

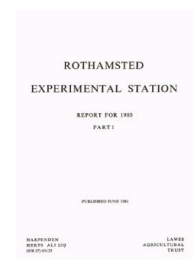
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Report for 1980 - Part 1

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Nematology Department

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A. R. Stone (1981) *Nematology Department* ; Report For 1980 - Part 1, pp 149 - 164 - **DOI:**
<https://doi.org/10.23637/ERADOC-1-137>

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Introduction

Following the pattern set in the 1979 *Report* attention is again focused on one aspect of the Department's work. For the past 15 years much of our effort has been in investigating control of plant-parasitic nematodes by chemical agents and most of the emphasis has been placed on control of cyst nematodes because of their economic importance. We believe that, for these nematodes, work with the currently available compounds has largely been taken as far as necessary although we shall continue to investigate new application techniques and new formulations. This Report therefore contains a review of achievements in this field during the past 15 years and a summary of current activity. In addition, work in the past year on aspects of plant-parasitic nematode biology, taxonomy, morphology and control by resistant crops and by pathogens of nematodes is reported.

Control by nematicides

In the last 15 years much effort has been devoted to the search for effective nematicides suitable for field and glasshouse use in Britain and to devising efficient techniques for

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applying them to infested soils. As a result, several compounds were found, which not only minimised nematode damage to sensitive crops but also limited or prevented nematode increase on them in a wide range of soils. These compounds are now used on commercial farms. For example, in 1979 some 16 000 ha of potatoes (about 12% of the main crop) and half the onions were grown in nematicide-treated soils.

Root ectoparasitic nematodes. Root ectoparasitic nematodes (especially *Trichodorus* spp. and *Longidorus* spp.) stunt sugar beet and other crops in sandy and peaty soils ('Docking disorder'). Row fumigation before sowing was shown to prevent the disease and killed 80% of the nematodes attacking the seedlings and was practised on several thousand hectares of sand land but fumigation has been replaced by application of granular nematicide-insecticides. However, in years when heavy rain closely follows sowing, the soluble nematicides are leached from the seedling rhizosphere, lessening nematode control and this remains a problem. (Whitehead, Tite and Fraser)

Effects of nematicides on root ectoparasitic and root lesion nematodes under grass and spring wheat, and cereal cyst-nematodes under maize are reported on pp. 152–154.

Cyst nematodes. Unlike *Trichodorus* or *Longidorus*, which increase 10-fold or less on annual field crops in Britain, cyst nematodes can increase 50-fold on susceptible plants, so 98% of the juveniles may have to be killed or immobilised to prevent nematode increase. In glasshouses, where potato cyst-nematodes can damage tomatoes, over 98% of potato cyst-nematodes (*Globodera pallida*) were killed by injecting methyl bromide, dichloropropene/dichloropropane ('D-D') mixture or 'D-D'/methyl isothiocyanate mixture at rates of 450–1300 kg ha⁻¹ into soil sealed by polythene sheeting. Dazomet at 440 kg ha⁻¹ was less effective, whether the soil was covered with polythene sheeting or not. In uncovered soils out-of-doors, dazomet granules controlled potato cyst-nematodes (*G. rostochiensis*) better than 'D-D' mixtures but both fumigants were much less effective in peat soils than in sandy soils. Despite many field experiments with soil fumigants applied in different ways, no reliable method of fumigating all potato soils has been found and so attention was turned to other classes of compound.

Of the many non-fumigant pesticides we have assessed as nematicides against potato cyst-nematodes, the most effective have been oximecarbamates, especially aldicarb ('Temik') and oxamyl ('Vydate'). Such polar compounds, at 5 kg a.i. ha⁻¹, are more effective than large amounts of soil fumigants and work well in a wider range of soils. Similarly, the organophosphates fenamiphos and ethoprophos and a carbamate (carbofuran) were effective, except in organic soils. All these non-fumigant nematicides do not kill the nematodes, except when applied in large amounts, but immobilise them in the soil; when they are absorbed by the roots they prevent the nematodes invading or establishing themselves in the roots. Non-fumigant nematicides are of relatively short persistence in the soil and did not affect the yields of sugar beet, barley or wheat following potatoes but when they controlled potato cyst-nematode populations large residual yield increases were obtained in a following potato crop without further application of nematicide.

Having relatively little vapour action, oximecarbamates, organophosphates or carbofuran granules must be thoroughly incorporated into the soil. For cyst nematode control they must be mixed into the top 10–15 cm just before sowing the crop; seed-furrow or narrowband row treatments are usually much less effective. Against potato cyst-nematodes, aldicarb and oxamyl were found more effective when incorporated in the top 15 cm of the soil than when incorporated half as deep. Mixed into the top 15 cm, aldicarb and oxamyl at 5 kg ha⁻¹ prevented damage to potatoes by potato cyst-nematodes and reduced

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their increase by about 90%. Smaller amounts of either compound were usually less effective. When granules were applied to the soil surface and harrowed in, 70% of them remained in the top 5 cm of the soil but after rotavation they were fairly evenly distributed down to the working depth of the rotavator, so controlling the nematodes better. On peaty soils, a spike rotavator was as effective at mixing the granules into the soil as an L-bladed rotavator. However, rotavation may damage the soil structure and brings unweathered soil to the surface. By blowing granules into vertical bands 12.5 or 25 cm apart in the top 10–15 cm of the soil followed by rotary harrowing, nematicides were well incorporated without damage to soil structure. This technique, patented in five countries by NRDC, is just as effective as incorporation by rotavation, is faster, and safer because granules are not distributed on the soil surface. Non-fumigant nematicides incorporated into the top 15 cm of the soil control nematodes only in the top 20 cm of the soil. Potato and beet cyst-nematodes are frequently abundant to 40 cm or more but pot and field experiments suggested that most damage to potatoes is done by nematodes in the top 15–20 cm of the soil.

Foliar application of nematicides would avoid problems of incorporation. Of the available compounds, oxamyl is transported to some extent from leaves to roots but was much less effective when applied to potato foliage than when incorporated in the seedbed.

The benefits of treating lightly and heavily infested soils before growing resistant or susceptible potato cultivars was studied in several soils. Although Maris Piper (resistant to *G. rostochiensis*) showed some tolerance to attack, it usually yielded better when the soil was treated with aldicarb or oxamyl. Cara, which is also resistant to *G. rostochiensis*, was even more tolerant to attack by this species but was less tolerant to *G. pallida* and responded well to oxamyl. Amongst cultivars susceptible to both species there was a wide range in yield response to oxamyl. Some cultivars (Record, Pentland Dell, Croft and Desirée) were more severely damaged by potato cyst-nematode (*G. rostochiensis*) than were Pentland Crown or King Edward but in untreated, severely infested soil all susceptible cultivars failed completely. Tuber yields of most cultivars were greatly increased by oxamyl in heavily infested soil and some of them also responded well to treatment of lightly infested soil. With King Edward numbers of potato cyst-nematodes increased twice as much as with any other susceptible cultivar. Multiplication of *G. pallida* and *G. rostochiensis* was less on two *Solanum tuberosum* × *S. vernei* hybrids (8890 ab42 and 8917 b3) from the Scottish Plant Breeding Station, than on susceptible cultivars but 8890 ab42 was hypersensitive to attack.

