveniles, and placed in a sand plunge out of doors. In the following May, aldicarb and carbofuran placed with the seed had decreased nematode invasion to 11·5 and 24·7% respectively of the untreated plants, whilst the other treatments were less effective. At harvest, all the treatments had prevented infestation of the seeds, although seed infestation in the untreated plants was only slight. We conclude that of the application methods tested, only row treatments give reasonable control of stem nematode in winter beans. Previously, a field trial had shown that aldicarb applied to seed furrows controlled stem nematode in spring beans (*Rothamsted Report for 1981*, Part 1, 159). (Bromilow and Williams, CLU)

Effects of aldicarb and benomyl on forage maize. Previously, treatment with aldicarb has been shown to increase yields of forage maize at Woburn (*Rothamsted Report for 1980*, Part 1, 153–4). In 1982 treatment with aldicarb (5 kg a.i. ha^{-1}), benomyl (22 kg a.i. ha^{-1}) and aldicarb plus benomyl were compared on cv. Fronica on sandy loam soil in Butt Close; previous crops were maize, 1980 and spring barley, 1981. Yields, both fresh weight of forage harvested per plot and dry matter percentage, were high (the season was exceptionally good for maize), in addition plant establishment under netting was excellent with basal insecticide ensuring no frit-fly attack. Yields of dry matter, t ha^{-1} were: untreated 19·18, benomyl 18·63, aldicarb + benomyl 22·08, aldicarb 21·50 (SED 0·803). Benomyl did not affect yields significantly but aldicarb increased them overall by almost 3 t ha^{-1} (13%); benomyl and aldicarb together did not further increase yield.

TABLE 1

Numbers of nematodes at mid-season and post-harvest under forage maize, soil to 20 cm depth

	Untreated	Benomyl	Ald. + Ben.	Aldicarb	SED
Mid-season:					
Pratylenchus l^{-1}	238	150	25	25	91
Tylenchorhynchus l^{-1}	463	1175	100	200	222
Post-harvest:					
H. avenae, eggs g^{-1}	9·4	8·5	9·7	6·5	2·2
Pratylenchus, l^{-1}	156	256	25	31	52
Tylenchorhynchus, l^{-1}	2350	2238	100	125	518

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Pre-treatment numbers of *Heterodera avenae* eggs averaged 16 g^{-1} soil, with 238 *Pratylenchus*, 725 *Tylenchorhynchus*, 200 *Tylenchus* and 863 *H. avenae* juveniles l^{-1}. Mid-season (July) and post-harvest (September) numbers of nematodes in the top 20 cm soil are in Table 1. *Tylenchorhynchus dubius* was most numerous (1200 l^{-1}) in the top 40 cm soil and almost absent at 40-60 cm. As in two previous experiments in this soil, *Tylenchorhynchus dubius* increased four-fold in one season on maize.

Benomyl, variously reported as having a nematicidal effect, did not significantly decrease nematode numbers in this trial. The substantial yield increases associated with aldicarb treatments are most likely to have resulted from nematode control.

Benomyl appears to have affected numbers of vesicular-arbuscular mycorrhiza present in roots at mid-season while aldicarb did not. Visual estimates of root infection (Phillips and Hayman, *Transactions of the British Mycological Society* (1970) **55,** 158–161) were: untreated 6·0%, benomyl 1·7%, aldicarb + benomyl 1·5%, aldicarb 4·4%. However, the site is not phosphate deficient so yields are unlikely to have been affected by mycorrhiza. *Glomus mosseae* and *G. caledonius* occur on the site. (Williams and Beane)

Some work with nematicides is reported in the following section.

Effects of nematodes on crops

Tolerance by potatoes to cyst nematode attack

Importance of root growth. Studies of root growth in the field are extremely labour intensive and tedious but have been used to show that Cara (a very tolerant cultivar) has a very vigorous root system which responds to nematode infestation by producing extra roots, less tolerant cultivars have smaller root systems when infested and very intolerant cultivars can have severely stunted roots. Top growth of intolerant cultivars is very much decreased by nematodes but hardly affected in tolerant ones. The ratio of shoots to roots is similar for *all* cultivars examined at a given nematode soil population density and is much decreased when the population density is great.

An easier method of observing root growth has been developed, using observation boxes 90 × 120 × 30 cm with a perspex front panel. The boxes are filled with baked clay granules and tilted forwards at an angle of 20°. A slow-release fertilizer is added and tubers planted close to the front face at the top. Light is excluded with black polythene sheet and root growth is recorded by tracing the roots on celluloid with a wax pencil. By using pencils of different colours a permanent record of root development can be made for measurement with an opisometer. Using this method Cara has been shown to have roots which grow more quickly than those of Pentland Crown, one of the most tolerant, non-resistant cultivars known, and to have a visible root length more than double that for Pentland Crown plants of similar age. In addition, Cara had a greater proportion of roots that penetrated the soil profile vertically so that on the observation dates its roots reached between 25 and 100% deeper down the profile. Pentland Crown showed advantages over the intolerant cv. Pentland Dell similar to those showed by Cara over Pentland Crown. When compared with King Edward, Cara had no advantage in terms of total root length but again reached consistently further down the profile on any one observation date.

