ROTHAMSTED RESEARCH

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Nematology Department

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Introduction

In *Reports* for 1979 and 1980 attention was focused on particular aspects of the Department's work. This report returns to the format of earlier years in being more general but, as in the past 2 years, inclusion of substantial quantities of data, which will appear in published papers, has been avoided.

Nematodes are ubiquitous, occurring in all biotopes, and those that occur in agricultural soils include types that feed on plant tissues. Of these plant parasites those which are the most highly adapted are paradoxically the most damaging in the agricultural context. The sedentary cyst nematodes and root-knot nematodes are the major nematode pests in temperate and tropical agriculture respectively and form the main focus of our attention but work on stem nematodes, which exist in a number of host specific races, is increasing. Relatively little is known about the great range of migratory nematodes,

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largely because they do not cause readily identifiable problems in crop production; some work on migratory forms is reported. The results of nematode investigations in the multidisciplinary experiments are reported elsewhere.

Work on tropical nematodes continues to be funded by the Overseas Development Administration and this year we have received support from the Perry Foundation for work on cyst nematode interactions with root microorganisms and from the United States Department of Agriculture for work on fungal pathogens of cyst nematodes.

Work with nematicides

Potato cyst-nematodes

Culture technique for screening nematicides. A faster method has been tested for assessing the effect of non-fumigant nematicides on potato cyst-nematode, *Globodera rostochiensis*. Potato sprouts 1–2 cm long with 1–2 cm cubes of tuber tissue were dipped in 'Chloros' (0·08% available Cl) containing 'Teepol' (2%), washed in sterile water and then dipped in chlorothalonil fungicide (450 ppm). The treated sprouts were grown on 2% water agar containing chlorothalonil (150 ppm), streptomycin sulphate (50 ppm) and the nematicide. Second-stage juveniles were placed close to the tips of roots 3 cm long. The cultures were kept at room temperature. In cultures not treated with a nematicide, the nematode completed its life cycle in about 4 weeks. The streptomycin and chlorothalonil kept the roots free of bacteria and fungi, which may otherwise make observations difficult or impossible when contamination is severe. This technique could be used to determine LD50 values of nematicides and to screen potato breeding lines against nematode pathotypes. (Akhtar and Whitehead)

New nematicides. In pots of peaty loam infested with potato cyst-nematodes (*G. rostochiensis* and *G. pallida*) two new organophosphates ('Hoe 00668' and 'RH 9358') and two new carbamates ('DS 47187' and 'DS 46995') mixed with the soil minimised or prevented nematode increase on susceptible Arran Banner potatoes. The two organophosphates were tested in the field at Woburn in sandy loam heavily infested with *G. rostochiensis*, where they controlled the nematode and very greatly increased yields of Pentland Crown potatoes. (Whitehead, Tite, Fraser and Nichols, with Bromilow, CLU)

Methods of incorporating nematicides in soil. This year we built and tested a simplified version of the patent Vertical Band granule applicator, described in previous annual reports. The technique consists of blowing nematicide granules into vertical bands 20 cm apart in the top 12–15 cm of the soil and then incorporating them laterally within the soil with a rotary harrow (Lely 'Roterra'). In contrast to spreading the granules on the soil surface and incorporating them with a rotavator, application is faster, safer and leaves a better seed bed. In fen peat soil at Woodwalton, rather more granules (40–50% of those applied) were recovered from 10–15 than from 0–5 or 5–10 cm deep in the soil and this distribution was independent of 'Roterra' rotor speed. Similar distribution was obtained with the earlier version of the machine (*Rothamsted Report for 1978*, Part 1, 170). Granules applied to the soil surface and incorporated with an L-bladed rotavator were more uniformly distributed in the top 15 cm of soil, with small amounts (15% applied granules) from 15–25 cm deep. However, the nematodes were equally well controlled and the yield of King Edward potatoes was increased equally by aldicarb or oxamyl in the heavily infested soil, whichever technique was used. Similar results were obtained in sandy clay loam infested with *G. rostochiensis* and *G. pallida* at Ramsey, with oxamyl and Maris Piper potatoes. (Whitehead, Tite, Fraser and Nichols, with Bromilow, CLU)

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Cultivar responses. As in 1980, we measured the yield responses of a range of potato cultivars to oxamyl, incorporated in the top 15 cm of the soil just before planting. At Ramsey, Hunts., in peaty loam moderately infested with *G. pallida*, oxamyl increased yields of Cara, Maris Piper, Pentland Crown, King Edward, Desirée and Record by 30–40% (to 52–72 t ware ha^{-1}) and of Croft and F 49/52 (80% resistant to *G. pallida*) by about 59% (to 51 t ware ha^{-1}). Oxamyl increased yield of Pentland Dell by 124% (to 51 t ware ha^{-1}). At Woburn, in sandy loam heavily infested with *G. rostochiensis*, susceptible varieties grew and yielded poorly in untreated soil (5–19 t ware ha^{-1}) but grew and yielded well in treated soil (34–59 t ware ha^{-1}). Cara and Maris Piper, which have the H_1 gene for resistance to *G. rostochiensis*, grew well in untreated soil (41 and 40 t ware ha^{-1}, respectively) but also responded to oxamyl (58 and 53 t ware ha^{-1}, respectively). In contrast, the early potato Maris Anchor, which also has gene H_1, yielded only 5 t ware ha^{-1} in untreated soil and 29 t ware ha^{-1} in treated soil. Some cultivars appear more prone to injury by potato cyst-nematodes than others and different population thresholds may need to be set for nematicide treatment of different cultivars. (Whitehead, Tite, Fraser and Nichols)

***Effect of wild* Solanum *spp. on* G. rostochiensis *and* G. pallida.** The possibility of decreasing numbers of potato cyst-nematodes in the soil by growing wild *Solanum* spp. in the autumn after an early harvested crop, was investigated in pots. Seeds of British wild *Solanum* spp. were kindly supplied by Dr Jennifer Edmunds, Botany School, Oxford. No females of *G. rostochiensis* or *G. pallida* developed on the roots of *S. chenopodioides*, *S. nigrum nigrum* or *S. nigrum schultesii* grown in infested soils but soil populations were decreased no more than by bare fallowing the soils. (Whitehead, Tite, Fraser and Nichols)