Beet cyst-nematode (*Heterodera schachtii*), a potential threat to the beet sugar industry in Britain, is at present controlled by crop rotation. Damage to the crop in peaty loam soils was prevented by aldicarb or oxamyl at 2.5 kg ha⁻¹. In 4 years out of 5 both compounds decreased nematode multiplication, although in untreated plots nematode increase was much less than expected even in lightly infested soils, suggesting an effective predator of the nematode because this species passes two or more generations per annum on sugar-beet roots.

Pea cyst-nematode (*H. goettingiana*) and cereal cyst-nematode (*H. avenae*) were also controlled by incorporating aldicarb or oxamyl at 5.6 kg ha⁻¹ in the top 15 cm of the soil but such treatments although very effective were uneconomic. Neither ethylene dibromide at 4.9, 9.7 or 17.5 kg ha⁻¹ nor similar amounts of 1,3-dichloropropene ('Telone II') applied in the seed furrows during sowing increased the yield of barley grain in soil infested with cereal cyst-nematode, although the numbers of juveniles invading the roots were decreased by ethylene dibromide. This technique with ethylene dibromide is widely and economically used in South Australia to control cereal cyst-nematode on wheat. (Whitehead, Tite, Bromilow, Fraser and Nichols)

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Stem nematodes (*Ditylenchus dipsaci*). Stem nematodes are damaging pests of numerous crops, e.g. onions, oats, field beans, lucerne, red clover, narcissus and tulip. They can be difficult to control because there are numerous races with differing host ranges and they may increase 1000-fold or more on host plants in one growing season. Small amounts of several non-fumigant nematicides, especially aldicarb, applied as granules to the seed furrows during sowing prevented serious yield loss in spring and summer-sown onions. Although attacks later in the growing season were sometimes controlled by a second dose of granules metered over the rows of young onions in the spring, only 2.5 kg or less aldicarb ha⁻¹ can be applied to onions without leaving unacceptable residues (>0.15 µg g⁻¹) in the harvested bulbs.

At Rothamsted, onions, Manod oats, peas, field beans and maize were infested by our 'oat race' of *D. dipsaci* and Maris Tabard oats, wheat, sugar beet and lucerne were uninfested. Aldicarb granules applied in the seed furrows during sowing greatly increased yields of the susceptible crops but also increased yields of wheat, lucerne and Maris Tabard oats, which were uninfested. Manod oats, supposedly resistant to *D. dipsaci*, were susceptible and Maris Tabard, known for susceptibility to *D. dipsaci*, were resistant to the Rothamsted 'oat race'. In pots of the infested soil, the oat cultivars Manod, Maris Osprey and Early Miller were susceptible, Maris Tabard and Maris Quest were poor hosts and Pennal, Peniarth, Panema, Milford and Pennant were resistant. The outer (oldest) leaves of all cultivars were infested with *D. dipsaci* but eggs were only found in the leaves of susceptible cultivars. Heavy infestation of the stem base was not necessarily associated with bloat in young onions or oats. In field plots, the Rothamsted 'oat race' was increased by Manod and Maris Osprey oats but was not increased by Panema, Pennal, Peniarth or Maris Tabard.

Work on the use of nematicides in conjunction with resistant cultivars is expected to form a major part of future research with potato cyst-nematodes while investigations of the biology, pathogenicity and control of stem nematode will expand. (Whitehead, Tite, Bromilow, Fraser and Nichols)

Effects of nematodes on crops

In some cases a particular plant-parasitic nematode is clearly implicated in damage to a particular crop but a diversity of nematodes occur under most field crops and assessing their contribution to yield losses is difficult.

Root ectoparasitic nematodes and grasses. Little is known of the effects of nematodes upon grassland and because grass is a resilient crop, it is unusual for symptoms of pest attack to be obvious. However, an established pasture at Wilberfoss, N. Humberside had many patches of poor growth throughout 1979; association occurred between the patches and numbers in autumn of *Helicotylenchus vulgaris* and *Paratylenchus* (mostly *P. microdorus*), in soil up to 11 000 litre⁻¹ and 20 000 litre⁻¹ respectively, which together were about 90% of the plant parasitic nematode population. The patches were still readily apparent the following spring when oxamyl at 8.4 kg a.i. ha⁻¹ was applied to half plots; plots were located in areas of poor and healthy grass. Treatments gave no consistent improvement in dry matter yields through the season. The dry spring may have inhibited nematode activity during early growth of the grass, which was enhanced by a basal dressing of 125 kg N ha⁻¹. Nematode numbers at the end of the season were similar to those before treatment. (Spaul)

Nematode damage to grasses is likely to be greatest at sward establishment. Plots on sandy loam at the Grassland Research Institute (Broad Oak VI) were treated with aldicarb raked into the seedbed at rates of 0, 5 or 10 kg a.i. ha⁻¹ before sowing with pure swards

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of one of three ryegrass cultivars: Baroldi (*Lolium westerwoldicum*), RvP (*L. multiflorum*), or S24 (*L. perenne*) at 1250 viable seeds m^{-2} . Large numbers of *Helicotylenchus varicaudatus* (up to 24 000 litre $^{-1}$) and *Paratylenchus* spp. (up to 13 000 litre $^{-1}$) were present and longidorid and trichodorid nematodes were also patchily distributed in small numbers across the trial area. At the first cut 8 weeks after sowing (14 October 1980) aldicarb at 5 kg a.i. ha^{-1} gave an average 71% increase in dry matter yield over untreated plots. Aldicarb at 10 kg a.i. ha^{-1} further increased yield significantly, although the increase was smaller with Baroldi and S24 than RvP. The yield of RvP was doubled with the larger aldicarb application, compared with untreated plots. A second cut taken 4 weeks later showed average yield gains of 61% over untreated plots for the smaller application and 73% for the larger. Baroldi had the smallest response at either rate and only RvP showed any marked additional yield from the larger aldicarb dosage, where yield was again double that from untreated plots. (Spaull, with Dr R. O. Clements, Grassland Research Institute)