A root system which quickly reaches parts of the soil profile where nematodes are scarce and water is usually plentiful will help a plant to tolerate nematode attack. The deeper roots will have fewer nematodes and help to alleviate the symptoms of water stress that potato plants heavily infested with cyst-nematodes normally show. Thus, features which will contribute to nematode tolerance include vigorous root growth, roots which are able to regenerate after damage and root systems which penetrate the soil deeply. Cara has all of these features. (Evans, Greet and Inge)

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Water use and calcium uptake by infested plants. Studies of the relationship between water use and calcium content of entire plants (*Rothamsted Report for 1980*, Part 1, 155) were continued. Arran Banner plants were grown in pots containing 1 kg of soil infested with *Globodera pallida* at 0, 10, 50 or 250 eggs g^{-1} and their growth and water use monitored. Weekly measurements showed that at first the plants grew more slowly the greater the number of nematodes. However, after six weeks plants in soil with the smaller numbers of nematodes resumed growth at the same rate as control plants, but plants in soil with the greatest infestation grew slowly throughout the experiment. Analyses of calcium content of the dried plants showed a highly significant correlation between calcium content and water uptake rates and that infested plants took up more calcium per unit of water transpired; earlier findings are thus confirmed. Calcium uptake rates per unit weight of fresh root were more or less constant for heavily infested plants throughout the experiment but the uptake rate decreased in control plants. Because calcium normally enters root systems by mass flow through the younger parts where the endodermis is unthickened, the effects of nematode infestation may be to make older parts of the root system more permeable to calcium through disruption of the endodermis, and thereby increase the proportion of the root system through which calcium may enter. (Fatemy and Evans)

Resistant responses to potato cyst-nematodes. Changes in cell morphology which occur when second-stage juveniles invade roots of susceptible potatoes and induce syncytial transfer cells as feeding sites have been described but the reaction in roots of resistant potatoes is much less well understood.

By growing potato plants from small tuber pieces on agar it is possible to inoculate chosen sections of root and subsequently obtain clean preparations of root pieces in which juveniles have been present for a known time. Such pieces were sectioned and stained for light microscopy using standard techniques, and the response to invasion examined in the roots of the following potatoes: Désirée (susceptible); Maris Piper (with gene H_1, conferring resistance to *G. rostochiensis* Ro1 only); 8917 and 10016 (with 80–90% resistance); 8899 and 9559 (with lesser resistance to *G. pallida* but full resistance to Ro1 conferred by the presence of gene H_1). The numbered clones were developed and supplied by SCRI. In all potatoes with gene H_1 the reaction to pathotype Ro1 was well defined, with initiation of a feeding site within 48 h of inoculation, appearance of a hypersensitive reaction, including enlarged nuclei, dense cytoplasm, and thickened cell walls by 4 days and development of this reaction in all cells in contact with the syncytium by 7 days. The syncytium was undeveloped compared with the susceptible response, and had a highly vacuolated cytoplasm. The reaction to *G. pallida* Pa1 and Pa3 in roots of clones 8899 and 9559, and also to *G. rostochiensis* Ro1 in clones 8917 and 10016 did not involve a hypersensitive reaction around the syncytium. Within 4 days considerable syncytial development had taken place and this continued but the syncytia showed a much more vacuolated cytoplasm than in the susceptible response. The degree of vacuolation varied with clone, nematode population and nematode individual. There is a clear difference between the response conferred by the single major resistance gene H_1 and that conferred by the unknown number of resistance genes derived from *S. vernei*. The variation in the latter response may result from the differing numbers of genes for resistance in the ex *vernei* clones and genes for virulence in the individual nematodes.

A response separate to that around the syncytium was observed in all combinations of host and nematode where resistance occurs. This was hypersensitive reaction around the second-stage juvenile and occurred within 24 h. Nuclei of cells adjacent to the juvenile become enlarged, their cytoplasm more granular and they stained readily. The changes were distinct from those resulting from mechanical damage by the juvenile as it invaded

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the root. Because this reaction occurred in all the cases where resistance was elicited regardless of the genetic basis, and because it is easily detected and occurs soon after invasion, it may provide the basis for an early, *in vitro* screen for resistance. (Rice and Stone)