Cereal cyst-nematode. At Woburn, small amounts of ethylene dibromide or 'Telone II' (dichloropropene mixture) applied to the seed furrows during sowing failed to increase yields of Maris Tabard oats in soil lightly infested with cereal cyst-nematode, *Heterodera avenae*, possibly because they were phytotoxic. In contrast, 1·5 and 3·0 kg oxamyl ha^{-1}, similarly applied, increased oat grain yields from 3·7 t ha^{-1} in untreated plots to 5·4 and 5·5 t ha^{-1}, respectively. (Whitehead, Tite, Fraser and Nichols)

Stem nematodes. At Rothamsted, oat and giant races of stem nematode, *Ditylenchus dipsaci*, were well controlled on winter beans by aldicarb applied to the seed furrow at sowing followed by thiabendazole watered on to the plants in spring. Dressing seeds with aldicarb, carbofuran, oxamyl, phoxim or thiabendazole (about 0·5 mg a.i. per seed) did not lessen nematode attack in the plants. In an adjacent experiment, aldicarb applied to the seed furrows at sowing controlled the nematode in spring beans, whereas phorate similarly applied did not. Oxamyl applied to the seed furrows was less effective than aldicarb. Top dressing the rows of bean plants with aldicarb, phoxim, thiabendazole or phorate did not improve control achieved by aldicarb alone. (Whitehead, Tite, Fraser and Nichols)

Effects of nematodes on crops

Tolerance by potatoes to cyst nematode attack. The ability of the host plant to grow and yield well despite the presence of many nematodes is referred to as 'tolerance'; 'resistance' is confined to describing the host plant's ability to prevent nematode reproduction. True resistance to potato cyst-nematode was first reliably reported in 1948. Earlier references claiming to have identified resistance in potatoes may have described tolerance, and be useful sources of information about tolerant cultivars. O'Brien and Prentice, 1931

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(*West of Scotland Agricultural College. Research Bulletin* No. 2) described a number of cultivars as 'resistant'. A selection of these have been grown in plots infested with *Globodera rostochiensis* Ro1 and compared with Desirée, a rather intolerant cultivar. Immune Ashleaf is very intolerant and Kerr's Pink and Arran Consul very tolerant, as found by O'Brien and Prentice. However, in contrast to their findings, Golden Wonder was the most tolerant cultivar tested and King George and Great Scot were relatively intolerant. Desirée was rated fifth out of the eight cultivars tested.

Measurements of nutrient uptake in two field trials (one site infested with *G. rostochiensis* the other with *G. pallida*), in which cultivars were grown with and without oxamyl treatment, confirmed that the amounts of potassium and phosphorus in plant dry matter are decreased and calcium increased in all cultivars when infested. The magnitude of these effects is always less in more tolerant cultivars and allows a crude classification of cultivars as either tolerant or not. (Evans)

Studies of water use efficiency by different cultivars were continued. When early, main crop and late maturing cultivars were compared in pots under glass, plants infested with *G. rostochiensis* had smaller transpiration ratios (water lost per unit increase in dry weight) than uninfested plants during the first 43 days from planting and plants of the late maturing cultivar had smaller transpiration ratios than the earlier maturing cultivars. Perhaps earlier maturing cultivars are not subjected to a selection pressure for efficient water use because they are grown at a time of year when water supply is not usually limiting for growth. *G. pallida* had as much effect on growth and water use efficiency of H_1 resistant cultivars as *G. rostochiensis* had on non-resistant cultivars. (Fatemy)

Growth and yield of the susceptible cultivars Maris Peer (intolerant) and Pentland Crown (tolerant) were compared with those of the *G. rostochiensis* resistant cultivars Maris Anchor (intolerant) and Maris Piper (tolerant) in an experiment with a range of population densities of *G. rostochiensis* and *G. pallida* in which half the plants were treated with measured inocula of *Verticillum dahliae*. In the absence of *V. dahliae* Maris Peer yielded worst, Pentland Crown and Maris Piper were hardly affected by either nematode and Maris Anchor was intermediate but affected more by *G. pallida* than *G. rostochiensis*. Addition of *V. dahliae* in the presence of nematodes had little effect on Maris Peer, Pentland Crown or Maris Piper but Maris Anchor grew much more poorly. Growth of Maris Anchor was particularly bad with *G. pallida* and *V. dahliae*, but *V. dahliae* alone was associated with 40% tuber yield loss. The poor performance of Maris Anchor in some field trials with potato cyst-nematodes may depend on the presence of *V. dahliae* and be a factor in this cultivar's intolerance to the nematodes. (Evans and Greet)

Suppression of *Rhizobium* nodules in pea roots. Invasion by pea cyst-nematode of pea roots grown in nitrogen-free agar (*see* p. 171) and inoculated 14 days previously with *Rhizobium* suppressed nodule formation. Nodulation was not as fully inhibited as in field conditions, in which nematodes invade over a longer period and usually in much greater numbers, but nodules developing were unusually small and limited to lateral roots, suggesting they were formed only after invasion by the nematodes had stopped. Possibly inhibition of nodule formation by pea cyst-nematodes is due to direct competition for sites in the roots but in similar experiments the endoparasite *Pratylenchus thornei* did not affect nodule numbers and stem nematode, *Ditylenchus dipsaci*, was associated with an apparent increase. (Green and Hornsey)

Fungal pathogens and root-knot nematode in black pepper. Root rot and foot rot of black pepper (*Piper nigrum*) caused by *Nectria haematococca* f. sp. *piperis* (*Fusarium solani* f. sp. *piperis*) and *Phytophthora palmivora* are regarded as the most important diseases of this

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crop in the Amazon region of Brazil. Root-knot nematodes are also usually present. Plants inoculated with the *Meloidogyne incognita* plus *P. palmivora* and plants inoculated with the fungus alone showed wilt symptoms almost at the same time, and prior infestation with the nematode did not make black pepper more susceptible than uninfested controls. The cultivar commonly grown in Brazil and six others from elsewhere all showed no resistance to the fungi or the nematode. (Freire)

