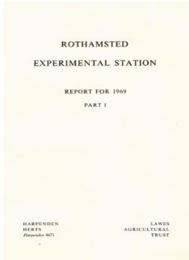
Report for 1969 - Part 1


ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1969
PART 1

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Nematology Department

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NEMATOLOGY DEPARTMENT

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The department studies the control, life histories, behaviour, relationships and host ranges of eelworms (nematodes) that harm crops. All these are microscopic, and most live in the soil, where they feed on or in plant roots. They are all worm-like when young and most remain so throughout their life, but the females of a few species are swollen, rounded and immobile. The swollen females of cyst-nematodes develop leathery walls which protect the many eggs they contain, enabling them to survive long periods in soils and facilitating their spread by movement of infested soil or crops. These cyst-nematodes are all specialised parasites, each infesting only a few species of crop plants, but most of the crops commonly grown in the United Kingdom can be harmed by at least one species. Species that are mobile throughout life are usually less specialised and can feed on the roots of many kinds of plants, crops and weeds. They can not only greatly stunt the growth of seedlings by their feeding but some also transmit viruses to the plants on which they feed.

Feeding mechanisms

When *Ditylenchus destructor* feeds on the epidermis of vetch stem and carrot crown, both its subventral and dorsal pharyngeal glands produce granular secretions, whereas when feeding on hyphae of the fungus *Botrytis* only the dorsal gland does. These secretions produce refractive zones around the point where they are injected into plant cells. Measurements from ciné-film show that the zone forms a few minutes after the feed begins and remains the same size (about 250 μ^3) until a few seconds after it ends, about three-quarters of a hour later. The nematode takes in food by irregular pulsations of the median-bulb pump, which do not diminish the size of the zone of secretions in the plant cell until the last few pulsations, which are vigorous and collapse the zone. The zone differs physically from the plant contents and is bounded by a definite interface or membrane through which plant sap must flow to be ingested by the nematode.

Feeding mechanisms of tylenchid nematodes were filmed. The median-bulb pump of *Aphelenchoides blastophthorus* and *Ditylenchus dipsaci* has an outlet valve only, which is closed by increased turgor in the wall of the median bulb when the muscles contract to dilate the pump. It opens again and is filled from the pump when the muscles relax. Unidirectional flow of fluid backward along the pharynx of *D. dipsaci* can be explained by Poiseulle's formula for the flow of viscous fluid through a capillary tube: $Q = PR^4/8VL$, where Q is the volume of liquid flowing per second under pressure P, when R and L are the radius and length of the capillary respectively, and V the viscosity of the fluid. With the pump midway along the pharynx, and the radius of the pharyngeal lumen 0·08 μ in front and 0·23 μ behind, as in *D. dipsaci*, the resistance of the anterior tube to liquid flow

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will be $0{\cdot}23^4/0{\cdot}08^4$ or about 68 times that of the posterior tube. With the posterior (i.e. the outlet) valve closed, the pump will fill *via* the anterior tube under action of the strong radial muscles. When the pump is full and the radial muscles relaxed, the pressure in the pharyngeal wall will expel the fluid both through the anterior tube and, *via* the valve, through the posterior tube, but the relative resistance will ensure that 68 times as much flows into the posterior tube and thence into the intestine. The anterior tube is always open and acts as a leaky valve but over the whole cycle the net flow is rearwards.

Some members of the Tylenchida have a pump with an opening and closing inlet valve. This is well developed in *Hemicycliophora* but poorly in *Hexatylus*. In *Hexatylus*, portions of the triradiate pharyngeal lumen open and close successively and rapidly from the front backwards, causing food to flow backwards into the intestine. The pharynx is not divided into distinct regions and most of its length retains the pumping function, whereas in more specialised Tylenchida the pumping region is very short and confined to the median bulb. (Doncaster)

Examination under the light microscope suggested that the oesophago-intestinal 'valve' of some dorylaimids is tipped with a sheath, apparently without an opening. Sections of the oesophagus of a species of *Thornenema* viewed under the electron microscope show that it has a triradiate lumen lined with cuticle. Near the oesophago-intestinal 'valve' the lining becomes thinner and the lumen narrower until it disappears in the cells of the sheath. At this point the sheath is a compact group of cells with their walls closely interdigitated, with distinct cell membranes resembling tight junctions. Where the tip of the sheath protrudes into the lumen of the intestine, there are two central cells and an outer ring of four to six cells. A passage through the sheath was not found. The sheath has an outer coat of intestinal cells bordered with microvilli. The intestine contains membraneous material, probably protein, which may have been liquid in the living animal, and many particles, some apparently bacteria and others virus-like.

The lack of a passage connecting oesophagus and intestine is puzzling, and how this genus and related ones feed is unknown. It seems improbable that particles could be forced through the 'valve' or carried in cell vacuoles.

Thornenema sp. has three small longitudinal muscles that run down the outside of the oesophagus at the mid-point of each of the three sectors seen in cross section. They may be the structures in dorylaimids previously thought to be nerves. The walls of ducts of the paired subventral glands that lie in the wall of the oesophagus are lined with closely packed, finger-like, membrane-bound projections resembling small microvilli. Their function is unknown but they may be discarded membranes from secretory granules discharged into the ducts. The cuticles of *Thornenema* and *Xiphinema index* are similar, except that the layers next to the hypodermis differ slightly. (Shepherd and Yeates)

Cuticle in cyst-nematodes. Because the names given to the layers in nematode cuticle are confusing, a system of letters and numbers is used, starting from the outer edge inwards, and no attempt made to homolo-

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gise the layers in cyst-nematodes (*Heterodera* spp.) with those of other genera.

The ultrastructure of the cuticle of the young fifth-stage females of five lemon-shaped species of cyst-nematodes was basically similar. All had two well defined main layers, A (outermost) and B (innermost), each further subdivided. The main differences were in layer A and from these the species could be identified. The thickness of the cuticle differed in different parts of the body in individuals of the same species, and between different species, but the patterns, especially in layer A, remained characteristic.

Among round-cyst nematodes, the cuticle of *H. tabacum* closely resembled that of the lemon-shaped species. The B layer has four zones, B1 to B4, about 3·0, 6·0, 0·5 and 0·75 μ thick respectively. Zone B1 of most species of *Heterodera* has fibrils tending to run parallel, whereas the fibrils in zones B2 to B4 run irregularly. Layer A is about 2·5 μ thick, irregularly indented on the outside, with an inner zone containing electron-dense areas interspersed with a network of lighter coloured veins or channels, and an osmiophilic outer zone. Layer A of *H. rostochiensis* is narrower (0·5 μ) and barely distinguishable from B1. What seems to be zone B3, is 10 μ thick and is further subdivided into four to eight bands of orientated fibrils, those of adjacent bands running at different angles. Zones B1 and B2 are together 10 μ thick. In sections under the light microscope, the layers and zones stain differentially with toluidene blue. After staining with picro-sirius red, layers B1 and B2 of *H. schachtii* and B1 of *H. rostochiensis* were birefringent under polarised light, a test that usually indicates collagen. None of the zones stained strongly with the protein stains bromophenol blue or naphthol yellow. (Shepherd and Clark, with Dart, Soil Microbiology Department)

One hypothesis of how hatching agents act requires the existence of a permeability barrier within the eggshell or larval body wall. If this is correct, species of *Heterodera* that respond differently to hatching agents might be expected to have chemically different barriers. Previous analyses of cyst walls, which are derived from larval body walls (*Rothamsted Report for 1967*, 119; *for 1968*, 152) showed quantitative differences between the cyst wall components of *H. rostochiensis* and *H. schachtii*, and a qualitative difference in hexosamine content has now been found. Whereas hydrolysates of the cyst walls of *H. schachtii* contained glucosamine (1·5% by weight), those of *H. schachtii* contained galactosamine (3·3%). (Clarke)

Internal structure of cyst-nematodes

To improve understanding of the internal structure of cyst-nematodes and help to identify organs under the electron microscope, serial sections 2·5 μ thick were cut of fourth-stage female larvae, young adult females and larvae in the intervening moult. In the species chosen, *Heterodera cruciferae*, the somatic muscles are still present in the fourth-stage females. The gut is filled with globules, has no apparent lumen and is attached to the body wall at six places. The gonads, which have started to elongate and in which the vagina and vulva are developing, seem to be engulfed by the gut but

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lie close to the somatic muscles. At this stage the vulva does not open to the exterior. During the fourth moult the somatic muscles break down and the gut almost fills the body cavity. The gonads continue to lengthen and the vulva opens to the outside. The gonads of young adults are arranged regularly on either side of the body cavity, but have enlarged and started to coil at the base.