Interactions of potato cyst-nematodes and *Verticillium dahliae*. Further tests of the responses of potato cultivars to infection with *V. dahliae* and *G. rostochiensis* or *G. pallida* have been made. Previously (*Rothamsted Report for 1981*, Part 1, 160) it was shown that Maris Anchor developed severe symptoms when inoculated with *V. dahliae* whether or not cyst-nematodes were present and that the symptoms were worse if the nematode was *G. pallida*, to which it is not resistant. Maris Peer, on the other hand, showed few symptoms when inoculated with *V. dahliae* alone but much worse symptoms when inoculated with *V. dahliae* and *G. rostochiensis* or *G. pallida*. Following this, four cultivars were tested, each plant grown in 1 kg of soil. Suspensions containing sufficient propagules of *V. dahliae* to give 4×10^5 propagules ml^{-1} soil were added to half of the pots 10 and 31 days after planting. The soil was either nematode-free or contained 100 eggs g^{-1}, of *G. rostochiensis* or *G. pallida*. Home Guard showed the same symptoms as Maris Anchor, yellowing and wilting in the presence of the fungus even when no nematodes were added, but Pentland Javelin showed little evidence of *V. dahliae* attack, even when growing in soil infested with *G. pallida* (to which it is not resistant) and even when other cultivars receiving the same treatment had died. Maris Peer was intermediate in behaviour. Interaction between *V. dahliae* and potato cyst-nematodes may be due to the nematodes providing an invasion pathway for the fungus through the endodermis. If this is so, there must be differences in the way roots of Maris Anchor and Pentland Javelin react to the nematodes. A method of determining the amount of damage caused by the nematodes to the endodermis in different cultivars is required. (Evans, Greet and Inge)

Interactions between nematodes and *Rhizobium* of peas. Infestation of pea roots by *Heterodera goettingiana* decreases numbers of *Rhizobium*-induced nodules while infestation of pea foliage by *Ditylenchus dipsaci* increases their number. However, in both cases plants appear chlorotic and the nitrogen-fixing efficiency of the nodules may have been decreased. Stem nematode can be induced to invade pea roots (see p. 164) and absorption spectroscopy of extracts from nodules formed by *R. leguminosarum* strain 1001 showed that they had less leghaemoglobin when roots were invaded by this nematode or *H. goettingiana* than when uninvaded. Those on roots invaded by *D. dipsaci* had least leghaemoglobin and were often greyish or greenish in colour. Absorption bands of leghaemoglobin decomposition products were found in spectra of extracts from some nodules from infested roots but not in those from uninfested roots, suggesting breakdown of the leghaemoglobin when the nematodes were present. The excessive nodulation of roots invaded by *D. dipsaci* but not the inhibition of nodulation caused by *H. goettingiana* could be explained by this effect. (Green and Hornsey)

Root-ectoparasitic nematodes. Problems with establishment of cereal and grass crops on light sandy land in the ADAS Northern Region have been associated with the root-ectoparasitic nematode *Paratrichodorus anemones*. To compare effects on winter- and spring-sown barley two sites were selected where damage to cereals had been associated with number of *P. anemones* in 1981. Both sites were on loamy sands, one at Docking, Norfolk, and the other at Holme-on-Spalding Moor, N. Humberside. The same barley cultivars were drilled at both sites; winter—cv. Igri, spring—cv. Triumph. Both sites compared the effect on yields of oxamyl broadcast at 5 kg a.i. ha^{-1} with untreated plots.

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At Docking two other treatments were included, oxamyl drilled at 1·5 kg a.i. ha^{-1} and aldicarb broadcast at 2 kg a.i. ha^{-1}. All broadcast treatments were incorporated with a harrow.

Initial numbers of nematodes at Docking were relatively small with 350 *P. anemones* l^{-1} soil; *Tylenchorhynchus dubius*, *T. maximus* and *Helicotylenchus digonicus* were also present. At Holme *P. anemones* was the most prevalent species at 1450 l^{-1} soil. Final numbers of *P. anemones* at Docking were similar to pre-season counts and at Holme numbers on untreated winter-sown plots were maintained. Numbers had decreased on treated plots at Holme but also on the untreated spring barley plots, possibly due to a very dry period a few weeks before sampling.

There was no significant difference between treatments at Docking on either the spring or winter-sown crops although the winter barley did show a trend of improved yield: control; aldicarb broadcast 2 kg a.i. ha^{-1}; oxamyl drilled 1·5 kg a.i. ha^{-1}; oxamyl broadcast 5 kg a.i. ha^{-1}. At Holme yields of spring barley were not significantly improved by oxamyl but the winter-sown plots yielded 4·07 t ha^{-1} (treated) compared with 3·77 t ha^{-1} (untreated), a significant improvement of 8% ($P=0·01$). This suggests *P. anemones* at *circa* 350 l^{-1} soil) were insufficient to affect yields but a population some four times larger did decrease yield of winter barley.

On another light sandy soil site in N. Humberside, with 1300 *P. anemones* l^{-1} soil, dry matter production from a newly sown short-term grass ley was 5·1 t ha^{-1} from plots treated with 1 kg a.i. oxamyl ha^{-1} and 5·6 t ha^{-1} from plots treated at 5 kg ha^{-1}, compared with 4·5 t ha^{-1} from untreated plots. In this experiment additional yield from plots treated with the smaller quantity of nematicide was estimated to offset the cost of treatment while resulting in improved ley establishment. (Spaull and Mewton)

Cyst nematode biology

Hatching mechanisms and behaviour. Additional information is given for several aspects of this work previously reported.