Paratrichodorus and other nematodes on spring wheat. Because root ectoparasitic nematodes typically occur in mixed populations it can be difficult to establish a causal relationship between a species and damage. These nematodes are also susceptible to handling and are difficult to culture for experimental work. The effect of *Paratrichodorus anemones* and other nematodes with which it occurs was assessed on spring wheat using field soil with a natural population of 500 litre $^{-1}$ *P. anemones* and 1500 litre $^{-1}$ other plant parasitic nematodes including *Tylenchorhynchus*, *Helicotylenchus* and *Pratylenchus*. The soil was treated to produce different initial populations:

- A. field soil untreated
- B. field soil greatly compacted before use: *P. anemones* 20 litre $^{-1}$ + 1310 litre $^{-1}$ others
- C. field soil extracted by Whitehead tray and the residue air-dried: *P. anemones* 15 litre $^{-1}$ + 220 litre $^{-1}$ others
- D. field soil autoclaved at 1 bar for 15 min: *P. anemones* none + 40 litre $^{-1}$ others
- E. field soil treated with dichloropropene ('Telone II') equivalent to 280 litre ha^{-1} : *P. anemones* none + 180 litre $^{-1}$ others
- F. field soil autoclaved as D 1 month previously and then treated with dichloropropene as E: *P. anemones* none + 20 litre $^{-1}$ others.

Spring wheat cv. Sicco was planted in pots of each soil. Numbers of *Paratrichodorus anemones* at harvest remained significantly greater in A than in B–F, in which there was little or no multiplication of this species but numbers of other nematodes in A, B and C were significantly greater than those in D, E and F. Roots of plants grown in untreated soil were distinguished by poor differentiation of protoxylem and endodermis. Shoot and root weights and root lengths (see p. 161) were measured at 4 and 20 weeks (harvest). Growth at 4 weeks was significantly less in A than in any other soil but D, but remained least in A at harvest, indicating that the *Paratrichodorus* had the greatest effect on yield and that the freshly autoclaved soil was not best for plant growth. (Spaull and Murphy)

The effects of nematodes on the growth and yield of forage maize. Aldicarb at 1.7, 3.3 and 5.0 kg a.i. ha^{-1} was applied before a maize crop in Butt Close, Woburn. Cultivars Aurelia and Fronica were sown in April with two rates of nitrogen fertiliser, 50 and 100 kg N ha^{-1} . Germination and emergence was slow because of dry conditions; when complete, chlorfenvinphos was applied to control frit fly. Soil and root samples were taken in July and soil samples in October after harvest. Root weights were not affected by aldicarb, nitrogen or cultivar. Root lesion nematodes (mainly *Pratylenchus neglectus*) were few and effectively controlled by aldicarb: 36 g^{-1} root untreated, 1 g^{-1} treated.

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H. avenae (15 eggs g⁻¹ soil before planting) were also few in number: 19 g⁻¹ root untreated; 4, 2, 1 g⁻¹ respectively at the different aldicarb rates. Numbers were not affected by cultivar or nitrogen. Numbers of migratory nematodes in soil in July are given in Table 1.

TABLE 1
Migratory nematodes per litre soil

	<i>Pratylenchus</i>	<i>Tylenchorhynchus</i>	<i>Tylenchus</i>	<i>Helicotylenchus</i> / <i>Rotylenchus</i>	Others*
No aldicarb	256	369	94	44	3744
Aldicarb 5.0 kg ha ⁻¹	31	63	75	6	2200

* Includes Rhabditidae, Mononchidae, *Criconemoides*, *Hemicycliophora*

All three rates of aldicarb significantly improved dry matter yields at harvest though no rate was significantly better than others. The best improvement was in Fronica with least nitrogen (37%). Extra nitrogen significantly increased yields without aldicarb and at the lower rates of aldicarb but not at the highest rate.

Numbers of plant-parasitic nematodes in roots and soil in July—notably *H. avenae* and *P. neglectus*—were small, probably due to spring drought (only 10 mm rain between 6 April and 17 May). At the end of the year there was a 4-fold increase in the numbers of *Tylenchorhynchus* in untreated soil, but little change in *Pratylenchus*, and *H. avenae* declined to 6 eggs g⁻¹ soil. However, these and other nematodes apparently contributed to the measured yield losses. As few as 30 *H. avenae* g⁻¹ root have been associated with maize yield losses in France even although maize is a poor host. The incidence of vesicular-arbuscular mycorrhizal fungi, which might affect maize yield, was not affected by aldicarb. (Williams and Beane)

Rice root-knot nematode on deep water rice. The rice root-knot nematode, *Meloidogyne graminicola*, is an important pest of upland rice but has not been investigated on deep water rice. We found that in Bangladesh the species causes severe galling of young deep water rice roots to a depth of 1.5 m of water. In the mature crop galling does not occur at a depth of 1 m but soil sampling after flooding showed that *M. graminicola* survives as well in flooded as in upland soils. Bangladesh rice varieties and others (total 13) were all very susceptible to *M. graminicola* which caused stunting and decreased tillering and yields. Some crops normally grown after deep water rice in Bangladesh were found to be hosts of *M. graminicola* including tomato (cvs Moneymaker, Roma VF and Roma VFN) wheat and onion. Initial experiments have shown that *M. graminicola* has a very short life cycle of 13–15 days on rice roots. In flooded conditions the nematode can develop within submerged rice roots. *M. graminicola* may be an important pest of flooded rice in the deep water rice growing areas of Bangladesh and elsewhere in S. Asia. (Bridge, Page and Jordan)

***Meloidogyne acronea* on cotton.** An unusual cotton root-knot nematode, *Meloidogyne acronea*, from Malawi was found to be restricted to soils having a large water-holding capacity in which moisture is maintained during the dry season. The life cycle of *M. acronea* takes 21 days at 33°C (the mean soil temperature in the main cotton growing area of Malawi) but its rate of development increases as the temperature is raised to 37°C. On cotton (*Gossypium hirsutum*) the nematode causes reduced growth, delay in flowering, abnormal lateral root growth and prevents deep penetration of the tap root. Other Malawian susceptible hosts are the crops pigeon pea (*Cajanus cajan*), leucaena (*Leucaena leucocephala*), and sorghum (*Sorghum bicolor*). Local Malawian cultivars of bulrush millet (*Pennisetum typhoides*) and finger millet (*Eleusine coracana*), do not support

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development of the nematode to maturity. All cultivars of *G. hirsutum* tested so far are highly susceptible to *M. acronea* including cvs Auburn 623 and Cleve-wilt which are resistant to *M. incognita*. Infection by vesicular-arbuscular mycorrhiza, *Endogone* spp., in cotton roots is detrimental to invasion by *M. acronea*, and this is being examined closely as it could have implications for the use of fungicidal seed dressings. (Page and Bridge)