Contrary to Mackintosh's opinion (*Nematologica* (1960) **5**, 158–165), *H. cruciferae* has rectal glands, which can be seen in whole mounts of second-stage, third-stage and adult females, and in sections of moulting fourth-stage and adult females. From the anus a substance of unknown function passes into the gelatinous egg sac. (Clark and Doncaster)

Hatching factors and sex attractants of cyst-nematodes

Nematodes live in the spaces between soil particles and are active only in moist soils. The eggs of some species do not hatch until the quiescent larvae within them are alerted by specific substances, usually given out by host plant roots. Some species are stimulated to moult by substances in root exudates and most plant-feeding nematodes are probably attracted by chemicals roots exude. Similarly, female nematodes seem to secrete substances that alert and attract their males. The kinds of substance that can act as sex attractants (pheromones) or relate parasite to plant host (phytomones) are probably limited by the moist environment around soil particles and the spaces between them, which are filled with an atmosphere that scarcely moves. Such an environment is dominated by water and unsuitable for aromatic air-borne scents. What little is known of the substances that influence nematodes in soil suggests that they are water-soluble glycosides, neutral or nearly so, and non-volatile or only slightly volatile. Nematodes seem to sense them at great dilution and their receptors probably respond to a few molecules. Concentrating and purifying them is difficult and bioassaying them tedious.

The method of purifying the hatching factor for the potato cyst-nematode, *H. rostochiensis*, produced by potato roots (*Rothamsted Report for 1968*, Part 1, 153) was modified and improved. The raw material is still an extract from potato roots, and not root diffusate absorbed and eluted from charcoal but the new procedure includes two improved methods of column chromatography. The product resembles previous partially purified material in that, when further purified by thin layer chromatography, it gives a broad zone of active material about 0·3 R_f units wide. Further purification by column chromatography, or by electrophoresis, yields four components that stimulate hatching. (Clarke)

Time-lapse ciné records of *Heterodera rostochiensis* in root-observation boxes showed that females sometimes produce surges of secretions from their posterior ends that may attract males. The secretions remain fluid and disappear when males or other soil organisms disturb them. (Doncaster)

Attempts to concentrate and purify the male attractants emitted by *Heterodera rostochiensis* females have so far failed. They are partially destroyed by distilling extracts at 100°C and atmospheric pressure, but

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not by either vacuum distillation at 50°C or freeze-drying. Appreciable amounts of attractive material distil over, suggesting that the attractant or at least one of its components is about as volatile as water.

Stronger extracts were obtained by leaving 500 young females on moist glassfibre filter-discs at 15°C for a week than by washing females repeatedly in small amounts of water. So far we have been unable to separate attractive fractions by column or thin layer chromatography and only partially by electrophoresis. The attractant seems not to dissolve easily in acetone, ether or benzene, but traces can be carried in them either in water solution or as solids. These are not deposited in definite zones but scattered along the solvent track, where they can be detected by the sensitive bioassay. Nevertheless, paper chromatography suggests there are at least two attractive components. (Greet)

The hatching factor for *H. rostochiensis* and the sex attractant emitted by females have some common physical characteristics and both operate initially by alerting either larvae or males. The effect is to initiate movement after quiescence. As at least one component of the sex attractant is volatile, the hatching factor was re-tested but lack of volatility was confirmed. Also, the sex attractant did not initiate hatching and the hatching factor did not activate or attract males. The hatching factor is acidic, absorbed by anionic exchange resins and moves to the cathode during electrophoresis, whereas the sex attractant is near neutral and only slightly absorbed by anionic exchange resin, cellulose or Sephadex. Both are absorbed by activated charcoal. (Green)

Earlier observation suggested that females of the beet cyst nematode, *H. schachtii*, became less attractive to males for a while after being mated (*Rothamsted Report for 1966*, 158). Table 1 shows that *H. rostochiensis* behaves similarly. Some males and females were allowed to mate, and others not, either because they were separated by a dialysis membrane that allows secretions to pass or because they were kept separate. After 15 hours the females were put on agar plates and tested with fresh males after 0·5, 3 and 24 hours. Males were similarly tested with fresh females.

TABLE 1

Influences of mating or proximity on attractiveness of females to males and vice versa

Log scores in bioassay of attraction

	Hours after mating or not		
	0·5	3	24
Females			
Virgin	1·62 (32)*	1·92 (31)	1·93 (28)
Mated	1·20 (29)	1·42 (29)	2·09 (23)
Separated from males by dialysis membrane	1·26 (28)	1·62 (27)	1·92 (23)
Males			
Virgin	1·89 (15)	2·10 (14)	2·09 (14)
Mated	1·73 (14)	1·96 (14)	2·16 (8)
Separated from females by dialysis membrane	1·75 (10)	1·96 (9)	2·39 (9)

* Figures in parenthesis indicate the number of tests.

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Recently mated females and those exposed to males but separated by a membrane were less attractive than virgin females but they partly recovered their attractiveness in 3 hours and completely in 24 hours. Exposing males to secretions from females did not affect their behaviour nor was it affected by previous mating. (Green)

The ability of females of *H. rostochiensis* (pathotype A), *H. rostochiensis* (pathotype B), *H. tabacum*, *H. virginiae*, *H. mexicana*, and Osborne's cyst nematode, an unnamed species, to attract each others' males was tested. In contrast to results from similar tests done last year (*Rothamsted Report for 1968*, Part 1, 154), no difference was found that might lead males of one species to be selected or rejected by females of any other. As the females in this closely related group of round-cyst nematodes attracted all males strongly, presumably they secrete the same or a similar sex attractant, which would be in keeping with their close morphological similarity and the fact that the host plants of all seem confined to the Solanaceae. (Green)

Survival of different stages of potato cyst-nematode at high temperatures

During hot weather larvae of the potato cyst-nematode infesting plants in the glasshouse often fail to produce cysts. Therefore we put infested plants, at different intervals after they were inoculated, at temperatures between 26° and 38°C for periods of 24 and 96 hours to see whether this affected the number of adults produced and the sex ratio. Fewer adults matured after exposure at 32, 35 and 38°C, than after exposure at 26 and 29°C (Table 2). Larvae were least sensitive to raised temperatures when youngest and became increasingly sensitive as they aged. Fewest became adult when the temperature was raised 16 or 20 days after the plants were inoculated.