Calcium associated with the inner lipoprotein membrane of the eggshell of *Globodera rostochiensis* is removed by treatment with a solution of the natural hatching factor, and a role for this process in hatching has been proposed (*Rothamsted Report for 1981*, Part 1, 161). Further work has now shown that when eggshells were treated with the artificial hatching agents $ZnCl_2$ or $LaCl_3$, the cation was bound to the shell and Ca^{2+} displaced. The total cation content (Ca^{2+}, La^{3+} or Zn^{2+}) was greater for the treated than the untreated eggshells. However, the Ca^{2+} content of the eggshell was not altered by treatment with solutions of $CaCl_2$ or $MgCl_2$, neither of which is a hatching agent. This supports the postulate that Ca^{2+} displacement by natural hatching factor is involved in potato cyst-nematode hatching. (Clarke and Perry)

The divalent cation ionophore 'A23187' was reported by Atkinson and Ballantyne (*Annals of Applied Biology* (1979) **93,** 191–98) to have hatching activity. The authors suggested that ionophores might interfere with the normal control of hatching by carrying Ca^{2+} through the egg-shell. We found that the solubility of 'A23187' in aqueous solutions was $<1·2$ μM, and we therefore tested suspensions of the ionophore. Our tests showed that in this form the ionophore did not stimulate the release of juveniles from eggs within cysts, nor did it synergize the hatching activity of potato-root exudate, on the contrary it inhibited hatching. We also found that free Ca^{2+} did not activate juveniles immobilized by immersion in 0·4M trehalose i.e. under the conditions of osmotic stress thought to exist inside the egg-shell (see *Rothamsted Report for 1977*, Part 1, 177).

When freshly collected *G. rostochiensis* second-stage juveniles were kept in a standard 'artificial' tap water (Greenaway, *Journal of Experimental Biology* (1970) **53,** 147–163) or

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distilled water for 7 days, the proportion of juveniles moving fell to <25%. By contrast, when juveniles were stored in potato-root exudate under the same conditions the majority continued to move actively. Also, fewer juveniles migrated through columns of sand moistened with the standard tap water or distilled water than through columns moistened with potato-root exudate. Juveniles immobilized by storage in water resumed active movement on exposure to potato-root exudate. The results indicate that the motility and mobility of the juveniles is strongly influenced by the presence of potato-root exudate, and demonstrates a role of potato-root exudate additional to its activity in stimulating hatch. Juveniles kept in potato-root exudate contained less lipid and polysaccharide than juveniles stored in water, suggesting a greater metabolic activity in the former condition. (Clarke and Hennessy)

Carbohydrates extracted from *Heterodera goettingiana* cysts, cyst walls, eggs and juveniles consisted of high molecular weight polysaccharides, oligosaccharides and low molecular weight compounds. The analyses showed that the disaccharide trehalose was present in the fluid surrounding the unhatched juvenile at a concentration of about 0·5M. When hatched juveniles were transferred from standard tap water or distilled water to 0·5M trehalose their water content fell to 66·5%, the value observed for unhatched juveniles in eggs equilibrated with water. Few juveniles moved after 7 days immersion in 0·5M trehalose, but dilution with water to give a sugar concentration of ⩽0·1M resulted in over 90% of the juveniles moving after 24 h. Hatching was also inhibited when cysts were immersed in solution of pea-root diffusate containing 0·5M trehalose. These experiments, together with evidence of an increase in juvenile water content before hatching when eggs are immersed in pea root exudate, suggest that loss of solutes from the egg fluid is an essential prelude to hatching. *H. goettingiana* thus shares some features of the hatching mechanism for *G. rostochiensis* discussed above. (Perry, Clarke, Hennessy and Beane)

Duration and repetition of stimulation by pea-root exudate are of major importance in the hatch of *H. goettingiana* from free eggs. Exposure periods of 18 h and over to root exudate were necessary to achieve hatches commensurate with those obtained from continuous exposure to diffusate. This contrasts with results previously obtained for *G. rostochiensis* where hatching was initiated by exposure periods as short as 5 min and duration of stimulation was of only marginal importance in hatching (*Rothamsted Report for 1981*, Part 1, 161–162). (Perry and Beane)

Selection for virulence in *G. pallida*. Selection within populations for genotypes able to reproduce (virulence) on *G. pallida* resistant hybrids of *Solanum vernei* has been demonstrated (*Rothamsted Report for 1979*, Part 1, 156–57) and now continued for a fifth generation. The resistance in *S. vernei* is mediated by an unknown number of genes but is not dependent upon a single major gene. Some populations did not multiply successfully on the hybrids throughout the experiment but six were maintained on one or both of clones 62.33.3 and 65.346/19, and showed an increasing proportion of the numbers of cysts produced by the same generation on susceptible control plants. A common slope fitted to data for the separate populations described an increase of about 10% per generation. This rate was used in the population model of Jones and Perry (*Journal of Applied Ecology* (1978) **15,** 349–71) and compared with a simulated population in which virulence was conferred by one double recessive allele, operating against a single major resistance gene in the host.