***Hirschmanniella* sp. causing a disease of taro.** Corms of taro (*Colocasia esculenta*) from the Solomon Islands suffering from a disease known locally as miti-miti, were found to contain high numbers of *Hirschmanniella* sp. The nematode was isolated from red necrotic streaks in the corms, a characteristic symptom of the disease. Inoculation of the nematode onto healthy taro plants produced identical disease symptoms. The species is being described. (Bridge, with Mrs J. J. Mortimer, Reading University, and Dr G. V. H. Jackson, Dodo Creek Research Station, Honiara, Solomon Islands)

Tolerance by potatoes to cyst nematode attack. Some potato cultivars tolerate attack by potato cyst-nematodes better than others and the most tolerant ones accumulate less calcium when uninfested (*Rothamsted Report for 1975*, Part 1, 199) perhaps because they use water more efficiently (*Rothamsted Report for 1977*, Part 1, 176–177). Limited watering improved water use efficiency of healthy potato plants in pots without limiting growth but the efficiency was impaired when plants were infested with potato cyst-nematode unless the cultivar were tolerant. Cultivars with resistance gene H_1 were less affected by *Globodera rostochiensis* Ro1 than by *G. pallida* Pa3. Cara (with gene H_1) was not the most efficient cultivar tested, although it is reported as significantly more tolerant of cyst nematode attacks than others (*Rothamsted Report for 1979*, Part 1, 145).

Four potato cultivars were grown in plots at Woburn which contained either few or many *G. rostochiensis* Ro1. Cara grew best and leaves of this cultivar contained more abscisic acid (ABA) than those from Pentland Crown, Pentland Dell or Maris Peer. Leaves of all cultivars taken from plots with many nematodes contained more ABA than those from plots with few. An increase in ABA levels generally results in more efficient water use by causing partial closure of stomata, which has a greater effect on the water vapour diffusion pathway than the CO_2 diffusion pathway, thereby restricting transpiration more than photosynthesis. The field observations of increased ABA levels after nematode invasion do not concur with the decreased water use efficiency of nematode-infested plants in pots. Measurements from large (130 × 65 cm) root observation boxes showed that Cara had much deeper and more vigorous roots than other cultivars. Field measurements of shoot:root ratios varied little between cultivars; those with the most vigorous root systems had the largest tops and best yields (9 weeks after planting, shoot:root ratio averaged 5.5 for plants in heavily infested plots and 11.9 for plants in lightly infested plots).

Tolerance seems to depend on more than one feature so that, although water use efficiency is important in dry seasons (and can be related to Ca content of leaves) other features are important in wet seasons—such as root system vigour and ability to regrow after nematode invasion. With initial infestations of *G. rostochiensis* Ro1 averaging 100 eggs g^{-1} on heavily infested plots and < 10 eggs g^{-1} on lightly infested plots, roots of heavily infested Cara plants weighed 114 g at 9 weeks from planting compared to 90 g in lightly infested plants; Pentland Crown 54 g compared to 57 g; Pentland Dell 27 g compared to 55 g. Since shoot:root ratios were similar for all varieties at each nematode level, Pentland Dell grew and yielded worse than the other varieties when heavily infested. (Evans, Greet, Minter and Wilson)

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Interactions between nematodes, *Rhizobium* and fungi of peas. Loss of yield and decreased growth of peas in a field in Worcestershire were related to the numbers of *Helicotylenchus vulgaris*, *Heterodera goettingiana* and *Pratylenchus thornei*. Effects of the species seemed to be additive although that of *Hel. vulgaris* was masked by the greater effect of pea cyst-nematode because the incidence of these two species was inversely related. *P. thornei* was more strongly associated with decreased growth late in the season than the other species. At equal numbers *P. thornei* appeared to cause five times and *Hel. vulgaris* twice the damage of *Het. goettingiana* but the greater numbers of the latter species made it the more important parasite.

Nodulation of pea roots in a field crop was inversely related to the number of *Het. goettingiana* juveniles that invaded the roots. The greater weight of plants with few juveniles and more nodules could not be attributed specifically to either factor but differences in foliar nitrogen concentration were more closely correlated with greater nodulation than with nematode invasion or plant weight.

Pea plants were grown in soils from three fields in which crops had responded differently to aldicarb application. Sterilisation of these soils with methyl bromide decreased plant growth for 2–3 weeks, and reduced the amount of root nodulation, but thereafter had little or no effect. Aldicarb applied to the soil increased growth of plants in two soils after 3 weeks and increased nodulation in one of these soils. In the third soil aldicarb did not affect growth, *Pratylenchus* or *Helicotylenchus* were more abundant in the two soils in which plants responded to aldicarb application. A direct growth stimulation effect by aldicarb seems unlikely as the plants only responded in two soils. Increased growth due to only nematode control seems unlikely as sterilisation by methyl bromide did not have a similar effect and the responses appear due to interaction between nematodes and other factors, possibly mycorrhiza. (Green)

Nematodes and *Fusarium* wilt of cotton. Surveys of cotton (*Gossypium hirsutum*) fields around Lake Victoria, Tanzania, showed a number of nematode species, in particular *Meloidogyne incognita acrita*, were associated with *Fusarium* wilt caused by *F. oxysporum* f. sp. *vasinfectum*. In a field trial, greatest incidence of *Fusarium* wilt occurred in plots with large populations of *M. incognita acrita*; plots treated with aldicarb had very small nematode populations and the least incidence of wilt. Other nematode species found in association with wilt were *Xiphinema elongatum*, *Rotylenchulus reniformis*, *Scutellonema* spp. (*S. brachyurum*, *S. clathricaudatum*, *S. magniphasmum*) and *Siddiqia* sp. (Bridge, with Mr R. J. Hillocks, Ukiriguru Research Station, Mwanza, Tanzania)

Cyst nematode biology

Pathotypes. Selection of *Globodera pallida* on the *Solanum vernei* hybrids with resistance to this species was continued for a further generation (*Rothamsted Report for 1979*, Part 1, 144). Regression analysis showed a linear increase in reproduction of populations of pathotypes Pa1, Pa2 and Pa3 over four generations ($P=0.01-0.001$). A linear increase in succeeding generations indicates that major genes conferring ability to overcome resistance (virulence genes) are being selected in the nematode populations. Resistance in *S. vernei* may be mediated by major genes to which the virulence genes in the nematodes correspond (the gene-for-gene hypothesis) and the commonly observed intermediate efficacy of *S. vernei* hybrids in preventing multiplication of potato cyst-nematodes then results from only a fraction of the individuals in a nematode population possessing the requisite virulence genes.