Rice root-knot nematode on deep water rice. In experiments which simulate deep water rice growing conditions, *Meloidogyne graminicola* (a pest of deep water as well as upland rice, *Rothamsted Report for 1980*, Part 1, 154) significantly decreased growth of deep water rice before and, to an even greater extent after, flooding. On submergence, most plants with large infestations in their roots were unable to grow above the water level but plants without nematodes rapidly elongated to remain above the rising water. Juveniles did not invade rice roots in flooded soil but remained viable for at least 27 days and immediately infested roots when the water was removed. *M. graminicola* was not found in flooded rice roots after 5 months at water depths of 29 cm and 1 m but survived in the flooded soils for this period and caused severe galling to rice planted immediately after the water was removed. Nematodes that invaded roots before flooding occurred developed and reproduced normally within the tissue for at least 36 days. Females laid their eggs mainly within roots and their progeny remained within the roots producing new infection sites but nematodes also were present in the water and could thus be dispersed. A greater number of large galls were produced in flooded roots than in roots growing in well-drained soils. (Bridge, Page and Jordan)

Cyst nematode biology

Hatching of *Globodera rostochiensis*. Calcium is a major inorganic constituent of *G. rostochiensis* egg-shells. Its distribution in variously treated egg-shells has been examined by x-ray microanalysis. When intact eggs were treated with 5 mM-1,2-di(2-aminoethoxyl)-ethane-N,N,N^1,N^1-tetra acetic acid (EGTA), about one-third of the Ca^{2+} present in the egg-shell was removed. However, when opened egg-shells were similarly treated almost all of the Ca^{2+} was lost. Neither intact nor opened egg-shells lost Ca^{2+} when extracted with 10 mM-acetic acid. Opened egg-shells from intact eggs which had previously been treated with EGTA lost the remaining Ca^{2+} on treatment with a solution of the hatching factor. The results indicate that the Ca^{2+} of intact egg-shells, which is accessible to EGTA, is present in the outer chitinous layer of the shell and that the inaccessible Ca^{2+} is associated with the inner lipo-protein layer. This suggests that the removal of Ca^{2+} by the hatching factor is an important part of the hatching mechanism. Loss of Ca^{2+} from the lipo-protein layer of the egg-shell may be responsible for the observed change in permeability and the release of egg-fluid solutes which precedes hatching. (Clarke and Perry with Turner, Plant Pathology Department)

Early work on the hatching mechanism was thought to indicate involvement of free Ca^{2+}. The reported increase in number of juveniles emerging from cysts when 0·5 mM-$CaCl_2$ is added to dilute decationised potato-root exudate is confirmed. However, we attribute the increase in hatch to the greater concentration of free hatching factor obtained with solutions containing $CaCl_2$. We suggest that Cl^- displaces ionically bound hatching factor from basic groups present in cyst wall protein and possibly elsewhere in the cyst. (Clarke and Hennessy)

It is becoming apparent that potato root exudate has a rapid action in initiating hatching of *G. rostochiensis* and *G. pallida*. A 5 min exposure is sufficient to induce some hatch of free eggs of *G. pallida* (*Rothamsted Report for 1978*, Part 1, 186–187) and physiological

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changes in the unhatched *G. rostochiensis* juvenile occur during the first 24 h after the hatching stimulus. Experiments were carried out to investigate the response of *G. rostochiensis* to brief exposures of potato root exudate. Cysts (Ro1), grown on cv. Arran Banner were soaked in artificial tap water before eggs were freed. For eggs kept continuously in root exudate or soil leachate only the total percentage hatch after 5 weeks was 69% and 2% respectively. Hatches of 51% were obtained from free eggs stimulated by immersion in potato root exudate for only 5 min per week for 5 weeks; increasing the period of stimulation up to 24 h did not significantly increase hatch. Repeated stimulation and the use of fresh exudate significantly ($P < 0{\cdot}01$) enhanced hatch when compared to the hatch resulting from single exposures to exudate or to the hatch obtained when the same exudate was used each week. Very brief exposures to root exudate are sufficient to 'trigger' the sequence of events leading to hatch; the enhancement of hatch by repeated stimulation may indicate a receptor threshold level being reached whereas an equivalent period of single stimulation does not reach the threshold level. (Perry and Beane)

When, in another series of experiments, cysts of *G. rostochiensis* were exposed to potato root exudate for 24 h and then dried at 0% relative humidity they subsequently showed a significantly decreased hatch compared with untreated cysts when again exposed to root diffusate. Exposure to exudate before desiccation did not alter the rate of hatch but reduced the number of juveniles able to respond. Juveniles hatched by mechanical pressure from cysts treated in this way did not show any less ability to withstand desiccation than juveniles from untreated eggs. The increased susceptibility to desiccation of unhatched juveniles treated with root exudate appears due to alteration in eggshell permeability rather than changes in juvenile physiology. (Perry and M. Hill)

G. rostochiensis hatches freely only when stimulated by host root exudates. It was once thought that the nematode could be controlled by using potato root exudate to induce hatch in the absence of the host plant but root exudate appeared not to persist in soil and was considered impractical as a means of control. However, Tsutsumi (*Japanese Journal of Nematology* (1976), **6,** 10–13) suggested persistence for up to 100 days after removal of the plant although the data were limited. To evaluate persistence, the effect of soil leachate on the hatch of *G. rostochiensis* was investigated before and after removal of host plants. Potato plants 5 cm high (cv. Arran Banner), transplanted without tuber pieces, were raised in sterile peaty-loam soil in 9 cm pots for 14 weeks and then removed; controls were similar but without potato plants. After removal of the plants leachate was collected until the hatch induced by the leachate from soil which had contained plants was similar to that in leachate from the control pots, which had never contained plants. Hatches >60% occurred with leachate obtained 2 weeks after plants were removed and after 4 weeks the mean hatch was >50%. Some activity persisted until 8 weeks after removal of the plants. Cysts treated with soil leachate from control pots gave small percentage hatches ranging from 0·5 to 4·4%. Small pieces of root left behind in the soil after removal of the plants may have continued to produce exudate for a period but when relatively large amounts of Arran Banner roots (3·5 g per pot) were chopped and mixed with soil in pots similar to the controls and the leachate collected at 2, 4 and 6 weeks, it induced hatches of only 11, 6 and 5% respectively. Potato root exudate seems to retain its activity in the soil for a period after potatoes are removed. A similar effect has been noted with *Heterodera goettingiana*. (Perry and Beane)

Differentiation of *G. pallida* pathotypes. A new pathotype of *G. pallida*, named New Leake, was recognised by Fuller, Howard and Stone (*Plant Pathology* (1977), **26,** 135–138) because it multiplied on D47/11, a potato clone derived from *Solanum tuberosum* ssp. *andigena* CPC 2802 with resistance to *G. pallida*. However ADAS trials with this clone in 1980 identified a number of field populations of *G. pallida* with limited reproduction on