With an initial population density of 5 eggs g^{-1} soil and one generation per year, the latter population was selected more rapidly at first but after 8 years there was little difference between the two types of population modelled. Build up in field populations of virulence against the polygenically inherited resistance in *S. vernei* derived potatoes

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may not be very different from that which might occur in selection against a single major gene for resistance. However, unlike the case of major gene resistance to *G. rostochiensis* in Maris Piper and allied cultivars, virulence against *S. vernei* resistance is already known to exist in British field populations of *G. pallida*.

The hypothesis that potato cyst-nematodes and their hosts have co-evolved argues that resistance is most likely to be mediated by vertically acting genes operating on a gene-for-gene basis (*Rothamsted Report for 1978*, Part 1, 181–82). Furthermore, Parlevliet and Zadoks (*Euphytica* (1977) **26,** 5–21) postulate this type of resistance is universal. In modelling polygenic gene-for-gene interactions, they found that a model with genes at as few as five loci had a high stability. Thus, lack of stability of resistance to *G. pallida* in the *S. vernei* hybrids suggests that the number of resistance genes in the hosts is small. (Stone, Dr Susan J. Turner, Dept. Agriculture for Northern Ireland and Perry, Statistics Department)

Stem nematode biology

Stem nematodes (*Ditylenchus dipsaci*) are insidious and damaging pests of many British field crops, especially lucerne, red clover, white clover, field beans, onion, garlic, oats, maize, narcissus, tulip and sugar beet. Although generally regarded as a single species, stem nematode exists as a number of races or pathotypes, of varying host specificity. Damage resulting from them is often overlooked or confused with other causes. Controlling stem nematodes chemically may be impractical, especially in perennial crops and controlling them by crop rotation is difficult, partly because of their longevity in soil and partly because of apparent inconsistencies in the host ranges of the different races. Resistance to stem nematodes needs to be broadly based if it is to be reliable.

Population studies. Previous work suggested that onion might be a common host for stem nematodes of different races. Fifty-six populations taken from a range of hosts were inoculated into leaves of onion cv. Robusta to see if they multiplied but not all did so and it is concluded that onion is host to many populations of different races but is not a common host to all populations.

In pot tests, eleven English isolates of lucerne race of stem nematode induced hypertrophy in the shoot apices of young lucerne seedlings of the supposedly resistant cultivars Sverre and Vertus as well as the susceptible cultivar Europe. Furthermore, all isolates multiplied freely in the shoots of Sverre and some did so in those of Vertus. Neither of these cultivars can be regarded as resistant. (Whitehead, Fraser and Nichols)

D. dipsaci is a parasite of plant stems and other foliar parts and readily invaded stems of pea plants growing in sterile agar medium but also invaded roots. Root invasion by this species has not been reported previously. The nematodes remained in the root cortex often close and parallel to the endodermis. Eggs and juveniles were found frequently in the tissue showing that reproduction occurred but numbers were fewer than in the stem. The invasion of roots doubtless occurred because of the abnormal conditions of *in vitro* culture and suggests barriers to its invasion of roots by the nematode under more normal conditions are behavioural rather than physiological. (Green and Hornsey)

Stem nematode on field beans. A survey of all field bean (*Vicia faba*) crops on the Rothamsted farms failed to find any new outbreaks of stem nematode although it did occur on a few sites with a history of this nematode. There was a very serious infestation of the giant race of *D. dipsaci* on spring beans cv. Maris Bead on a 169 ha field near Shrewsbury with extensive patches of badly damaged plants. Some of the seed used for sowing was infested and infestation of the seeds harvested from various parts of the field

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varied from 8 to 22%, indicating how easily this nematode can proliferate and be dispersed. (Hooper, Cowland and Spratt)