Pathotypes of *G. pallida* are defined by their performance on *S. vernei* hybrids and their characteristics will depend on the particular gene frequencies in the nematode

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populations chosen when the pathotypes were defined. It seems unlikely that all field populations encountered will have the same gene frequencies as the standard populations and a survey of recent ADAS pathotyping tests indicates that this is so. (Stone and Turner)

Resistance to potato cyst-nematodes. At 12 days after inoculation with active second-stage juveniles *c.* 70% of *G. rostochiensis* Ro1 (Feltwell) in roots of the susceptible cv. Arran Banner were at the third juvenile stage and *c.* 22, *c.* 10% and *c.* 30% in the roots of the clones Maris Piper, SPBS 8917 and SPBS 9559, resistant to this pathotype. Development of *G. pallida* Pa3 (Cadishead) was similarly retarded in clone 8917, resistant to this pathotype, but in all potatoes this population developed faster than the *G. rostochiensis* population and differences between development in susceptible and resistant hosts were apparent from the fourth juvenile stage onwards: 50% of individuals in Arran Banner roots and 12% in 8917 at 16 days after inoculation. At 30 days >90% of *G. rostochiensis* in Arran Banner roots were fourth-stage juveniles and *c.* 12, *c.* 30 and *c.* 20% in Maris Piper, 8917 and 9559; *c.* 90% of *G. pallida* in Arran Banner and *c.* 50% in 8917 were also fourth stages.

Clones 8917 and 9559 are *S. vernei* hybrids but 9559 has the *ex andigena* resistance gene H₁, present in Maris Piper. Resistance against *G. rostochiensis* Ro1 derived from *S. tuberosum* ssp. *andigena* (Maris Piper, 9559) and from *S. vernei* (8917), and to *G. pallida* Pa3 derived from *S. vernei* (8917) all involved slowing nematode development. Because juvenile stages are easily released from potato roots in a macerator and can be counted this may provide a rapid method of screening for resistance. (Turner and Stone)

Hatching of pea cyst-nematode. *H. goettingiana* is sometimes a serious pest but laboratory investigations have been hampered by difficulty in stimulating hatching *in vitro* by pea root leachates or artificial hatching agents, although hatch in the field is thought to be stimulated by host roots. However, we have achieved hatches *in vitro* of between 20 and 40% of cyst contents.

Cysts were recovered from moist soil which was first stored at 2°C for 24 weeks (a typical period of storage before use) and then kept at 15°C for several weeks. Cysts were set to hatch at this temperature in soil leachings obtained from peas (four plants, cv. Kelvedon Wonder, in 12 cm pot) collected as described by Fenwick (*Journal of Helminthology* (1949) **23**, 157–170) at two weekly intervals. The largest hatches, of over 40% in 5 weeks, were from cysts immersed in leachings from 4- and 6-week old plants; little hatching (<10%) occurred when cysts were placed in leachings from 2- or 10-week old plants. Thus, in common with other cyst nematodes, the hatching response is related to the age of the plant producing the diffusate. Hatching may also be influenced by the period and temperature of storage of cysts prior to experimentation. Pea root diffusate may retain its activity in the soil after removal of the plants, for leachate from soil in which peas had been growing 12 weeks before, induced hatches of almost 25%. (Perry, Clarke and Beane)

Stem nematode

Stem nematode (*Ditylenchus dipsaci*) in field beans. In a pot experiment, field beans (*Vicia faba*) cv. Minden were planted at weekly intervals over a period of 7 weeks in the spring. All pots were inoculated with the giant race of *D. dipsaci* at the end of the period to give plants inoculated at sowing and at 1–6 weeks old. The degree of infestation of the bean stems, assessed 4 months later, decreased with the increased age of the plants at the time of inoculation. Plants in pots inoculated before the plants emerged (weeks

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6 and 7) had the most severely infested stems in which some tops were stunted and distorted with a 'mop top' appearance also seen sporadically on infested field sites; such plants tend to produce much infested seed. These pots also produced plants with extra tillers due to the killing off of the primary shoot by heavy infestations of *D. dipsaci* but not all of the tillers became infested. In contrast, only few plants which were 6 weeks old (30 cm high) when inoculated became infested and then only at the base of the stems but 4-week old plants (16 cm) became well infested. These results corroborate other pot and field observations that cool, moist conditions at time of sowing and hence slow emergence, tend to result in more heavily infested plants but it is notable that established plants are susceptible, though less so, to attack. (Hooper)

Dormancy and persistence of stem nematode. Fourth-stage juveniles survive overwinter in the absence of a host and although populations show a severe decline, enough may remain to damage a host crop in the following spring. The possibility that starvation was responsible for the overwinter population decline was investigated. Measurements were made of lipid utilisation by fourth-stage juveniles obtained from soil and incubated at 5°, 17° and 25°C for 6 weeks. The initial lipid content was high and at 25°C over 25% of the total content was utilised during incubation. However at 5°C, less than 17% of the total lipid content was used. Measurements of lipid content of soil populations during the winter months supported the experimental evidence, indicating that starvation is unlikely to be responsible for the population decline. (Clayden)

Movement of stem nematode before hatching. Second-stage juveniles in the egg have been observed to undergo specific behaviour as hatch approaches. Simple, symmetrical contractions of the body develop into undulatory movements. The juvenile markedly increases in length before hatch and rearranges itself from a simple coil to figure-of-eight forms. The elongation indicates that a change in egg shell permeability, leading to entry of water and hydration of the juvenile, may be part of the hatching process, as in the case of *Globodera rostochiensis* (Rothamsted Report for 1977, Part 1, 177–178) and *Ascaris suum* (Rothamsted Report for 1979, Part 1, 148). Stylet activity is at first undirected but develops into an ordered thrusting at the egg shell which creates a line of weakness that bursts to release the juvenile. The stylet appears more flexible than in later stages and is bent by movements of the head during thrusting at the egg membrane; this may be an adaptation to thrusting in the confined interior of the shell. (Seymour and Doncaster)

Pathogens of nematodes

***Nematophthora gynophila* and sugar beet cyst-nematode.** This fungus which contributes to the decline of cereal cyst-nematode in many UK soils had not been found in fields infested with sugar-beet cyst-nematode (*H. schachtii*) although both nematodes are probably indigenous in W. Europe and *H. schachtii* was parasitised when introduced into soil containing the fungus (Rothamsted Report for 1975, Part 1, 202). Soils collected from 16 fields infested with the beet cyst-nematode were planted with sugar beet in pots and plunged in sand out-of-doors in April. Three pots of each soil were sampled on three occasions from July to September and the females examined for infection by the fungus. The occurrence of the cereal cyst-nematode in these soils was assessed by planting three pots from each site with barley and examining the roots after 16 weeks. *N. gynophila* was found in seven and *H. avenae* in nine of the soils. Four fields contained both *N. gynophila* and *H. avenae* but three contained the fungus but not cereal cyst-nematode. *N. gynophila* parasitised females of *H. avenae* and *H. schachtii* in the same soil and *H. schachtii* alone. (Crump and Kerry)