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D47/11. Either the New Leake pathotype is widespread as a component of field populations or D47/11 is not fully resistant to other *G. pallida* pathotypes. In pot trials with this clone five of six *G. pallida* populations (Ballyloughan Pal, Garvaghey Pal, Dunminning Pal, St Brelades Pa2 or 3, D1001 Pa2 or 3, and Dutch E Pa3) had Pf/Pi ratios $\geqslant 1{\cdot}0$ producing on average 60–88 new cysts per plant at inocula of 15–20 eggs g^{-1} soil. The resistance of D47/11 to *G. pallida* pathotypes other than New Leake is apparently not complete and differentiation of the new pathotype is therefore imprecise. (Stone, Parrott and Payne)

Inheritance of virulence in *G. rostochiensis* Ro4 and Ro5. Reciprocal matings were made between the standard populations of *G. rostochiensis* pathotypes Ro1, Ro4 and Ro5. The progeny (cysts containing F_1 juveniles) were tested against differential potato clones used in the European pathotyping scheme (*Solanum kurtzianum* hybr. 60.21.19 and *S. vernei* hybr. 58.1642/4) both resistant to Ro1, and an ex *andigena* hybrid (cv. Maris Piper) resistant to Ro1 and Ro4. Viability of the progeny was tested on susceptible cv. Desirée.

TABLE 1

Pf/Pi ratios of progeny from reciprocal crosses of G. rostochiensis *Ro1, Ro4, and Ro5*

	Ro1	Ro4	Ro5	Ro1 × Ro4	Ro4 × Ro1	Ro1 × Ro5	Ro5 × Ro1	Ro4 × Ro5	Ro5 × Ro4
S. tuberosum ssp. *tuberosum*	9·8	6·6	18·5	5·5	4·4	8·7	17·3	10·4	13·0
S. tuberosum ssp. *andigena* CPC 1673 hybr.	0·2	0·0	3·6	—	—	0·1	0·1	<0·1	<0·1
S. kurtzianum hybr. 60.21.19	0·5	3·1	1·0	0·6	0·4	0·9	2·4	—	—
S. vernei hybr. 58.1642/4	0·2	1·0	4·6	0·1	0·1	0·2	0·5	—	—

The resulting Pf/Pi (final number cysts/initial number cysts) ratios (Table 1) suggest that the nematodes able to reproduce on the *andigena* and *S. vernei* clones were homozygous for recessive genes, the reproduction of the progeny from the crosses being no greater than that of the non-virulent parent. This was probably also true for the Ro4/*S. kurtzianum* relationship but the progeny of the Ro1 × Ro5 cross were as virulent, or more so, on this clone than the Ro5 parent population. This suggests the gene(s) in Ro5 conferring virulence on *S. kurtzianum* is dominant and the result is unexpected, other pathotypes of potato cyst-nematodes tested apparently having recessive genes for virulence (*Rothamsted Report for 1978*, Part 1, 182). Tests on the F_2 generation and backcrosses should clarify the situation. (Parrott)

Development of *Heterodera schachtii* on cotyledons of rape. Females developed on the cotyledons of rape growing in sterile culture, and produced eggs containing second-stage juveniles. Transfer cells were observed near to the vascular tissue in thin sections of the cotyledons examined under the light microscope. This is the first observation of such cellular changes caused by *H. schachtii*, although *H. trifolii* females have been observed on clover leaves by others. (Rice, Mullen and Kerry)

Stem nematode biology

Stem nematodes (*Ditylenchus dipsaci*) are damaging pests of a number of field crops in Britain, especially lucerne, red clover, field beans, onions, garlic, carrots, oats, maize,

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narcissus and tulip. Controlling stem nematodes by crop rotations is difficult, partly because of their longevity in soil and partly because of apparent inconsistencies in the host ranges of the different 'races'.

Population studies. Ninety populations of common races of stem nematodes were collected in Britain and Europe. As an essential preliminary to detailed studies of the host ranges of these 'races' the efficacy of different culture techniques was assessed. Stem nematodes in 1% agar, on the growing points of young seedling hosts growing at 5–10°C in humidified pots usually invaded and multiplied in the shoots. Inoculations of onion, narcissus and tulip bulbs and of Duke of York potato tubers were unreliable. Inoculations of red clover, lucerne and oat stems were unsuccessful but inoculations of onion leaves and broad bean stems were successful. (Whitehead, Tite, Fraser and Nichols)

Persistence. Soil populations of *D. dipsaci* fourth-stage juveniles may decline by up to 99% over winter. Measurements of lipid reserves indicate that starvation is unlikely to be the cause (*Rothamsted Report for 1980*, Part 1, 158). The decline does not appear due to movements of nematodes into deeper soil. Thirteen per cent of fourth-stage juveniles inoculated at 1·0 cm depth into 10 × 30 cm tubes of soil sunk in outdoor sand plunges over winter were recovered from the upper 2·5 cm of soil after 20 weeks, and 10% recovered from a similar soil volume inoculated at 15 cm depth. There was greater mobility into adjacent soil layers by the nematodes inoculated at 15 cm depth and overall more of them survived. (Clayden and Green)

Migratory nematodes

Depth distribution of *Paratrichodorus*. Little work has been done on the population dynamics of trichodorid nematodes, though their distribution is thought to be restricted to light sand soils. In Yorkshire and N. Humberside such soils frequently overlie very different subsoils and soil type may change rapidly with depth. Six sites in this region were sampled at 2-month intervals from April to October for numbers of *Paratrichodorus anemones* in the different depth fractions 0–9, 10–19, 20–29, 30–39 and 40–49 cm. At three of these sites there was a layer of clay at *c.* 30 cm. Crops differed at the sites but could be divided into those already planted when sampled in April and those planted after this. In April the populations of *P. anemones* at the three unplanted sites were largest in the 0–9 cm fraction and decreased considerably with depth but where the crop was already present the nematodes were spread further down the soil profile. In subsequent samples when all crops were established, numbers were usually greater below 10 cm than in the top fraction. Distribution of nematodes and roots appeared to be correlated, and nematodes occurred in soil types with which they would not typically be associated. (Spaull and Mewton)