Pathogens of nematodes

Integrated control of the beet cyst-nematode. Females and eggs of the beet cyst-nematode, *Heterodera schachtii* are parasitized by the same species of fungi that prevent populations of *H. avenae* increasing in cereal monocultures. Field soils infested with *H. schachtii* often also contain *H. avenae* and the nematophagous fungi *Nematophthora gynophila* and *Verticillium chlamydosporium* (*Rothamsted Report for 1980*, Part 1, 158). In such fields sugar beet has usually been grown in rotation with cereals and so females of cyst nematodes would have been available in most years, enabling the fungi to multiply. To test the effects of nematicides and crop rotation on the population dynamics of *H. schachtii* in the presence of nematophagous fungi about 30 t of *H. schachtii* infested soil was rotavated into an area (27 × 30 m) of Butt Close field, Woburn. In previous years at this site *H. avenae* had failed to multiply on susceptible cereals and *N. gynophila* and *V. chlamydosporium* were present. In 1982 no treatments were applied and sugar beet cv. Monoire was sown in all plots to ensure the establishment of *H. schachtii*. In July, and thereafter at 2-week intervals, nematode females and eggs on the sugar beet roots and in soil were examined for fungal parasites. In July there was a mean of 24 females per plant, of which about 35% were infected by *N. gynophila*. Parasitism by fungi did not prevent a large second generation of the nematode developing and by October all plants were infected (mean 713 females per plant). By the end of October about 30% of females contained fungi and the number of full cysts was decreasing but in-row numbers of eggs remained high at 146 eggs g^{-1} soil. As *H. schachtii* was successfully established in a soil which normally suppresses multiplication of *H. avenae* it seems likely that the former species with more than one generation in a season requires greater densities of antagonists to prevent its populations increasing. (Kerry, Crump, Mullen, Gilmour and Hornsey)

Incidence of fungal pathogens in soils. Following the survey for fungal parasites of the beet cyst-nematode in soil from 16 fields from sugar beet growing areas of East Anglia (*Rothamsted Report for 1980*, Part 1, 158) a further 25 soil samples were obtained from a beet cyst-nematode survey made by the ADAS Eastern Region. Spores of *N. gynophila* and *V. chlamydosporium* were recovered from 14 and 18 soils respectively. In general quantities of spores were small, with a mean of 16 g^{-1} for *N. gynophila* (range 5–68) and 22 g^{-1} for *V. chlamydosporium* (range 4–47) of air-dried soil. Numbers of spores did not increase to those observed when cereals are grown in monoculture in soils infested with *H. avenae*. (Crump, Kerry, Mullen and Gilmore)

Effect of formalin and captafol on fungal pathogens. In 1980 a field trial was set up at Broom's Barn on land previously cropped with sugar beet for 12 consecutive years and where *H. schachtii* and fungal antagonists were present. Formalin, a general soil sterilant, and captafol, a fungicide that is not nematicidal, were applied to replicated plots before drilling at a rate of 3000 l ha^{-1} and 60 kg ha^{-1} respectively. The trial was repeated in 1981, when captafol was applied every sixth week at the same rate throughout the growing season and formalin not applied, and in 1982, when captafol was applied every third week.

In 1980 and 1981 numbers of *H. schachtii* failed to increase in untreated soil, remaining at 17-19 eggs g^{-1} soil. In captafol and formalin treated plots infestation increased by 3·2 and 4·0 times respectively in 1980, and captafol increased populations a further 1·7 times in 1981. As formalin resulted in increased sugar beet yields in 1980, the increase in

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nematode multiplication might have been a result of the larger plants allowing more nematodes to develop but captafol treated plots did not show a similar increase in beet yield. It is not clear whether the increases in nematode numbers observed with captafol and formalin were due solely to a reduction in the activity of nematophagous fungi. Both treatments could affect root infecting fungi which may influence nematode multiplication. Hence the effects of such treatments are difficult to interpret and more detailed observations are necessary.

In 1981 numbers of spores of *N. gynophila* and *V. chlamydosporium* increased in all soils, but most markedly in untreated soil. However, spore numbers were small, suggesting that other antagonists could be limiting numbers of nematodes in the untreated soil. (Crump and Kerry)

Morphology and function

Feeding pump of stem nematode. The action of the oesophageal pump of this species has been analysed by cinemicrography. Only 30% of the cross-sectional area of the central region of the pump is composed of myofibrils and there is still less muscle towards the anterior and posterior ends of the pump. Muscular actions during opening and closing of the pump are complex and involve several different elements, the functions of which have been elucidated. Opening of the sclerotized pump lining from its closed, triradiate form to the open, triangular cross-section involves transient distortion of the lining into compound curves of unstable shape but the fully-open (triangular) condition is quite stable. On closing it is destabilized by a nearly longitudinal pull from the posterior radial muscles. It is believed the pump lining is bistable and forms part of a click mechanism. The pump lining rotates within the pump during pumping. Muscular activity in normal pumping is highly isometric and hence energy-efficient although transient activities observed with pumping included twitching of isolated groups of radial muscles which shortened by up to 18% but never opened the lining. Sometimes the pump lining oscillated markedly and regularly during pumping, and very low-amplitude pumping was also seen. Pumping, stylet thrusting and moving about characterize various activity phases leading to feeding, but were occasionally seen out of their proper sequence. Dorsal gland secretions were displaced by radial muscle action and by that of an anterior radial muscle complex that stiffens the oesophageal wall just anterior to the pump, but cannot open its thickened circular lining. Passive flow of food from a cell through the oesophagus and closed feeding pump lining into the intestine is already known; the 'closed' lining is shown to have enough residual open lumen to present no greater obstacle to food flow than the stylet lumen. (Seymour)