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***Verticillium chlamyosporium* in eggs of *Heterodera avenae*.** *V. chlamyosporium* parasitises eggs in cysts and females of *Heterodera* spp. Chlamyospores (the normal resting stage of the fungus) have not been observed within eggs and after the egg contents have been destroyed the mycelium lyses. Cysts of *H. avenae* were extracted from soil stored at 5°C for 0, 1, 2, 4, 8, 12, 16, 20 and 24 weeks and the fungi within eggs isolated. About 9% of the eggs contained fungi and of those 57% were *V. chlamyosporium*. The length of storage did not affect the recovery of *V. chlamyosporium*. Survival of the fungus within the egg is apparently not dependent on a morphologically distinct stage. *V. chlamyosporium* isolates from eggs in cysts from different or the same sites vary greatly in their growth rate and spore production on corn meal agar. Such variability may account for differences in the rates of parasitism which have been observed in the field. (Kerry and Mullen)

Feeding behaviour

***Longidorus caespiticola*.** Feeding studies continue. Earlier workers thought that where the muscles of the feeding pump contracted to open pump lining, the bulb would become wider; we have shown the opposite to be so.

Contradictory observations were made by Towle and Doncaster (*Nematologica* (1978) 24, 277–285) that the lumen opened and closed sequentially, anterior-to-posterior, but also that both ends of the bulb lengthened or shortened simultaneously about a central point. The explanation is that more than half the length of the pump is open at full dilation, so that the whole bulb is fully elongated at that stage, and elongation does occur sequentially. The pump is surrounded by tissues that press on it equally from all directions, so in fact both ends of the bulb move apart from each other simultaneously, but not from a fixed point. (Seymour and Doncaster)

***Caenorhabditis elegans*.** We studied the behaviour of *Caenorhabditis elegans* feeding on *Escherichia coli*. Ciné-film analysis of ingestion shows how the action of the stoma and its valve flaps, and the anterior oesophagus are coordinated. A notable feature is the intermittance of the feeding mechanism; a bolus of bacteria accumulated over about 0.25 s is then swallowed suddenly (within 0.042 s). The valve flaps and the anterior oesophagus lining always act reciprocally; during accumulation the flaps at the base of the stoma are closed, holding bacteria in the stoma whilst liquid sucked between the valve flaps carries more bacteria into the stoma. When the stoma is full the valve flaps open suddenly; at the same time the triradiate lining of the anterior oesophagus closes centrally, but leaves three peripheral channels through which the mouthful is rapidly swallowed. The channels merge posteriorly, and as the bolus passes from them into the posterior oesophageal lumen, excess liquid taken in during accumulation and swallowing of the bolus is ejected forward through the channels and stoma. Thus *C. elegans* is shown to be a two-stage filter feeder, the filter mechanisms being (1) the stoma valve flaps and (2) the oesophagus lining with its anterior channels. (Seymour and Doncaster, with Dr K. A. Wright, University of Toronto)

Analysis of food flow. As part of studies on host–parasite relations, a technique is being developed for visualising flow towards the stylet in liquid media caused by feeding. The stylet pierces a synthetic membrane and enters a thin layer of liquid below the cover slip through which observations and film records are made. Flow is demonstrated by movement of suspended latex/polystyrene particles of 0.3 or 1.0 μm diam. Film analysis of particle trajectories shows pumping pulsations transmitted through the medium, how far pumping influence extends, and flow velocity and acceleration. Measurements of particle accumulation round stylets show volume ingested (particle number in unit

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volume being known). In a collaboration with the Entomology Department a stylet-bearing insect, the cereal thrips, has been successfully studied: it has been shown (apparently for the first time) to use its stylet apparatus for sucking up food (see Entomology Department Report). The recently built photodiode probe equipment (*Rothamsted Report for 1978*, Part 1, 184) has been used in this work to measure activity recorded on ciné-film. (Doncaster and Seymour, with Chisholm, Entomology Department)

Morphology and fine structure

Head structure in *Hexatylus viviparus*. As a fungal feeding member of the Tylenchida (which includes most plant-parasitic nematodes) *H. viviparus* shows several interesting and systematically important attributes, e.g. passive feeding and the associated structure of the gut (*Rothamsted Report for 1975*, Part 1, 193–194). Light microscopy suggests the head skeleton is octagonal but scanning and transmission electron microscopy show an unusually complex arrangement which is nevertheless six-fold, as in other Tylenchida. Each of the six radial arms of the head skeleton has a large foramen, leaving only thin spars on either side and the protractor muscles pass through these foramina into the tip of the head, resulting in 12 lightly sclerotised radial arms instead of six, or eight as was thought. The eight head sectors seen in the light microscope result from subdivisions of six basic sectors; the cephalic sensillae, stylet musculature and their nerves all have a basically hexaradiate symmetry. The fine morphology of these cephalic structures has been elucidated in detail. (Shepherd and Clark)

Taxonomy

Characterisation of *Meloidogyne*. Characters used in identification of *Meloidogyne* exhibit morphological variation with considerable overlap between species. Some of the current 47 *Meloidogyne* species and races, particularly the less well known, are being examined to establish more useful deterministic characters. Existing species descriptions are inconsistent and generally unsatisfactory but the most useful characters have been identified by comparison of range and mean measurements and by limitation to those visible in fixed specimens and exhibiting 10% or less intraspecific variation. Applied to test populations of *M. graminicola* and *M. graminis*, this resulted in a 60% reduction of the characters considered useful. Scanning electron microscopy has been used for comparison of head and stylet structure. The form of the head cap, notably the labial disc, is a useful specific character in males and juveniles examined. Male and female stylet dimensions, the shape of stylet, cone, shaft and knobs and distance from knobs to dorsal oesophageal gland orifice, are usually characteristic. SEM observation is related to light microscopy to provide characters accessible to most workers and light microscopy of 18 species in the Rothamsted slide collection has confirmed the utility of characters first observed by SEM.