Nematodes of ryegrasses. Pure swards of the ryegrasses Baroldi (*Lolium westerwoldicum*), RvP (*L. multiflorum*) or S24 (*L. perenne*) on a sandy loam at the Grassland Research Institute (Broad Oak VI) had been treated in August 1980 with aldicarb raked in to the seedbed at rates of 0, 5 or 10 kg a.i. ha^{-1} (*Rothamsted Report for 1980*, Part 1, 152–153). Ectoparasitic nematode numbers (especially *Helicotylenchus varicaudatus*) had decreased on treated plots by March 1981 when aldicarb was re-applied at the same rates. During the year the plots received a total of 350 kg N ha^{-1} and 100 kg ha^{-1} each of P_2O_5 and K_2O. Plots were cut six times during the year at approximately 5-week intervals from mid-May. Aldicarb significantly improved yield throughout the year, but grass varieties again differed in their response to aldicarb treatment; S24 usually responded less than

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either of the other varieties and after the third cut, aldicarb at either rate gave no significant improvement in its yield. The yields of the third and subsequent cuts were much smaller than the first two and the increment from aldicarb application to Baroldi and RvP became more marked. Over the year the lower rate of aldicarb gave the following increases compared with controls: Baroldi—3%, RvP—7%, S24—4%. The larger application gave increases of Baroldi—13%, RvP—12% and S24—6% compared with untreated plots. Yield increases appear inversely correlated with nematode numbers which increased between March and October but under the single spring application of aldicarb populations were significantly lower on all treated plots and the larger rate further reduced numbers. Samples taken in October indicated that multiplication was greater on plots of RvP than on either Baroldi or S24; no differences in host suitability had been noted before. Invasion by stem-boring diptera was measured in October but there was no significant difference between different rates of aldicarb. S24 had a significantly smaller percentage of infested tillers than Baroldi or RvP. RvP was the most infested. (Spaull and Mewton, with Dr R. O. Clements, GRI)

Pathogens of cyst nematodes

Distribution of cyst nematode pathogens. *Nematophthora gynophila* has been found in soil from Denmark in which populations of *Heterodera avenae* failed to multiply on continuous susceptible cereals, in soils infested with *H. schachtii* from Poland, Holland and California and in microplots in Tennessee in which *H. glycines* has failed to multiply. *Verticillium chlamydosporium* was in the samples from Denmark, Holland and California. About 40 samples from Peru infested with potato cyst-nematodes contained neither species of fungus. (Kerry, Crump and Mullen)

Effect of temperature. Total numbers of females of *H. schachtii* and the proportion infected by *N. gynophila* reached a maximum at similar temperatures when sugar beet cv. Amono plants were raised in soil containing fungal spores and sugar beet cyst-nematode juveniles, at constant temperatures of 10, 15, 20, 25, 30 and 35°C. Optimum temperatures for female cyst nematode production were 10–15°C, smallest numbers were produced at 35°C. At 15° 68% of females recovered were infected with the fungus and at 10°, 62%. Smaller numbers were infected at 20° (21%) and 25° (9%) and none at 30° or 35°. The optimum temperature for nematode and fungus coincides with typical English soil temperatures but the fungus also occurs in California where an optimum of 27° has been reported for *H. schachtii*. Possibly both nematode and fungus in California are adapted to higher soil temperatures than in the UK. (Crump and Kerry)

Host range studies of some nematophagous fungi. Soil from Butt Close field, Woburn Experimental Farm, in which *N. gynophila*, *Catenaria auxiliaris* and an undescribed lagenidiaceous fungus parasitised females of *H. avenae*, was used in pots to test the susceptibility of some other nematodes to these fungi. Appropriate host plants were infected with *Meloidogyne incognita*, *M. javanica*, *M. acronea*, *M. naasi*, *H. glycines*, *Tylenchulus semipenetrans* and *Rotylenchulus reniformis*. *H. glycines* was susceptible to all three fungal species and all their stages were recovered from diseased females. *M. acronea* was also parasitised by *N. gynophila* but only hyphae and no resting spores were found; the first time this fungus has been recorded in nematodes outside the genus *Heterodera*. None of the other nematode species tested was parasitised. (Kerry and Mullen)

Rickettsia-like organisms. Intracellular rickettsia-like microorganisms are known from three species of cyst nematodes and may be pathogens. Until now diagnosis of infections

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has only been possible by transmission electron microscopy of ultrathin sections of embedded nematodes, which is very time consuming. A rapid technique has now been developed for the diagnosis of infections by applying homogenates of juveniles or adults to coated electron microscope grids, negative staining and examining in the transmission electron microscope. Rickettsia-like organisms are easily distinguished from other microorganisms and mitochondria by their characteristic cell walls and the presence of distinctive intracytoplasmic inclusions (fascicles). The technique is quite sensitive and infection has been detected from batches of 200 juveniles, single cysts and single females. South American populations of potato cyst-nematodes have been screened and two new infected populations found. It is interesting to note that both came from Bolivia as did the original population of *Globodera rostochiensis* infected by the microorganisms. The technique also permits detection of viral infections of nematodes and virus-like particles have been observed in association with three different South American populations of potato cyst-nematode. (Walsh)

Morphology and fine structure

Male reproductive system in *Meloidogyne* and *Globodera*. Root-knot nematodes (*Meloidogyne*) and cyst nematodes (*Globodera*) although clearly related show many differences which include the distinctions in the male reproductive systems reported here.

Sperm structure was compared in *M. acronea*, *M. arenaria*, *M. graminicola*, *M. hapla*, *M. incognita incognita*, *M. incognita wartellei* and *M. oryzae*. Spermatogenesis differed from that in cyst nematodes, where the maturation divisions cease after the last moult. Both early and late stages of sperm development were present in the testis of adult males of all the *Meloidogyne* species studied, which include facultative meiotic and obligatory mitotic parthenogens. There were differences in sperm structure between species, mostly involving size, nuclear structure, differentiation of parts of the sperm cell, and the abundance of filopodia. None exactly resembled cyst-nematode sperm, but some were more like *Globodera*-type sperm, others more like *Heterodera*.