TABLE 2

The effect of temperature and time of treatment of larvae that become adult

Duration of treatment		Untreated control 16–24°C	Temperature 26°C	29°C	32°C	35°C	38°C
24 hours	Adults	1276	1382	1221	997	280	89
	♂/♀	1·9	1·7	1·8	1·8	1·8	1·3
96 hours	Adults	1276	1365	1147	366	163	3
	♂/♀	1·9	1·6	1·3	1·2	0·9	0·5

Duration of treatment		Untreated control 16–24°C	Days after inoculation when treatment began 1	4	8	12	16	20
24 hours	Adults	1276	1189	855	752	829	737	400
	♂/♀	1·9	1·8	1·3	2·1	2·3	1·8	1·1
96 hours	Adults	1276	774	689	611	511	270	—
	♂/♀	1·9	1·0	1·4	1·5	2·2	0·9	—

The pre-adult stage males were the most sensitive and raising the temperature to only 26°C 20 to 21 days after inoculation significantly decreased the numbers that became adult. Heating 1, 4 or 8 days after inoculation

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increased the proportion of the surviving larvae that became female, presumably because the death of some larvae meant less competition for space and food among survivors (*Rothamsted Report for 1966*, 159). Plants exposed to 26°C for 18 days produced a mean number of adults of 734, whereas those kept at 29° produced only 179. Air temperatures often exceed 26°C in glasshouses during summer, so unless pots are cooled larvae in them may be killed. (Trudgill)

A mathematical model relating the sex ratio of potato cyst-nematode to the numbers of larvae that invade host roots

The average size of females changes little as the density of infestation increases in potato roots. This contrasts with the behaviour of many invertebrate animals, which produce smaller adults when crowded. The sex of potato cyst-nematodes is determined after larvae enter the plant root and the proportion that become male increases when the plant tops are cut off or when larvae are crowded in the roots (*Rothamsted Report for 1965*, 146). Larvae need more food to become female than to become male and ultimately need 200 to 300 times more, so it was suggested that, having invaded the root at random, larvae compete for space to produce giant-cell groups and only those with large enough groups become female. This situation was simulated by a computer model. The stele of 1 cm of roots was represented as a cylinder and the giant-cell groups by rectangles placed at random on its surface. As more giant-cell groups were added, it was assumed that those placed in an unoccupied space could support a female, whereas those that overlapped an occupied space produce males. The size of the giant-cell groups occupying one-fourteenth and one-twentieth of the total surface area of the stele simulated the actual situation found in tomato and potato roots, respectively. Total numbers of giant-cell groups able to support females, for the mean of fifty random placements at each of ten larval densities, were printed. Table 3 shows that the sex ratio obtained by inoculating the main roots of tomato and potato with different numbers of larvae agrees well with that calculated from the mathematical model. Lateral roots are often so much thinner than main roots that larvae can rarely form giant-cell groups large

TABLE 3

The sex ratio on tomato and potato compared with that expected from the mathematical model at different population densities

Nematodes per cm of root	Sex ratio in tomato roots		Nematodes per cm of root	Sex ratio in potato roots	
	Observed	Expected		Observed	Expected
5·5	0·64	0·69	6·0	0·62	0·69
11·0	1·27	1·42	12·0	1·14	1·18
16·5	2·00	2·17	18·0	1·65	1·69
22·0	2·67	2·86	24·0	2·14	2·16
27·5	3·37	3·47	30·0	2·70	2·77
33·0	4·04	4·12	36·0	3·21	3·36
38·5	4·70	4·75	42·0	3·72	3·94
44·0	5·38	5·33	48·0	4·25	4·30
49·5	6·02	5·97	54·0	4·71	4·74
56·0	6·83	6·67	60·0	5·28	5·19

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enough for them to become female. (Trudgill with Ross, Statistics Department)

Size of adult potato cyst-nematode on resistant potato hybrids

Potato plants resistant to some populations of potato cyst-nematode restrict the development of giant-cell groups and prevent larvae from becoming female. In some plants this is accompanied by an increase in the numbers of males of usual size, but in others food may be so restricted that the larvae develop into small males or many larvae may die. Table 4 shows the mean numbers of males and females and the mean length of 80 males produced by two nematode populations on one susceptible potato variety and three resistant hybrids, each infested with 4000 larvae. The mean body length of both populations was significantly smaller on the ex *andigena* and ex *andigena* × ex *multidissectum* hybrids, and for the Jersey population on the ex *multidissectum* hybrid, than on the susceptible variety. Some of the small males were only one-quarter the bulk of males from the susceptible variety. The average size of the females that developed on the resistant hybrids was the same as on the susceptible variety.

TABLE 4

The mean numbers of males and females and mean lengths of males of two populations of the potato cyst-nematode on one susceptible and three resistant potato hybrids

	Population					
	Feltwell			Jersey		
	Males	Females	Male length mm	Males	Females	Male length mm
Susceptible	1433	356	1·078	986	438	1·082
ex *andigena*	595	1	0·908*	1402	91	1·025*
ex *multidissectum*	1128	91	1·044	1369	142	0·977*
ex *andigena* × ex *multidissectum*	285	1	0·947*	588	62	1·033*

* Significantly different from the susceptible variety at $P = 0{\cdot}01$.

(Parrott and Trudgill)

Potato cyst-nematode, pathotype or species?

More matings between individual males and females of different pathotypes of *H. rostochiensis* (*Rothamsted Report for 1967*, 147) were attempted, but this time two populations from the type locality of the species in the Rostock area of East Germany kindly supplied by Dr. H. Stelter, Gross Lusewitz, East Germany, which proved to be pathotype A, and four pathotype B populations from Northern Ireland were used as well as pathotype E from Cadishead and Frampton. Pathotype A reproduces on potatoes incorporating genes for resistance from *Solanum multidissectum* but not on those with genes for resistance from *S. tuberosum* ssp. *andigena*; pathotype B behaves in the opposite way and pathotype E reproduces on plants with genes for resistance from both sources.

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TABLE 5

Single male/single female reciprocal crosses of Heterodera rostochiensis *using three pathotypes*

Source of populations	No. of populations	No. of cysts on Arran Banner	Cysts produced relative to Arran Banner = 100: ex *andigena*	ex *multi-dissectum*	ex *andigena* × ex *multi-dissectum*	Main pathotype	Results of matings: % females with eggs / females: A	B	E
Feltwell, England	1	251	1	53	1	A	62	38	42
Rostock,* East Germany	2	924	1	66	1				
Northern Ireland	4	510	108	11	3	B	4	50	67
Cadishead and Frampton	2	252	102	77	29	E	17	54	58

* Obtained from the type locality of *H. rostochiensis*.

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Table 5 shows that, as in 1967, matings between A females and E males yielded many fewer females with eggs than matings between males and females of the same pathotype, whereas the reciprocal cross produced only slightly fewer. The pathotype B populations behaved similarly to those of pathotype E, suggesting that these are more closely related to each other than to pathotype A. On average judged by the number of females that produced eggs, matings between A and E or B were less than half as successful as selfings or matings between B and E.