Drying from acetone or infiltration with Spurr's resin produces distortion in males and juveniles, making them unsatisfactory for SEM. More satisfactory preparations have been obtained by fixation in cold 2.5% glutaraldehyde, passage through an ethanol series into amyl acetate and then critical point drying from carbon dioxide. (Jepson and Hoole)

***Heterodera*.** A newly discovered species was described from S. Italy and differs from the closely related *H. carotae*, *H. cruciferae* and *H. goettingiana* by presence of conspicuous bullae, a shorter second-stage juvenile tail and by its only known host, lentiscus (*Pistacia lentiscus*), a root-stock for cultivated pistachio. It is the first cyst nematode

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described from the woody family Anacardiaceae (Order Sapindales) of which there are no closely related herbaceous plants and few other cyst nematodes have been described from woody hosts. *Pistacia* is naturally distributed in the Mediterranean region. (Vovlas and Stone)

Miscellaneous studies

Hair worms (Gordiids): Gordiids occur in ponds and streams and look like nematodes but are systematically distant and can be much longer. Males of *Parachordodes wolterstorffii*, from a stream in the New Forest, Hampshire, were examined in the scanning electron microscope after cutting into sections which allowed examination of internal as well as external structures. Anteriorly and on the outer margins of the bifid tail the cuticle is relatively smooth but over much of the body there is an areolated pattern with minute tubercles in the depressions between the areoles. Over most of the body the areoles are elongated along the body axis but posteriorly they are more rounded dorsally and more elongated ventrally; the lateral margins are marked by four to five rows of irregularly placed bumps. The precloacal 'brush' consists of elongated bristles similar to those closely encircling the small cloacal opening but in the post-cloacal field the bristles are shorter, thicker, and cone-shaped. The body wall appears very like that of nematodes. The inner, fibrous layer of the cuticle has about 40 layers of parallel fibres, probably collagenous. Each fibre is about 0.2 μm in diameter and in successive layers describe right- and left-handed helices round the body. Only longitudinal body muscles are present; the theory of fibre-wound cylinders predicts that in a shortening worm, volume will tend to decrease and pressure rise, and the angle between the fibres and longitudinal axis of the worm increase. With the body muscles relaxed, the worm will recoil and elongate until at rest when a fibre/axis angle of $54^{\circ} 44'$ is predicted. Measurements of angles in cuticle from relaxed worms give a mean value of $54^{\circ} 41'$ ($\pm 30'$ SE). (Hooper, Cham and Seymour)

Techniques

A simple method for estimating root length. Plant roots often respond to nematode attack by producing many rootlets, which add little to the weight of the system but may increase its total length considerably. Physiological activity is thought to be more closely related to surface area or total length than to weight of a root system. Scores from a line-intersect method using grid squares of 1.27 or 2 cm were converted to length estimates using the formula $\text{root length} = 11/14 (\text{no. of intercepts}) (\text{grid-spacing unit})$, (Marsh, *Journal of Applied Ecology* (1971) 8, 265–267). The method was tested with white cotton threads 0.3–50.0 m long, scattered in a rectangular perspex dish over the grid. Lengths of 0.3–5.0 m were counted on the smaller grid and 3–50 m lengths on the larger. Estimates were usually within $\pm 5\%$ of the true length, with coefficient of variation $< 5\%$. The guide-lines for counting suggested by Tennant (*Journal of Ecology* (1975) 63, 995–1001) improved accuracy. (Spaull and Murphy)

Extraction of fungal resting spores from soil. A wet sieving method has been developed to estimate the number of resting spores of *Nematophthora gynophila* and *Verticillium chlamydosporium* in soil. Moist soil (25 g) is screened through 16 and 100 mesh sieves and spores and other fine particles collected on a 10 μm aperture sieve. The collected material is suspended in a solution of magnesium sulphate, density 1.33, centrifuged at 500 rev min^{-1} (39 g) for 5 min to precipitate soil particles and the supernatant, containing spores, decanted on to a 10 μm aperture sieve. The sediment is resuspended and the process repeated. Spores on the 10 μm aperture sieve are washed into 10 ml water and centrifuged at 2500 rev min^{-1} (850 g) for 5 min. The supernatant is removed with a pipette to leave

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0.5 ml of the spore suspension and 0.01 ml is pipetted on to a glass slide for counting. The method recovers 80% of the resting spores of both fungi added to sandy loam, peat or clay soils. One person may process four samples daily. In fields where *H. avenae* populations fail to multiply when susceptible cereals are grown, 254 and 255 spores g^{-1} soil of *N. gynophila* and *V. chlamydosporium* respectively were recovered from a sandy loam soil at Woburn, and 35 and 365 g^{-1} soil from a calcareous loam soil in Hampshire. In soil where the nematode was causing damage fewer spores were recovered; 3 g^{-1} soil *N. gynophila* and 35 g^{-1} soil *V. chlamydosporium*. (Crump and Kerry)

Extraction of cysts. *Globodera pallida* cysts in dried soil from a pot experiment were extracted with 80% efficiency by Oostenbrink elutriator but 70% of these sank when the extract was refloated in a filter paper cone, the usual final stage of separation from soil and debris. In a routine extraction >70% of cysts present in the soil would have been lost. The cysts were small, pale and contained unembryonated eggs and had not completed normal development. For efficient application of cyst extraction procedures where a second flotation follows immediately after the first it is necessary for females to have completed their maturation. (Parrott)

Staff and visitors

C. C. Doncaster and D. J. Hooper were elected Fellows of the Institute of Biology. Susan Turner was awarded a Ph.D., University of Birmingham. C. D. Green transferred to the Department from the National Vegetable Research Station. A. R. Stone visited nematology laboratories at North Carolina State University, Raleigh; Virginia Polytechnic Institute and State University, Blacksburg, and the USDA Agricultural Research Center, Beltsville, with support from the Hatley Foundation and ODA. Susan Jepson also visited North Carolina and Beltsville under ODA auspices. A. R. Stone, C. D. Green and J. A. Walsh gave papers at the XV Symposium of the European Society of Nematologists in Bari, Italy. B. R. Kerry visited the University of Georgia, Athens; the University of Florida, Live Oak, and gave an invited paper at the USDA Symposium on Biological Control, held at Beltsville, supported by USDA. A. G. Whitehead visited nematological centres in Europe. J. Bridge visited Tanzania on behalf of ODA. The Department was host in June to the Association of Applied Biologists Meeting on Nematicides. Seventy participants from eight countries attended the meeting which included a demonstration of nematicide applicators at the Woburn Farm. Staff members also contributed to the Association of Applied Biologists/Federation of British Plant Pathologists Meeting on Plant Disease Etiology held in London in December, to Royal Society Soirées in June and to the Royal Charter celebrations of the Institute of Biology. The film 'The stem nematode: A pest in agriculture' (C. C. Doncaster and D. J. Hooper) was shown at the XI Internationaler Agrarfilm, Wettbewerb, Berlin, January, and the 34th Congress of the International Scientific Film Association, Cologne, in September. The film 'Aphid-trapping potato plants' (Doncaster and R. W. Gibson, Plant Pathology Department) was awarded a Diploma of Honour at the International Scientific Film Association Congress.

Dr N. Vovlas (Italy), Mr W. K. K. Mmatta (Kenya) and Mrs Ellita Chikwita (Malawi) spent extended periods in the Department and Mr F. D. Friere (Brazil) joined the Department for 2 years.

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Publications

THESIS

- 1 TURNER, S. J. (1980) Resistance in *Solanum vernei* hybrids to potato cyst-nematodes. Ph.D. Thesis, University of Birmingham.