Feeding pump of *Longidorus caespiticola*. Behaviour of the oesophageal bulb feeding pump in *L. caespiticola* has been analysed: a primary analysis diagram was constructed on the basis of previous work (*Rothamsted Report for 1977*, Part 1, 173-174) and by making *a priori* assumptions about how the pump works. A second diagram, based on further detailed analysis of cine film, was compared with the first. This comparison showed when and how certain structures were being brought into play, even when such action could not be observed directly; in particular, the longitudinal muscles and their associated longitudinal bands of circumferentially orientated muscle fibres. Study of a working sectional scale model of the pump lining and muscles suggested how some parts of the bulb must be displaced and pressurized during opening to create an effective closing force. On the basis of analyses and model findings a scheme of operation of the oesophageal feeding pump in *L. caespiticola* has been developed and includes the nature of closing forces, functions of the greatly thickened pump lining plates, sequential

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control of pumping, transition zones between open and closed pump lining, and nature of the oesophago-intestinal valve. (Seymour)

Cell complement of *Aphelenchoides blastophthorus* oesophagus. Electron microscopy can reveal fine structural details of nematode feeding apparatus which may aid understanding of host-parasite relations and provide information on comparative morphology of importance to taxonomy. The feeding apparatus of three nematodes with different types of feeding behaviour is being examined: *A. blastophthorus*, with active pumping in of food; *Hexatylus viviparus*, a passive feeder (*Rothamsted Report for 1980*, Part 1, 160); *Ditylenchus dipsaci*, with a combination of both methods (*Rothamsted Report for 1977*, Part 1, 173).

Using computer based reconstructions from serial sections (see p. 168) the number and disposition of the various cell types (i.e. muscle, nerve and 'marginal' cells) in the oesophagus of *A. blastophthorus*, were determined for later comparison with the feeding structures in other nematode groups. This was achieved by working out the positions of the nuclei of each of these cell types. The cell bodies of most of the oesophageal cells and stylet protractor muscles lie in the metacorpus in this species. There are four muscle systems as follows: stylet protractor muscles (3+3 cells); constraining muscles (6 cells); anterior metacorpus valve muscles (6 cells); oesophageal pump muscles (either 6 binucleate or 6+6 cells). The rest of the tissues of the oesophagus comprise 13 nerve cells and 3+3 marginal cells. In addition there is the single neuron of the sensory microtubular organelle that lies between the stylet and its protractor muscles, the function of which is not known but may be proprioreception. This neuron passes through the oesophageal tissues but its cell body lies outside them, probably near the nerve ring. The various cell types tend to be housed in specific sectors in the metacorpus. Marginal cells surround the apices of the arms of the lumen where it is triradiate, or the corresponding sectors elsewhere. The nerve cell bodies are in the dorsal and subventral sectors and the muscle cells are interposed between the nerve and marginal cells. The stylet protractor muscle cell bodies are an exception; they lie in two layers in the dorsal and subventral sectors, corresponding to the position of the stylet knobs. (Shepherd and Clark)

Taxonomy

Nematode specimen collection. The Department's microscope-slide collection has over 11 000 slides and includes some 1800 type slides which have recently been rehoused within a fire-proof safe. For many older slides the traditional glass rod cover-glass supports have not been adequate to prevent eventual flattening of the specimen, also the drying out of slides due to inadequate seal is cause for concern.

Examination with the scanning electron microscope of specimens stored in vials for some 20 years indicates that those stored in FA 4:1 (4% formaldehyde 1% acetic acid) are in a better condition than those stored in TAF (2·8% formaldehyde, 2% triethanolamine): in the latter there is degeneration of nematode cuticle. Both are commonly used fixatives. The effect of TAF varies with different nematodes: with *Paraphelenchus pseudoparietinus* the cuticle over the lateral field has disappeared although intact over the rest of the body; with *Ditylenchus dipsaci* the cuticle has a shredded appearance being detached from the body and separated along the grooves between the transverse annulations; with an *Aphelenchus* and an *Aphelenchoides* sp. the cuticle has completely disappeared revealing the muscle bands beneath. (Hooper, Cowland and Spratt)

***Hirschmanniella* on Taro.** A new species of *Hirschmanniella* has been described from taro (*Colocasia esculenta*) corms in the Solomon Islands. The new species is closest to

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H. gracilis, *H. diversa* and *H. microtyla*. It differs from *H. gracilis* in shape of head and tail, length of oesophageal glands in relation to body length, and length of non-annulated part of tail. It has a shorter stylet than *H. diversa* and smaller, b, b′ and c′ values. It is distinguished from *H. microtyla* by the greater body length, a more rounded head, tail shape and a longer non-annulated tail terminus. This new species has been shown to be the primary causal agent of a corm rot disease of taro, known as 'mitimiti' in the Solomon Islands (*Rothamsted Report for 1980*, Part 1, 155) and has now been found parasitizing taro in Papua New Guinea. (Bridge, Page and Jordan, with J. J. Mortimer and G. V. H. Jackson, Agricultural Division, Ministry of Home Affairs and National Development, Honiara, Solomon Islands)