The wall of the functional testis in the pre-adult *G. rostochiensis* and the adult *M. incognita incognita* is similar, very thin over the germinal zone but slightly thicker and secretory in the region of the spermatocytes. It seems likely that the critical changes that initiate the reduction division are mediated or influenced by these secretions. In the adult *Globodera* this secretory function ceases. In the vicinity of the spermatids, the wall cells contain lysosomes that aid in the autolysis of the cast-off residual bodies that are engulfed by these cells. The posterior half of the genital tract, about 200–250 μm long, and its musculature are different in the two genera, being more complex in *Globodera*. The seminal vesicle, in which the spermatozoa are stored, is thin walled in *Meloidogyne* and ends at the vas deferens. This has a thick glandular wall and an occluded lumen that acts as a valve, allowing passage of sperm only at copulation. The cells of the vas deferens wall are uniform throughout its length of about 50 μm, and are filled with secretion globules. The vas deferens leads directly into the cloaca. In *Globodera*, the wall of the whole of this posterior *c.* 250 μm of the duct is secretory, and the lumen open except for the last 50 μm or so, where it is occluded as in *Meloidogyne*. So the vas deferens acts also as a seminal vesicle for most of its length. It consists of three distinct regions, each producing a characteristic secretion contributing to the seminal fluid bathing the sperm. There are also differences in the shape of the cloaca in the two genera.

The gonoduct musculature also is more complex in *Globodera* than in *Meloidogyne*. In both there is a dorsal and a subventral pair of muscles operating the vas deferens, each muscle a single cell. In *Meloidogyne* these same muscles also attach to and operate the cloaca, whereas in *Globodera* there are four additional pairs of cloacal dilator muscles (or

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muscle branches), and two unpaired, asymmetrical muscles whose function is unclear. These last may produce a twisting action when the spicules are protruded; they have no equivalent in *Meloidogyne*. A pair of protractor muscles and a pair of retractor muscles operate each spicule. The retractors pass anteriorly from the end of the spicule base to the body wall. The protractors attach to the base and the shaft, and pass posteriorly to the tail tip. There is an inner and an outer protractor. In *Meloidogyne*, both insert on to the body wall of the tail; the outer is branched and the branches insert side by side on the subventral wall of the tail tip. In *Globodera*, the inner protractor inserts on to the ventral body wall, the unbranched outer on to the dorsal wall of the cloaca, above the gubernaculum. The copulatory spicules are essentially similar in the two genera but the base is more deeply embedded in tissues in *Globodera* than in *Meloidogyne* and the spicules rest in a slightly different position. (Shepherd and Clark)

Feeding pump lining. The roughly elliptical median bulb pump lining of tylenchids becomes longer and thinner when it closes and wider as it opens. The sum of length (L) and width (D) of the pump of an individual *Ditylenchus dipsaci* measured from ciné film remained approximately constant as the pump oscillated. The standard error of mean (L+D) was $\pm 0{\cdot}54\%$ and L plotted against D fitted a straight line with correlation coefficient, $r = -0{\cdot}73$, significant at $P < 0{\cdot}001$. (For L+D to be constant the areas of the ellipses described by the pump must change as it operates.) If L+D is constant it may have taxonomic value. Sums for individuals of seven *Meloidogyne* species were similar within each species, e.g. for *M. arenaria* ♂♂, the mean (L+D) was 15·94 μm $\pm$ 1·42 s.e.; for *M. graminicola* jj², 7·69 μm $\pm$ 0·96. Significant differences occurred between species, e.g. $P = 0{\cdot}03$ for *M. arenaria* ♂♂ compared with *M. javanica* ♂♂; $P = 0{\cdot}0015$ for *M. africana* ♂♂ compared with *M. incognita* ♂♂. (Seymour and Jepson)

Egg-shell of *Globodera rostochiensis*. The hatching sequence in *G. rostochiensis* apparently involves a change in permeability of the egg-shell. The lipid layer probably determines the permeability characteristics of the egg-shell but although lipoprotein membranes have been found in the egg-shells of a number of tylenchids the ultrastructure and histochemistry of the potato cyst-nematode eggshell has not been reported previously. We have found the egg-shell consists of an outer vitelline layer, a chitinous layer and an inner lipid layer. The vitelline layer lacks a typical unit membrane-like appearance and has strands of particulate material attached to its outer surface. The chitinous layer is made up of fibres consisting of a chitin microfibril core, surrounded by a protein coat; these fibres are arranged randomly rather than helicoidally. The lipid layer consists of lipoprotein and this is consistent with chemical analysis of the egg-shell. Unit membrane-like structures closely associated with the inner layer of the egg-shell were clearly observed and comprised the major portion of the lipid layer. They varied in number, the most commonly observed pattern being two or three membranes loosely associated with the inner surface of the egg-shell. (Perry and Clarke, with Dr D. A. Wharton, University of Wales, Aberystwyth)

Taxonomy

***Aphelenchoides* sp. associated with crop loss of mushrooms.** An *Aphelenchoides* species has been found in mushroom compost from which there was a reduced yield of mushrooms. The species was first noticed on a mushroom farm in Hertfordshire in 1979 where it occurred again in 1981. This nematode has been shown to be a fungus feeder, reproducing readily on agar plate cultures of *Botrytis cinerea* and of mushroom mycelium. It resembles *A. composticola*, a nematode known to decrease mushroom growth, but

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differs in the shape of the male spicules and in the absence of a mucro on the female tail. (Hooper, with Mr P. Bassett, ADAS, Cambridge)

Pararotylenchus. A hoplolaimid nematode from St Ouens, Jersey, is being described as a new species. It is characterised by having virtually no overlap of the oesophagus over the intestine, seven to ten head annules, the anterior body cuticle is tessellated and the lateral field is areolated along most of its length. This new species was first described as belonging to the genus *Rotylenchus* but it has been transferred to the recently described genus *Pararotylenchus* Baldwin & Bell, 1981 which now accommodates species of *Rotylenchus* without an overlapping oesophagus. (Hooper, with Dr B. Boag, Scottish Crop Research Institute)

Longidorus. The male of *L. pisi* has been described for the first time. It was found associated with sugar cane at Nchalo, Malawi. Females from this site have been compared with other populations and the synonymy of *L. siddiqii* with this species, proposed elsewhere, is endorsed. (Hooper, with Mr D. J. F. Brown, Scottish Crops Research Institute, and Dr V. W. Saka, Agricultural Research Station, Limbe, Malawi)