GENERAL PAPERS

- 2 BRIDGE, J. & (MANSER, P.) (1980) Occurrence of the beet cyst-nematode, *Heterodera schachtii*, in tropical Africa. *Plant Disease* **64**, 1036.
- 3 BRIDGE, J. & PAGE, S. L. J. (1980) Estimation of root-knot nematode infestation levels on roots using a rating chart. *Tropical Pest Management* **26**, 296–298.
- 4 EVANS, K. & (BRODIE, B. B.) (1980) The origin and distribution of the golden nematode and its potential in the U.S.A. *American Potato Journal* **57**, 79–89.
- 5 FRANCO, J. (1980) Effects of potato cyst-nematode *Globodera rostochiensis* on photosynthesis of potato plants. *Fitopatologia* **15**, 1–6.
- 6 HOOPER, D. J. (1980) Stem nematode (*Ditylenchus dipsaci*), a seed and soil-borne pathogen of *Vicia faba*. *FABIS Newsletter* No. 2, 49.
- 7 JONES, F. G. W. (1980) Plant nematology. In: *Perspectives in world agriculture*. Farnham Royal: Commonwealth Agricultural Bureau, pp. 295–305.
- 8 JONES, F. G. W. & KEMPTON, R. A. (1980) Forecasting crop damage by nematodes: nematode population dynamics. *EPPO Bulletin* **10**, 169–180.
- 9 KERRY, B. R. (1980) Biocontrol: Fungal parasites of female cyst-nematodes. *Journal of Nematology* **12**, 253–259.

RESEARCH PAPERS

- 10 (ANDERSON, R. V.) & HOOPER, D. J. (1980) Diagnostic value of vagina structure in the taxonomy of *Aphelenchus* Bastian, 1865 (Nematoda: Aphelenchidae) with a description of *A. (Anaphelenchus) isomerus* n. subgen., n, sp. *Canadian Journal of Zoology* **58**, 924–928.
- 11 BRIDGEMAN, M. R. & KERRY, B. R. (1980) The sex ratios of cyst nematodes produced by adding single second-stage juveniles to host roots. *Nematologica* **26**, 209–213.
- 12 BROMILOW, R. H. (& LEISTRA, M.) (1980) Measured and simulated behaviour of aldicarb and its oxidation products in fallow soils. *Pesticide Science* **11**, 389–395.
- 13 BROMILOW, R. H., BAKER, R. J., FREEMAN, M. A. H. (& GÖRÖG, K.) (1980) The degradation of aldicarb and oxamyl in soil. *Pesticide Science* **11**, 371–378.
- 14 CLARKE, A. J. & HENNESSY, J. (1980) Release of juveniles of cyst-nematodes from eggs by hypochlorites. *Nematologica*, **26**, 358–368.
- 15 DONCASTER, C. C. (1981) Observations on relationships between infective juveniles of bovine lungworm, *Dictyocaulus viviparus* (Nematoda: Strongylida) and the fungi, *Pilobolus kleinii* and *P. crystallinus* (Zygomycotina: Zygomycetes.) *Parasitology* **82**, 421–428.
- 16 (FORREST, J. M. S.) & PERRY, R. N. (1980) Hatching of *Globodera pallida* eggs after brief exposures to potato root diffusate. *Nematologica* **26**, 130–132.
- 17 HOOPER, D. J. & CLARK, S. A. (1980) Scanning electron micrographs of the head region of some species of Aphelenchoidea (Aphelenchina: Nematoda). *Nematologica* **26**, 47–56.

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- 18 KERRY, B. R., CRUMP, D. H. & MULLEN, L. A. (1980) Parasitic fungi, soil moisture and multiplication of the cereal cyst-nematode, *Heterodera avenae*. *Nematologica* **26**, 57–68.
- 19 (LEISTRA, M.), BROMILOW, R. H. & (BOESTEN, J. J. T. I.) (1980) Measured and simulated behaviour of oxamyl in fallow soils. *Pesticide Science* **11**, 379–388.
- 20 MCEWEN, J., WEBB, R. M. *et al.* (1980) The effects of irrigation, nitrogen fertilizer and the control of pests and pathogens on spring-sown field beans (*Vicia faba* L.) and residual effects on two following winter wheat crops. *Journal of Agricultural Science, Cambridge* **96**, 129–150.
- 21 PERRY, R. N., CLARKE, A. J. & BEANE, J. (1980) Hatching of *Heterodera goettingiana* *in vitro*. *Nematologica* **26**, 493–495.
- 22 PERRY, R. N., PLOWRIGHT, R. A. & WEBB, R. M. (1980) Mating between *Pratylenchus penetrans* and *P. fallax* in sterile culture. *Nematologica* **26**, 125–129.
- 23 SHEPHERD, A. M., CLARK, S. A. & HOOPER, D. J. (1981) Structure of the anterior alimentary tract of *Aphelenchoides blastophthorus* (Nematoda: Tylenchida, Aphelenchina) *Nematologica* **26**, 313–357.
- 24 SPAULL, A. M. (1980) Effect of *Paratrichodorus anemones* on growth of spring wheat and barley. *Nematologica* **26**, 163–169.
- 25 VOVLAS, N., CHAM, S. & HOOPER, D. J. (1981) Observations on the morphology and histopathology of *Rotylenchus laurentinus* attacking carrots in Italy. *Nematologica* **26**, 302–307.
- 26 WHITEHEAD, A. G., TITE, D. J., FRASER, J. E. & FRENCH, E. M. (1980) Effects of aldicarb and oxamyl in peaty loam soil on potato cyst-nematode, *Globodera rostochiensis*, and on resistant and susceptible potatoes. *Journal of Agricultural Science, Cambridge* **95**, 213–217.
- 27 WHITEHEAD, A. G., TITE, D. J., FRASER, J. E. & FRENCH, E. M. (1980) Control of potato cyst-nematode, *Globodera rostochiensis*, in a three-course rotation. *Journal of Agricultural Science, Cambridge* **95**, 294–304.
- 28 WHITEHEAD, A. G., TITE, D. J. & BROMILOW, R. H. (1981) Techniques for distributing non-fumigant nematicides in soil to control potato cyst-nematodes, *Globodera rostochiensis* and *G. pallida*. *Annals of Applied Biology* **97**, 311–321.
- 29 WILLIAMS, T. D. & BEANE, J. (1980) The effects of nematode resistant and susceptible spring oat cultivars and aldicarb on the cereal cyst-nematode *Heterodera avenae* and yields in contrasting soil types. *Annals of Applied Biology* **95**, 115–124.
- 30 WILLIAMS, T. D. & BEANE, J. (1980) Some effects of differently-acting nematicides on the cereal cyst-nematode (*Heterodera avenae*) and on the appearance of 'scorch' in spring wheat on light loamy sand. *Annals of Applied Biology* **95**, 225–234.