The progeny of earlier crosses between pathotypes A and E were cultured separately on the fully susceptible potato variety Arran Banner. Parental cysts (dead females containing F_1 eggs) from the Sandy, St. Brelades and Gosberton females were used as inocula and the new females (cysts) produced were counted, whereas hatched F_1 larvae and eggs from the Woburn and Cadishead females were used as inocula and the males and females formed were estimated (Table 6). Not only did fewer females

TABLE 6

Numbers of larvae, males, females and cysts produced by the F_1 generation of single male–single female matings of pathotypes of potato cyst-nematode

Origin of parental females		Type of mating: Within pathotypes	Between pathotypes
	% parental females producing eggs in 1967	64	19
Woburn Cadishead	No. of parental cysts tested	95	12
	Mean no. of larvae hatched per cyst	49	3
	Mean no. of F_1 males per cyst	6	(total 3)
	Mean no. of F_1 females per cyst	7	0
Sandy St. Brelades Gosberton	No. of parental cysts tested	149	45
	Mean no. of F_1 cysts recovered per parental cyst	45	2

from matings between pathotypes produce eggs, but fewer larvae hatched from them and many fewer produced adults, than from matings within pathotypes. The viability of F_1 adults has yet to be determined. (Parrott)

The soluble proteins in extracts from nine populations of the potato cyst-nematode, made by crushing 400 adult females of each in isotonic buffer, were analysed by polyacrylamide gel electrophoresis, using a discontinuous buffer system in which the protein molecules separate according to their size and, after staining, the gel columns show a complex pattern of bands. The main protein bands from the nine populations fall into two groups, differing in that some bands vary in intensity and others do not occur in all.

The population from Woburn (pathotype A) has 12 strong bands (Table 7), whether extracts come from living yellow females or dead ones (cysts containing eggs with unhatched larvae). All four pathotype A populations produce similar patterns, although the Sandy population has an additional band (2a) between bands 2 and 3.

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TABLE 7

Percentage of females on three resistant potato hybrids (Arran Banner = 100) and the band patterns produced by polyacrylamide gel electrophoresis of extracts from females of nine populations of the potato cyst nematode

		Percentage of females on																			
Main pathotype	Population source	ex *andigena*	ex *multi-dissectum*	ex *andigena* × *multi-dissectum*	1	2	2a	3	4	5	5a	6	6a	7	7a	8	9	10	11	11a	12
A	Woburn, England	4	150	1	+	+		+	+	+		+		+		+	+	+	+		+
	Feltwell, England	1	53	1	+	+		+	+	+		+		+		+	+	+	+		+
	Rostock,* East Germany	1	87	1	+	+		+	+	+		+		+		+	+	+	+		+
	Sandy, England	8	88	2	+	+	+	+	+	+		+		+		+	+	+	+		+
B	Glarrygord, Northern Ireland	102	5	3	+	+		+				+	+	+	+	+	+		+	+	
	Garvaghey, Northern Ireland	81	17	4		+		+				+	+		+	+	+		+	+	
E	Jersey, Channel Islands	139	60	41	+	+		+			+	+	+	+		+	+		+	+	
	Cadishead, England	108	84	32	+	+	+	+				+		+	+	+	+	+	+		
	Frampton, England	95	70	26	+	+	+	+				+		+		+	+	+			+

Main bands, 1–12; subsidiary bands 2a, 5a, 6a, 7a and 11a.

* Obtained from the type locality in East Germany.

Band patterns from pathotypes B and E populations have eight bands in common with pathotype A but lack bands in positions 4, 5, 10 and 12. Additional bands sometimes appear between 5 and 6 (5a), 6 and 7 (6a), and 11 and 12 (11a). Pathotype B and E populations vary more, so probably they are genetically and physiologically more diverse than populations of pathotype A. Consistent differences between pathotype B and pathotype E populations have not been found. Selecting pathotype A populations on *andigena* hybrids may increase the proportion of larvae able to become females, change the band pattern and perhaps indicate which bands are associated with larvae unable to multiply in plants with genes for resistance derived from *Solanum tuberosum* ssp. *andigena*. (Trudgill with Carpenter, Plant Pathology Department)

The different protein-band patterns, the fact that pathotype A females are golden yellow, whereas those of pathotypes B and E are pale cream or white, the differences in spear length, body length and some other measurements between pathotype A and B and E, but not between B and E (Webley, *Nematologia* (1970) **16**, 107–112) and finally the inability of A to hybridise freely with B and E whereas B and E seem to hybridise freely, suggests that two species of potato cyst-nematode exist in the U.K.: *H. rostochiensis sensu stricto* is pathotype A, the golden nematode, because that is the pathotype of the type locality near Rostock and the other (pathotype B and E) is so far undescribed and lacks a specific name. The pattern of distribution of the species, with pathotype A dominant in South East England, central Scotland and probably also in Northern Ireland, and the others dominant in the basin of the river Humber, with admixtures of both in other areas, probably stems from original introductions of both species from the Andes plateau of South America and their subsequent spread in seed potatoes and by other means. The two species belong to the group of round-cyst nematodes (page 181 of this Report) that have many characters in common and probably merit being split off from cyst nematodes with lemon-shaped cysts as a separate genus. They were assigned to a sub-genus, *Globodera*, by Skarbilovich in 1959 but this has not so far been generally accepted.

Most of the work at Rothamsted extending over many years has been with *H. rostochiensis sensu stricto*, which is dominant in old allotments at Rothamsted and in the fields at Woburn Experimental Station. The host ranges reported by Jones (*Ann. appl. Biol.* (1950) **37**, 414) and Winslow (*Ann. appl. Biol.* (1954) **41**, 591) are those of this pathotype. (Jones)

Genetics of eelworm resistant potatoes

Resistant potatoes bred from ex *andigena* have a major gene that confers resistance to *H. rostochiensis* pathotype A and those bred ex *multidissectum* another that confers resistance to pathotype B. Hybrids with both genes are resistant to both pathotypes but not to pathotype E. Tests with a range of nematode populations and resistant hybrids show that some ex *andigena* plants contain additional resistance as do those bred from ex *multidissectum*. The additional genes for resistance from *andigena* operate primarily against pathotype B and E populations. The hybrids lacking

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this factor such as Maris Piper and Ulster Glade seem to distinguish sharply between pathotypes A and B or E. The presence or absence of minor factors in resistant hybrids goes some way to explaining the variation in the numbers of cysts formed on their roots. Nematode populations also vary in their reactions to the minor factors and in the number of cysts they form on plants that possess them. The resistant plants are probably best regarded not as non-hosts but as poor hosts able to support small populations. In a trial at Woburn using Maris Piper, in sandy soil, heavy infestations of *H. rostochiensis* pathotype A were decreased by 80% but light ones were maintained at a few eggs/g of soil. So far as is known, the cysts formed were golden yellow, i.e. pathotype A. (Trudgill, Parrott and Jones)

Woody nightshade, *Solanum dulcamara*, a hedgerow plant, and black nightshade, *S. nigrum*, a common weed of arable land, are the only widespread native Solanaceous plants in Britain. The common races of *S. nigrum* in South Eastern England seem not to be hosts of pathotype A, B or E of *H. rostochiensis*, whereas *S. dulcamara* is a host of pathotype A and of most round-cyst nematodes. Because of its value as a common host when attempting to cross round-cyst nematodes, its status as a host for pathotypes A, B and E was compared with tomato in miniature pots each inoculated with 50 larvae. Both were equally good hosts for pathotype A, and both supported pathotypes B and E but they multiplied only half as much as pathotype A. All three pathotypes produced a larger ratio of females to males on woody nightshade than on tomato. (Green)

Reproduction and sex attraction in some root-knot nematodes

Inoculating host roots with single larvae proved that *Meloidogyne ardenensis*, *M. naasi* and *M. thamesi* reproduce parthenogenetically, for 60 days later females had produced viable eggs.

M. hapla can also reproduce parthenogenetically, although it produces males. Tests on agar plates gave no evidence that *M. arenaria* females of any age attracted newly-emerged or old males. Similarly young females of *Meloidogyne arenaria* in observation boxes did not attract males placed near them in groups of ten.