Status of *Globodera* species. Five nominal species and one unnamed, putative species (Mexican cyst-nematode) in this genus parasitise Solanaceae. Only two, *G. rostochiensis* and *G. pallida*, the potato cyst-nematodes, are major agricultural pests but the others may be confused with them and their status is therefore of significance in agricultural nematology. The group also serves as a model for other cyst nematode species complexes. Studies of host range have failed to differentiate populations assigned to the different nominal species (*Rothamsted Report for 1978*, Part 1, 180–181) and hybridisation experiments failed to distinguish *G. solanacearum*, *G. virginiae* and Mexican cyst-nematode from each other (*Rothamsted Report for 1979*, Part 1, 140). These studies have now been extended to include *G. tabacum* using the technique described in 1979 except that tobacco as well as tomato was used as a host and proved more satisfactory for this species. *G. tabacum* hybridises freely with *G. solanacearum*, *G. virginiae* and Mexican cyst-nematode, producing cysts with healthy F_2 embryonated eggs. Measurements of second-stage juveniles and cysts of 57 populations of *Globodera* (five assigned to *G. rostochiensis*, four to *G. pallida*, nine to *G. tabacum*, ten to *G. virginiae*, nine to *G. solanacearum*, one to Mexican cyst-nematode and 18 from Mexico, unassigned to nominal species) were analysed by principal coordinate analysis and other multivariate techniques. The characters measured are of established value in the taxonomy of cyst-nematodes. Only *G. rostochiensis* was clearly differentiated, the other nominal species and the unassigned populations forming a continuum with some differentiation of *G. tabacum* and *G. pallida*. Although *G. pallida* is not clearly differentiated by these characters it is distinguished by other, qualitative, aspects of morphology. Thus only *G. rostochiensis* and *G. pallida* are distinguished strongly from the remainder of the complex and this, together with the evidence from host-range and hybridisation studies indicates that *G. tabacum*, *G. solanacearum*, *G. virginiae* and Mexican cyst-nematode are conspecific. (Stone, Burrows and Payne, with Perry, Statistics Department)

Cereal cyst-nematode complex. Of the forms currently recognised in this group only *H. avenae*, *H. avenae* pathotype 3 and *H. mani* present taxonomic problems of immediate relevance to agriculture. Pathotype 3 is of importance because it overcomes resistance in some cereals to other *H. avenae* pathotypes, it has been distinguished from *H. avenae* chiefly by the presence of an underbridge, an inconsistent character. *H. mani* is important because it is commonly confused with *H. avenae* but is not a cereal pest and some popula-

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tions cannot be determined by the characters (presence of an underbridge, tulip-shaped juvenile stylet knobs) used to distinguish *H. mani* from *H. avenae*. Juvenile measurements from populations assigned to *H. avenae* (six), *H. avenae* pathotype 3 (three), *H. mani* (four) or intermediate between *H. avenae* and *H. mani* (five) were compared by principal coordinate and other multivariate analyses. Seven populations of *H. arenaria*, a well-characterised species in the complex, were also included. The *H. avenae* pathotype 3 populations were well separated from those of *H. avenae* and *H. mani* and were as strongly distinguished as *H. arenaria*, emphasising the biological distinctiveness of this pathotype and supporting the contention that it is a distinct species. Centroids of the populations assigned to *H. avenae* other than pathotype 3, *H. mani*, and indeterminate populations clustered closely and this treatment of juvenile characters does not aid distinction of *H. mani* from *H. avenae*. (Hill and Stone, with Perry, Statistics Department)

Identification of root-knot species. Only 11 male, seven female and 11 second-stage juvenile characters aid species differentiation in *Meloidogyne*. Principal coordinate and canonical variate analyses of nine measurements of males (17 populations) and ten measurements of second-stage juveniles (14 populations) showed that most of the species could not be exclusively discriminated. Nevertheless, the analyses identified the most discriminating characters in males as stylet length, distance from stylet base to anterior end, distance from excretory pore to anterior end and body length, and in juveniles tail length, hyaline tail length and stylet knob width. Qualitative (i.e. non-measured) characters are frequently species-specific exhibiting little intraspecific variation. The value of such characters for differentiating species has been illustrated in a key to the males of 24 species using features of the head and stylet visible in the light microscope. The only measurements used to supplement the key were stylet length, stylet cone length, distance of the dorsal oesophageal gland orifice from the stylet base and head width. Another example of the importance of qualitative characters is in differentiation of second-stage juveniles by tail shape. Range of tail shape in the genus is broad with an almost continuous series from very short and broad to very long and narrow. Thirty-one species studied can be allocated to 12 distinct groups based upon tail shape. Within groups, however, qualitative differences are generally small and measurements must be used. Tail length and hyaline tail length separate most species within each group.

A new species has been described from sedge, *Carex acuta*, in Estonia, USSR, and is compared with nine related *Meloidogyne*, including important rice and cereal pests, which together constitute a group primarily parasitising Graminae and Cyperaceae and have been named the Graminae group. The species in the group all have long second-stage juvenile tails and hyaline tails and short male stylets. A close phylogenetic relationship between some of these species has been suggested in the literature because of their similar karyotypes. Common host families and some aspects of morphology support this but species of the Graminae group occur in six of the groupings based on juvenile tails and two based on male characters. However, practical aids to identification need not reflect phylogeny. (Jepson and Hoole)

Miscellaneous studies

Effects of subsoil working and deep PK. Some plant parasitic-nematodes are sensitive to cultivations, especially in coarse soils. The long-term effects of subsoil digging on the abundance of plant-parasitic nematodes in soil to 20 cm depth and from 30 to 50 cm deep were measured in Butt Furlong, Woburn, in September 1979. Deep digging in autumn 1973, with or without the addition of PK to the subsoil, significantly increased numbers of

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Trichodorus (stubby-root nematodes) 30–50 cm deep in plots which had grown two barley crops following a four-course rotation (potatoes, wheat, sugar beet and barley in 1977). The same treatments significantly increased numbers of *Pratylenchus* (root-lesion nematodes) 30–50 cm deep in plots which had grown two barley crops following crops of barley, potatoes, wheat and sugar beet in 1977. Overall, *Trichodorus* was much more abundant in soil 30–50 cm deep than in soil to 20 cm deep, whereas the reverse was true of *Pratylenchus*. (Whitehead, Tite, Fraser and Nichols)