Identification of root-knot species. The characters most useful in identifying *Meloidogyne* species have been discussed (*Rothamsted Report for 1981*, Part 1, 169). Stylet measurements of males and females greatly contribute towards species differentiation but qualitative characters of the stylets are also very important. Detailed morphology of excised stylets can be clarified by scanning electron microscopy, it now being possible to remove and prepare stylets from individual nematodes as a routine procedure. Electron micrographs may then be used in conjunction with the light microscope for practical identification. The important features are the general form of the stylet, the shape of the cone, shaft and knobs, the stylet length and relative cone length. The knobs are probably the most important diagnostic feature of the stylet, particularly their individual shape (longitudinally ovoid, round or transversely ovoid) and nature of their junction with the shaft (gradually tapering to offset). Not surprisingly there are similarities in the stylets of second-stage juveniles, males and females in individual species. (Jepson and Hoole)

Techniques

Computer graphics in the reconstruction of serial sections of nematodes. Three-dimensional reconstruction of serial sections can be achieved in several ways. Shepherd and Clark have previously traced outlines of nematode structures on to acetate sheet and then superimposed these sheets with appropriate spacers between them to give a translucent 3-D picture that can be viewed from any angle. A more versatile method involves the production of a computer model by tracing structures from individual sections on a digitizing tablet and using an interactive program to build up and display the selected sections in various orientations by rotating the resulting image on the screen. Tissues are allocated to categories before entering the data and any category or combination of categories can be selectively displayed. This cannot be done with the earlier method without redrawing. The programs we are using were devised by Mr W. J. Perkins and Mr R. J. Green. SSPROF is the serial section data entry program, SSRCON the serial section reconstruction program and SSALIN the serial section alignment program. The reconstruction can be displayed in colour on a monitor, or as hard copy on a drum or flat-bed plotter, in three possible ways: as stereo pairs, viewed with a stereo-viewer; as a red/green anaglyph, viewed with red/green spectacles; as three orthogonal views. Using this technique, not only can the shapes of complex structures or their disposition in space be elucidated but also accurate measurements can be made. (Shepherd and Clark, with W. J. Perkins and R. J. Green, National Institute for Medical Research)

Time lapse cinematography of nematode tracks. Fourth-stage juveniles of stem nematode may either be attracted to hosts or remain inactive in the soil (*Rothamsted Report for 1981*, Part 1, 164). In order to study the behaviour of individuals presented with plant tissues or extracts, a technique permitting time lapse cinematography of tracks the nematodes

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make on the surface of agar was devised. To show up the faint tracks on agar plates images of the tracks were thrown on to a translucent plastic screen in the camera's field of view; the tracks scattered the transmitted light so that their images appeared dark on a light background. To eliminate the grain of the ground surface, the screen was rapidly rotated. (Clayden and Seymour)

Miscellaneous studies

Influence of soils on *Meloidogyne acronea* of cotton. *Meloidogyne acronea* was found infesting only one of the two different soil-types that occur in the same cotton field in southern Malawi. *In vitro* experiments have shown that the soil type (vertisol) which did not support populations of *M. acronea* had a lower moisture content than the soil-type (alluvium) that did support the nematode, when kept at the same relative humidities. Eggs of *M. acronea* have been shown not to survive when kept at a relative humidity of less than 97% for nine weeks. This corresponds with a moisture content of 12·1% in the alluvium and 11·9% in the vertisol. The lower moisture level of the vertisol, when it is at permanent wilting point, during the dry season can account for the absence of *M. acronea* in this soil in southern Malawi. (Page, Bridge and Jordan)

Staff and visitors

J. Bridge visited Bolivia for four weeks to survey serious nematode damage to vegetable, tobacco and plantation crops, under ODA auspices. Bridge and Sam L. J. Page visited Papua New Guinea for 5 and 10 weeks respectively, undertaking the first survey of nematode pests in that country, at the invitation of the World Bank. B. R. Kerry and D. H. Crump organized an OILB workshop on pathogens of nematodes in Stuttgart, and Kerry gave papers at the University of Hohenheim, Germany, and University of Lund, Sweden. A. G. Whitehead visited the Centre National de la Recherche Agronomique at Versailles, to discuss protein crops in Europe and also visited nematological laboratories at Rennes, and at Zürich and Nyon, Switzerland to discuss stem nematode. Alison M. Spaull visited institutes in Wageningen to discuss nematode effects on grass and forage crops. A. R. Stone visited nematological centres and potato breeders in Eire and N. Ireland. Sixteen staff attended the 16th International Nematology Symposium at St. Andrews. Papers or other presentations were also given at meetings of the British Society for Parasitology, British Soil Science Society, European Grassland Federation, RASE meeting on Break Crops and the ADAS Entomologists' Technical Conference. In addition to the longer term visiting workers listed at the head of this report, a large number of home and overseas scientists visited the Department.

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