Tests on agar also showed that males of these species are not attracted to females of other species. *Heterodera cruciferae* females attract males of all other species of *Heterodera*, and *H. schachtii* males are attracted to all other species of *Heterodera* females, but *Meloidogyne* females did not attract *H. schachtii* males and *Meloidogyne* males were not attracted to *H. cruciferae* females. (Santos)

Nematodes in ploughed and unploughed land

Table 8 shows that the nematode fauna of the soil was similar after 3 and 4 years of growing wheat in unploughed land where weeds were killed with paraquat to that where the land was ploughed annually. The direct-seeded plots at Rothamsted probably yielded less than the ploughed plots because they were infected with couch grass, *Agropyron repens*, which was

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TABLE 8

Nematode populations under winter wheat grown with and without ploughing. Nematodes/l soil, detransformed from log (x + 1)

	Woburn, third year					Rothamsted, fourth year				
	Grain yield cwt/acre	Parasitic Tylenchs	Other Tylenchs	Doryl-aims	Other nematodes	Grain yield cwt/acre	Parasitic Tylenchs	Other Tylenchs	Doryl-aims	Other nematodes
Treated with weed-killer	29·8	2399	5495	813	14130	14·9	7244	8913	1413	31620
Ploughed	28·3 ± 1·24	2692	6026	525	11750	30·4 ± 1·53	5623	6166	813	14130
	September 1967	3311	7943	1072	19950	October 1967	9120	10000	9550	22910
	January 1968	4677	4786	813	13180	March 1968	7244	5623	9333	17780
	April 1968	1585	4786	447	10720	June 1968	3162	6166	617	15490
	July 1968	1585	5888	437	9772	September 1968	7943	8511	1000	30900

*, ** or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.

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not controlled by weed killer spray applied the previous autumn. The detailed analysis of nematodes in soil taken at approximately 3 months intervals show slight but inconsistent differences between numbers in the direct-seeded and ploughed plots. The changes between sampling dates followed the usual pattern, which is that all groups tended to be fewer during summer than at other times. Seemingly any compaction from not ploughing the Woburn sandy soil for 3 years or the Rothamsted clay soil for 4 years did not make the pore system of either less suitable for nematodes.

Damage to wheat roots by the lesion nematode *Pratylenchus fallax*

To gain information about *P. fallax* affecting wheat roots, roots were grown in sterile culture and inoculated with nematodes. Larvae invading the roots broke cell walls and some were discoloured. After 4 weeks many cell walls were broken and others thickened. *P. fallax* did not penetrate beyond the endodermis which greatly thickened near any nematode, became discoloured and produced peg like protrusions in the inner walls. These changes happened before the outside of the root showed any lesions. (Corbett and Webb)

Migratory nematodes in barley

Barley was planted again in 1969 at Papplewick, Notts, and Woburn, Beds, to see whether fumigants applied to soil in 1968 to control nematodes had any residual effects (*Rothamsted Report for 1968*, Part 1, 164–165. Table 9 shows the number of nematodes, estimated at sowing, and the grain yields.

TABLE 9

Residual effect of nematicides in barley

	Treatments before 1968 crop				
	Untreated	'D-D'	Aldicarb	Chloro-picrin	S.E.
	Papplewick, Notts.				
Barley cwt/acre	26·0	32·7	27·0	30·2	0·93
Log *Pratylenchus*/l soil	3·27	2·63	2·88	2·71	0·08
Log all parasites/l soil	3·54	2·82	3·21	3·18	0·06
Log all nematodes/l soil	4·27	4·20	4·11	4·45	0·04
Pratylenchus as % total	10·8	3·3	7·6	2·5	1·0
	Butt Close, Woburn				
Barley cwt/acre	29·0	34·7	29·9	32·3	0·64
Log *Pratylenchus*/l soil	3·47	2·81	3·14	2·85	0·13
Log all parasites/l soil	3·71	3·11	3·41	3·15	0·09
Log all nematodes/l soil	4·24	4·06	4·09	4·33	0·06
Pratylenchus as % total	17·6	5·8	11·8	4·2	0·97

At both sites plots treated with 'D-D' and chloropicrin yielded significantly more than untreated plots. At Papplewick, 'D-D', aldicarb and chloropicrin applied before the 1968 crop significantly decreased numbers of *Pratylenchus fallax* and all parasitic nematodes. At Woburn 'D-D'

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and chloropicrin significantly decreased *P. minyus* and *P. crenatus*. 'D-D', aldicarb and chloropicrin significantly decreased all parasitic nematodes. Only at Papplewick, in aldicarb treated plots, were all nematodes significantly fewer than in untreated plots. Apparently killing nematodes is at least partly responsible for fumigation increasing the yields of grain at both sites, and, as *Pratylenchus* was affected proportionately more than total nematodes by 'D-D' and chloropicrin, this genus may have been largely responsible for the smaller yields from the untreated plots. (Corbett and Webb)

Nematodes in the potatoes in the Woburn Ley-Arable

Fumigating the soil of plots in the Woburn Ley-Arable experiment with chloropicrin during autumn 1968, or applying Temik at planting 1968, significantly increased yield of potatoes and decreased the numbers of ectoparasitic nematodes. However, as populations of these nematodes and of the potato cyst-nematode (*Heterodera rostochiensis*) in untreated plots seemed too small to decrease yields, the increases may have been from the extra nitrogen mineralised by fumigation or the control of other pathogens.

The potato variety Maris Piper has been planted in this experiment since 1966. It is damaged when many larvae of *H. rostochiensis* invade its roots, but it prevents the nematode multiplying as it does following a susceptible variety. The block that grew potatoes in 1968 (rye in 1969) contained far fewer ectoparasitic nematodes in the plots fumigated with chloropicrin in autumn 1967 than unfumigated ones, but these again contained fewer than would be expected to cause measurable damage. Nevertheless the rye yielded better on previously fumigated plots. This, too, was probably a nitrogen effect, for the plants on fumigated plots matured later. Fumigation with chloropicrin greatly increased the 1968 potato yield (*Rothamsted Report for 1968*, Part 1, 150), but populations of *H. rostochiensis* were still appreciable in this block, despite growing the resistant variety. In 1969 the roots of potato plants grown in pots containing soil from unfumigated plots were invaded by twice as many larvae as roots of plants grown in soil treated with chloropicrin in autumn 1967. Hence the large yield differences (more than 10 tons/acre) after fumigating the soil for the 1968 potatoes were partly caused by *H. rostochiensis*. The block to be planted next year, like that planted in 1968, still contains an appreciable population of *H. rostochiensis* and its effect on potato yields will be tested. Salt (see page 171 of this Report) failed to find fungi attacking the potatoes that might explain the yield differences this year or last. (Evans)

Nematodes of Sitka spruce nurseries

Tylenchus sp. and *Tylenchorhynchus* spp. are plant parasites common in the Chemistry Department's forestry reference plots on Stackyard field, Woburn. *Paratylenchus*, *Pratylenchus* and *Trichodorus* spp. also occur, but never in large numbers. Differences between the abundance of *Tylenchorhynchus* spp. and *Tylenchus* spp. in soil examined in November 1968 and

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TABLE 10

Nematodes in 200 ml soil samples from forestry reference plots, Woburn, 1968 and 1969

	Fertiliser treatments										
	N P Mg	N P K Mg L	N P K	C	N P K Mg	O	N P K Mg F	N K Mg	N P K Mg C	O	P K Mg C
1968 *Tylenchus* sp.	676	452	812	2772	1156	418	720	1284	1072	181	134
1969	18	250	166	1332	212	3384	212	190	154	2156	2472
1968 *Tylenchorhynchus* spp.	1068	1088	1628	89	1884	20	32	83	652	31	59
1969	186	280	162	144	758	12	0	36	574	44	92
Other Tylenchids											
1968	21	26	12	1	3	4	21	1	20	—	7
1969	4	14	10	12	18	24	6	8	34	8	20
Other nematodes											
1968	681	1632	1620	1015	1118	345	1221	559	683	410	389
1969	104	192	136	416	302	298	120	90	186	282	128
Total											
1968	2546	3198	4072	3877	4162	787	1997	1929	2427	621	589
1969	312	736	474	1904	1288	3718	338	324	948	2484	2708
Tylenchus as % of total											
1968	26	14	20	71	28	53	36	67	44	29	23
1969	6	34	35	70	16	91	63	59	16	87	91
Tylenchorhynchus as % of total											
1968	42	34	40	2	45	2	2	4	27	5	10
1969	60	38	34	7	59	0	0	11	60	2	3

N = 'Nitro-Chalk'; S = Superphosphate; P = Potassium chloride; K = Kieserite; C = Compost; L = litter; F = Formalin.