Modelling of nematode dispersal. Because it is impossible to tell when a field first becomes infested by a plant-parasitic nematode or to monitor the early stages of spread by sampling, the spread of nematodes within fields can only be studied theoretically. Therefore, a model was made which allows for from one to six generations a year and for periods of latency during which the nematode multiplies until there is a greater than 90% chance that each gram of soil or plant tissue spread by harvesting will initiate a new infestation. The model is suitable for cyst nematodes attacking root crops or for stem nematode races attacking clover or lucerne. In the model, the newly infested area is measured in 'domains'. A domain is the area occupied by movement during one generation (Jones, In: *Comparative epidemiology* (1980), Ed. J. Palti & J. Kranz, Wageningen: PUDOC, pp. 71–92). Allowance is made for self-spread from the initial focus and from new ones generated by cultivation and harvesting and for the decrease in the rate of propagation of new foci as infested soil or plant material falls increasingly on land already colonised and also for competition between foci as they increase in area. (Jones, Computer Department)

Cuticular fibrils. Many nematodes have an extensible, multilayer trellis of collagen fibres in the cuticle. Studies on the functionally identical fibrous cuticle of a hairworm, *Parachordodes wolterstorffii* (*Rothamsted Report for 1980*, Part 1, 161) throw light on several features of the fibre system which have important implications for locomotion in nematodes. Nematodes and hairworms both have a multilayered fibrous cuticle and coelomyarian type, exclusively longitudinal body muscles. The cuticular fibres of *Parachordodes* are double helices, with 0·5 μm diameter fibrils coiled around each other. Measurements of the geometry of the fibre spirals enable predictions to be made about the ability of the worm to shorten, stretch and bend, and the predicted values are similar to those observed. (Seymour)

Analysis of food flow. The technique for visualising flow towards the stylet caused by feeding, using latex/polystyrene particles (*Rothamsted Report for 1980*, Part 1, 159) was extended when, in collaboration with the Entomology Department, film was made of cereal thrips feeding on isolated oat chloroplasts. Instead of aggregating into a globular mass at the stylet aperture as 0·3 and 1·0 μm particles did, the much larger (5 μm) chloroplasts were elongated and quickly drawn into the 1 μm diameter lumen. (Seymour, with Chisholm, Entomology Department)

Effect of osmotic stress on *Trichostrongylus colubriformis*. The infective third-stage juveniles of *Trichostrongylus colubriformis* possess remarkable abilities to survive adverse environmental conditions. Third-stage juveniles of trichostrongyles retain the cuticle of the previous stage as a protective sheath and Ellenby (*Journal of Experimental Biology* (1968), **49**, 469–475) suggested that the permeability of the sheath decreases as it dries thus ensuring a slow rate of water loss associated with enhanced survival of desiccation. We used changes in the water content of juveniles under osmotic stress to examine the role of the hydrated cuticle and sheath in control of entry or loss of water. In hypertonic

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solutions juveniles lose the ability to move after mechanical stimulation and there was also some increase in coiling. Juveniles can regulate their water content in hypotonic solutions but lose water slowly in hypertonic solutions. Removal of the sheath by exposure to sodium hypochlorite or to a natural exsheathment stimulus had little effect on the water dynamics of infective juveniles. The sheath thus appears to be freely permeable to water when hydrated whereas the permeability of the cuticle is very restricted. (Perry and Beane, with Dr D. A. Wharton, University of Wales, Aberystwyth)

Techniques

Axenic culture. Axenic cultures enable interactions between nematodes and micro-organisms to be examined without interference from contaminants. Roots of pea plants are readily invaded by juveniles of pea cyst-nematode, *Heterodera goettingiana*, when plants are raised on 1% agar in Petri dishes or flasks. Using batches of 50–200 juveniles and eggs, up to 30% develop into mature cysts. The nematodes and eggs are collected on a 5 μm aperture cellulose nitrate filter membrane via a micropipette, using a small suction pump. By using a finger-operated bleed to control suction, nematodes can be selected individually under the microscope. After collection the filter membrane and nematodes are surface sterilised in an aqueous solution of 1% Aretan and 0·05% streptomycin and placed directly on the agar. Solutions of malachite green and mercuric chloride were unsatisfactory because pea plants were damaged by sterilant transferred with the filter. The simple technique has been used also with stem nematode and other cyst nematodes and permits large numbers of cultures to be inoculated in a short time. (Green and Hornsey)

An improved method for staining nematodes in roots. Nematodes in roots can be stained by boiling the chopped roots for 3 min in a solution of equal parts by volume of glycerol, lactic acid and distilled water plus 0·05% acid fuchsin, and the roots cleared in a 50:50 solution of glycerol and distilled water. Roots clear more quickly than in the commonly used lactophenol, nematodes are well stained and the use of toxic phenol is avoided. (Bridge, Page and Jordan)

Staff and visitors

C. C. Doncaster, who joined the Department in 1950, retired in 1981. His long experience, particularly in the cinéphotography of nematodes and other small organisms will be greatly missed, as will his consummate skills as a naturalist. B. R. Kerry and D. H. Crump gave a paper at an OILB meeting on nematode pathogens, Zurich, Switzerland. A. R. Stone, B. R. Kerry, T. D. Williams and A. J. Hill gave papers at an EPPO symposium on cereal cyst-nematodes, Rennes, France, D. J. Hooper contributed to a workshop on grain and forage legumes in Lusignan, France, A. G. Whitehead visited the Foundation for Soil-borne Diseases, Assen, Netherlands, to discuss joint work. D. H. Crump visited the USDA Research Centre, Beltsville, Maryland, and USDA laboratories at Jackson, Tennessee, and also visited the University of California, Riverside. J. Bridge spent 3 months in the Netherlands and Philippines assessing impact of agricultural advice, and S. L. J. Page surveyed nematodes in Santa Cruz, Bolivia, both at request of the Overseas Development Administration. B. R. Kerry spent 4 months in the CSIRO Division of Soils, Adelaide. Staff members also contributed to the 150th Anniversary Meeting of the British Association; the East of England Agricultural Show; the Systematics Association and Association of Applied Biologists meeting on Concepts in Nematode Systematics, co-organised by A. R. Stone; the British Grassland Society Winter Meeting and the 3rd European Symposium on Aquatic Nematodes. In addition to the

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longer term visiting workers listed at the head of this report, more than a dozen overseas scientists visited the Department.

Publications

Theses

1 Bridgeman, M. R. (1982) *Sex ratios of* Heterodera avenae Woll. *and other cyst nematodes*. Ph.D. Thesis, Imperial College, University of London.

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18 Clayden, I. & Hooper, D. J. (1982) New weed hosts for the giant race of *Ditylenchus dipsaci* (Kühn) Filipjev. *Plant Pathology* **30,** 251–252.

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