1969 could not be related to fertiliser treatments or to root weights of the host plants. Populations were smaller in 1969 than in 1968, probably because the summer and autumn of 1969 were much drier (Table 10).

TABLE 11

Tylenchus *spp. and* Tylenchorhynchus *spp. as a percentage of total nematode populations in Stackyard, Woburn, in November*

November	Sitka spruce for 4–9 yrs 1968	1969	Cereals 1960*	Clover 1960*	Sugar beet 1960*	Potatoes 1960*	Potatoes 1969†
Tylenchus	44	67	5	3	9	7	11
Tylenchorhynchus	20	12	2	1	4	4	10

* The 6-course rotation.
† The ley-arable experiment.

Where Sitka spruce has been grown annually for 4 to 9 years, the proportions of *Tylenchus* spp. and *Tylenchorhynchus* spp. to other species were greater than elsewhere in the field (Table 11). *T. emarginatus* was the dominant species of *Tylenchus*, with *T. costatus* many fewer, and other unidentified species occurred occasionally. *Tylenchorhynchus* spp. were less numerous than *Tylenchus* spp. *T. dubius*, the most common species, occurs about the roots of many crops on Stackyard. *T. emarginatus* was probably introduced on conifer transplants from the forestry nursery at Kennington near Oxford, as this species does not occur elsewhere at Woburn.

Tylenchus emarginatus, *T. costatus*, *Tylenchorhynchus dubius*, *T. brevidens*, *Rotylenchus robustus* and *Trichodorus pachydermus* feed on the roots of Sitka seedlings growing in water agar and lay eggs but only *Tylenchus emarginatus* completes its life cycle. Eggs laid by the other species hatched, but the juveniles soon became quiescent. When placed in water they became active but did not mature even when moved to fresh roots. *T. emarginatus* reproduced readily without males. The mean numbers of

TABLE 12

Fecundity and longevity of T. emarginatus *females at different temperatures*

	10°C	15°C	20°C	25°C	17–23°C
Number of females surviving (replicates)	10	10	8	13	10
Mean number larvae produced	37	204	168	155	182
S.E.	6	±17	±26	±21	±14
Mean length of adult life in days	Still alive at end of experiment	128	46	33	57
S.E.		±10·3	±5·7	±4·2	±4·1

larvae produced at constant temperatures of 15°, 20°, and 25°C, and with a daily fluctuating temperature of 17–23°C, were not significantly different, although most viable eggs were laid at 15°C (Table 12). Nematodes lived longer at 10° and 15°C, and reproduced more slowly than at the higher

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temperatures. At 10°C females were still alive 3 months after the first eggs were laid, at 15°C adults lived about 128 days (72–168), at 25°C only 33 days (12–60). Egg-laying capacity is independent of temperature. Egg-laying depends on a continued supply of food; it is slowed and longevity increased by food shortage and/or cold.

T. emarginatus did not reproduce at 30° or 5°C, or when the temperature fluctuated between 3 and 8°C, and eggs failed to hatch after 3 weeks at these temperatures. It can be assumed that *T. emarginatus* cannot reproduce in field soils between October and April, when soil is usually colder than 10°C, and that it overwinters in either juvenile or adult stages. *T. emarginatus* has a shorter generation time than most other plant-parasitic species. At 25°C the life-cycle takes only 5–6 days, at 20°C or at temperatures fluctuating between 17 and 23°C 6–7 days, and at 15°C 13–15 days.

That *Tylenchus emarginatus* and *Tylenchorhynchus dubius* reproduce on Sitka spruce was shown in the glasshouse. After 9 months at temperatures between 15–30°C, which allowed some 20 generations of *T. emarginatus*, numbers increased from the initial 50 and 500 in the inoculum to 1216 and 12 768 of *Tylenchus* and from 213 to 5832 of *Tylenchorhynchus* (Table 13). The weights of the Sitka spruce tops and roots were not significantly affected. In agar cultures *Tylenchus* spp. and *T. dubius* fed on epidermal root cells, but never penetrated deep into the roots, halted growth or caused obvious injury. (Gowen)

TABLE 13

Reproduction of Tylenchus emarginatus *and* Tylenchorhynchus dubius *on Sitka spruce seedlings in pots*

	*Tylenchus emarginatus**		*Tylenchorhynchus dubius*	
Inoculum added	50	500	50	500
Numbers extracted				
Mean ($n = 10$)	5253	3869 ($n = 9$)	3479	1505 ($n = 9$)
Range	(1216–12 768)	(2024–7248)	(231–5832)	(213–4017)
S.E.	±995	±538	±541	±383

* Including some *T. costatus*.

Cereal cyst-nematode at Woburn

The experiment studying the effects of treatments applied in 1966 on populations of *Heterodera avenae* and the yield of spring wheat and spring barley ended. A barley resistant to the Woburn population of *H. avenae* (kindly supplied by the Welsh Plant Breeding Station) was grown and all plots were given the same amount of nitrogen fertiliser (1·0 cwt N/acre). Neither yield nor nematode numbers were affected by giving different amounts of nitrogen in previous years, so all replicates for each main treatment were pooled.

The 'D-D' applied in 1966 significantly ($P = 0{\cdot}01$) increased the yield of the nematode resistant barley in 1969 (Table 14), possibly partly by controlling the nematode, for the resistant barley is invaded by *H. avenae*

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larvae, or by controlling other pathogens, and partly by inhibiting nitrification. The fact that it did not increase yield in 1968, although varieties of wheat and barley susceptible to the nematode were grown may be explained by the severe lodging in the wet summer. In 1969 a wet spring was followed by a dry summer, conditions that favour invasion of roots by larvae and increase the stress on plants with damaged roots. Early in 1968 it seemed that the 1966 'D-D' was beneficial to wheat, but the benefit did not show in increased yield.

TABLE 14

Effects of rotavation and 'D-D' (1966) on resistant barley and H. avenae *1969*

	A Oats to harvest 1966	B Oats rotavated May, 1966	C Oats rotavated + 'D-D' (400 lb/acre) 1966
After barley (1967 and 1968)			
Pre-crop eggs/g soil	6·2	2·4***	1·2***
H. avenae/g root	114·2	74·5	43·3***
Grain cwt/acre (85% D.M.)	32·3	32·7	37·9**
After wheat (1967 and 1968)			
Pre-crop eggs/g soil	5·3	2·5***	1·1***
H. avenae/g root	100·7	80·4	44·9*
Grain cwt/acre (85% D.M.)	35·7	36·7	39·9**

*, **, or ***, significantly different from A at 5%, 1% or 0·1% levels of probability.

TABLE 15

Total grain production, 1967–69, after different treatment in 1966

cwt/acre (85% D.M.)

	Treatment in 1966		
	Oats to harvest	Oats rotavated May	Oats rotavated + 400 lb 'D-D'/acre
	Total yields 1967, 1968, 1969		
For sequence, barley, barley, resistant barley	98·5	102·9	108·9
For wheat, wheat, resistant barley	103·2	108·7	117·6

Table 15 shows the total yields over the three years of this experiment. The differences in yield between plots where oats were grown to maturity in 1966 and those where they were rotavated in during May, with and without applying 'D-D', probably underestimates the effects of these treatments, because the largest N dressing given in 1967 and 1968 depressed yields. These modest responses in yield cannot justify the cost of using a sterilant such as 'D-D' for cereal growing alone, but they add an extra return where land is treated primarily for crops such as potatoes and sugar-beet, with which 'D-D' can produce substantial yield increases. When this experiment began in 1966, the *H. avenae* before sowing were fewer than 1 egg/g soil; at the end of 1967, after two susceptible crops it reached 6 eggs/g in untreated plots. It was still 6 eggs/g after the susceptible crop was grown in 1968, confirming the tendency noted earlier for populations of *H. avenae* at Woburn to stabilise at the relatively small value of

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TABLE 16

Heterodera avenae, Ophiobolus graminis—*their effect on each other and the growth of winter wheat seedlings at 14°C*

	Uninoculated	Inoculum				
		O. graminis only	*H. avenae* only	*O. graminis* first	*H. avenae* first	*O. graminis* + *H. avenae* simultaneously
Dry shoot wt, g	0·22	0·14	0·20	0·16	0·18	0·13
Fresh shoot wt, g	1·25	0·75	1·04	0·81	0·77	0·72
Moist root wt, g	4·5	1·3	3·9	1·5	2·2	1·0
♂♂ emerged/treatment	—	—	89	49	69	46
Total ♂/g root	—	—	27	142	47	102
Total ♀/g root	—	—	5	9	13	4
Total ♂/treatment	—	—	534	1009	494	321
Total ♀/treatment	—	—	100	70	150	25

5–10 eggs/g, unless the land is treated with formalin, when they increased considerably. (Williams)

The interaction between cereal cyst-nematode and the take-all fungus

After an indication in 1965 (*Rothamsted Report for 1965*, 149) that *H. avenae* became fewer when cereals were much affected by take-all and increased when they were not, the interaction between *H. avenae* and *O. graminis* was studied in pots planted with winter wheat. Some pots were inoculated with *H. avenae*, some with *O. graminis*, some with both, and some with neither. In some pots both were inoculated simultaneously, and in others at different times.

H. avenae alone (at 500 larvae/plant) had no detectable effect on root or shoot weights (Table 16). Take-all alone significantly ($P = 0{\cdot}001$) decreased shoot weights and *H. avenae* did not enhance its effects. Although there were more males/g root when *O. graminis* was added first, this was probably because the delay in adding the larvae meant more immature males were in the roots when these were macerated.

Female *H. avenae* (per g of root or per pot) were fewer when larvae were inoculated at the same time as the fungus ($P = 0{\cdot}05$) than when they were inoculated first, possibly because when established first they had more chance of becoming females. Only limited conclusions can be reached from this experiment because some males were lost and could not be counted.

In another experiment the males were counted by transferring plants from soil to Cornish grit in plastic baskets standing in trays before males began to emerge. *Ophiobolus graminis* from Woburn soil (25 mesh sieve fraction) and 1600 *H. avenae* larvae were added simultaneously to the pots. Table 17 shows that roots were heaviest in the un-inoculated pots

TABLE 17

The effects of Heterodera avenae *and* Ophiobolus graminis *on each other and on winter wheat seedlings at 14°C*

	Control	*H. avenae* only	*O. graminis* only	*H. avenae* + *O. graminis*
Shoot weight/pot (fresh)	3·4	3·6	2·8	3·0
Root weight/pot moist	6·7	5·1*	4·7***	3·7***
Take-all lesions % roots infected	—	—	55	50
Total males/pot	—	362	—	157
Total females/pot	—	139	—	56

* or ***, significantly different from control at 5% or 0·1% levels of probability.

and lightest in pots with *O. graminis*. *H. avenae* did not significantly increase the effect of *O. graminis*, although alone it significantly decreased the weight of moist root ($P = 0{\cdot}05$). There was little sign of the 'knotting' of seminal roots which follows *H. avenae* invasion of spring wheat in the field. Take-all invasion of roots was not influenced by *H. avenae*, but *O. graminis* greatly decreased the number of male and female nematodes that matured ($P = 0{\cdot}001$). In pots where take-all developed extensively the sex ratio (♂ : ♀) was 4·2, compared with 2·8 where it failed to develop

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extensively, and 2·6 in uninoculated pots. It was 9·1 in one pot in which 85% of the roots had take-all lesions. (Williams and Hornby, Plant Pathology Dept.)

Fumigation of potato soil to control nematodes and *Verticillium* wilt

Heterodera rostochiensis worsened *Verticillium* wilt of potatoes grown in pots (*Rothamsted Report for 1968*, Part 1, 157). Hence attempts were made in an infested field at Woburn to control either pest or fungus or both. Aldicarb (660 lb/acre of 10% granules) was rotavated in before planting to kill nematodes; benomyl was applied as dust to seed tubers to try and control the fungus, and methyl bromide (2 lb/100 sq ft) was applied under gas-tight sheets to control both organisms.

Benomyl was ineffective and did not affect the tuber yield (Table 18). Aldicarb and methyl bromide killed nematodes so effectively that there were few females on roots during June and even fewer cysts and eggs in the soil after harvest, but methyl bromide increased the yield by 7·7 and aldicarb by only 4·2 tons/acre. (Corbett and Hide, Plant Pathology Department)

TABLE 18

Effect of methyl bromide, aldicarb and benomyl on potato yields and numbers of the cyst nematode

(Counts are log $(x+1)$ with detransformed numbers in parenthesis)

		Tuber yields tons/acre	White females on roots in June	Cysts/200 g soil at harvest	Eggs/200 g soil at harvest
Untreated	Control	10·0	1·30 (20)	1·77 (59)	1·78 (60)
Aldicarb	Nematicide	14·2	0·83 (7)	1·03 (11)	1·20 (16)
Benomyl	Fungicide	10·3	1·78 (60)	1·79 (62)	1·98 (96)
Methyl bromide	Nematicide and fungicide	17·7	0·61 (4)	1·11 (13)	0·95 (9)
S.E.		0·9	0·17	0·14	0·18

Control of 'Docking disorder' in sugar beet

In plots 4 yards × about 500 yards on Honeyhills, Docking, Norfolk, where the soil was infested with *Trichodorus* (chiefly *T. cylindricus*) and *Longidorus attenuatus*, 'D-D' injected on 26 March 6 in beneath the predetermined sugar-beet rows greatly increased the yield of sugar-beet sown on 21 April. One ml 'D-D'/ft of row (6·4 gal/acre) increased seedling weight in June ten-fold, 1½ ml increased it twenty-fold and 2 ml increased it twelve-fold. Seedlings in untreated soil on one side of the field grew well during summer but on the other side, where the soil was coarser, they remained stunted. Although total yields were increased sugar was less than the maximum because the plant population was excessive and gave many roots too small to harvest. At Bircham, Norfolk, where the soil was lightly infested with *Trichodorus* and where herbicide killed many seedlings, Docking disorder did not occur and 'D-D' neither increased seedling vigour nor yield (Table 19).

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TABLE 19

Effect on sugar yield of 'D-D' injected beneath rows before sowing

Docking			Bircham		
Treatment (gal 'D-D'/acre)	Sugar (cwt/acre)	Plants/acre (thousands)	Treatment (gal 'D-D'/acre)	Sugar (cwt/acre)	Plants/acre (thousands)
Untreated	31·7	46·7	Untreated	45·3	24·1
6·4	43·7**	46·0	5·8	48·3	21·1
9·6	43·5**	46·9	8·7	48·7	20·2
12·8	46·4***	47·0	11·6	49·9	25·0

*, **, or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.

At Bircham, because of heavy rain, sugar-beet was sown 6 weeks after fertilisers were applied to the seedbed. In spite of this an extra 122 lb N/acre added to the seedbed as ammonium sulphate or as ammonium sulphate with 2% of the nitrogen as 'N-serve' (2-chloro-6-trichloromethyl-pyridine), which is said not to be leached, did not increase yields. (Whitehead and Tite)

Control of the needle-nematode *Longidorus elongatus*

In fen peat soil (more than 50% organic matter) near Stoke Ferry, W. Norfolk, *Longidorus elongatus* injures spring-sown crops, especially cocksfoot-ryegrass leys, sugar-beet and kale. Dazomet 100 lb (prill)/acre rotavated into the top 6 in of soil during August killed about 70% of the nematodes down to 8 in. Aldicarb, 40 lb granules (10% active ingredient)/acre rotavated into the top soil, or 'D-D' 400 lb/acre injected 6 in. deep during August, killed half of the nematodes but as much as 200 lb 'Mocap' granules (*O*-ethyl *S,S*-dipropyl phosphorodithioate) (10% active ingredient) did not kill any. None of the treatments improved the good yields of the 1969 cocksfoot-ryegrass sown in autumn 1968 after the treatments had been applied. Although soil from untreated plots contained more than 300 *L. elongatus*/litre during spring, the autumn sown grass was undamaged whereas the spring sown grass failed. Other new leys sown in spring 1969 on similar peat soils at Stoke Ferry were badly damaged by *L. elongatus*. Damage by this pest to grass is therefore best avoided by sowing in autumn, when it is presumed the nematodes are not feeding. (Whitehead and Tite)

Control of potato cyst-nematode

In Butt Furlong, Woburn, where the sandy soil (about 10% clay) is infested with potato cyst-nematode, 'D-D' injected 9 in. deep into preformed ridges 5 weeks before potatoes were planted decreased the number of larvae invading the roots and increased the yield of ware-sized tubers (Table 20). Applying 32 gal 'D-D'/acre doubled the yield of ware, as it did on the same plots in 1968 but it controlled the nematode less well than in 1968. In Long Mead, Woburn, where the soil is a loam with 39% clay, dazomet (98% granules (prill)) and aldicarb ('Temik') granules (10%

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active ingredient) rotavated into the top 6 in. controlled the nematode better than 'D-D' applied to preformed ridges, and greatly increased yields.

In a new experiment on sandy loam in Butt Close, Woburn, 780 lb methyl bromide/acre was applied under gas-tight polythene sheeting during spring, and dazomet rotavated into the top 6 in. of soil either during autumn or 8 weeks before planting. Both controlled potato cyst-nematode better than did 'D-D' or 'Telone', whether these were applied during autumn or to preformed ridges in spring, and greatly increased yields of ware tubers (Table 21).

TABLE 20

Nematicides and potato cyst-nematode at Woburn

Treatment	Amount gal/acre (lb/acre)	Ware tubers var. Majestic tons/acre; (larval invasion % untreated plots) Butt Furlong (sandy loam)	Long Mead (sandy clay)
Untreated		4·5	2·1
Spring, 1969			
'D-D'	4 (8)	4·7 (81)	
	8 (95)	5·6 (59)	2·3 (100)
	16 (190)	**7·6 (56)	3·0 (100)
	32 (380)	***9·2 (48)	**6·0 (100)
Dazomet (98%)	(100)		**5·9 (80)
	(200)		***8·3 (30)
	(400)		***13·6 (19)
Aldicarb (10%)	(23)		**7·2 (25)
	(46)		**7·8 (16)
	(92)		***13·2 (4)

*, ** or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.

TABLE 21

Nematicides and potato cyst-nematode in sandy loam, Butt Close, Woburn

Treatment	Amount gal/acre (lb/acre)	Ware tubers var. Majestic ton/acre (larval invasion % untreated plots)
Untreated		4·0
Autumn, 1968		
'D-D'	33 (400)	7·2 (14)
'Telone'	19 (230)	5·4 (39)
Dazomet	(400)	***15·3 (5)
Spring, 1969		
'D-D'	8 (95)	7·3 (39)
	16 (190)	6·5 (74)
	32 (380)	**7·9 (32)
'Telone'	6 (73)	5·4 (80)
	12 (145)	5·4 (44)
	24 (290)	**7·7 (17)
Dazomet	(100)	***10·5 (16)
	(200)	***12·4 (9)
	(300)	***16·0 (2)
Methyl bromide	(780)	***13·9 (4)

*, ** or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.

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TABLE 22

Nematicides and potato cyst-nematode in peaty loam soil, Mepal

Ware tubers ton/acre (larval invasion % of untreated plots)

Treatment	Potato variety	Amount (gal, lb/acre)				Means (vertical comparisons only)
		Experiment A				
'D-D'		Untreated	29 gal	58 gal	87 gal	
1967 only	K. Edward	1·6 (100)	1·8 (100)	2·6 (100)	3·1 (100)	2·3
1967 and 1968	K. Edward	1·4 (100)	3·8* (59)	6·5*** (51)	8·3*** (28)	5·0*
		Untreated	23 lb.	46 lb	92 lb	
Aldicarb at planting	K. Edward	2·2 (100)	6·2** (29)	7·7*** (15)	9·1*** (5)	6·3**
	Maris Piper†	8·1 (21)	10·2 (11)	10·5* (4)	11·7** (3)	10·1***
		Experiment B				
		Untreated	8 gal	16 gal	32 gal	
'D-D' to ridges in spring	K. Edward	2·6 (100)	3·0 (84)	2·7 (64)	3·3 (67)	2·9
		Untreated	100 lb	200 lb	400 lb	
Dazomet, November 1968	K. Edward	2·0 (100)	2·6 (51)	3·0 (50)	5·9*** (17)	3·4
		Untreated	23 lb	46 lb	92 lb	
Aldicarb at planting	K. Edward	2·7 (100)	8·1*** (36)	8·2*** (16)	8·2*** (5)	6·8***

*, **, or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.

† Larval invasion of Arran Banner potato roots determined from soil samples collected after aldicarb treatment but before Maris Piper planted.

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'D-D', dazomet and aldicarb were tested for a second year in fen peat soil (25–30% organic matter) at the Arthur Rickwood Experimental Husbandry Farm, Mepal, Isle of Ely (Table 22). Yields of ware-sized tubers from untreated plots were small. 'D-D' injected 6 in. deep in rows 12 in. apart in November again increased potato yields but controlled potato cyst-nematode poorly. Smaller amounts of 'D-D' injected into preformed ridges during spring neither controlled the nematode nor increased the yields. Dazomet rotavated into the top 6 in. of soil in November controlled the nematode better but damaged the plants. Aldicarb rotavated into the top 6 in. of soil just before planting controlled the nematode well and greatly increased yields. In contrast to 1968, when the soil was less heavily infested, aldicarb also significantly increased the yield of Maris Piper potatoes.

'D-D' and dazomet were also tested in fen silt soil (73% fine sand) near Terrington St. Clement, Norfolk (Table 23). The soil was heavily infested and yields of Maris Piper and Majestic potatoes from untreated plots were small. Although 'D-D' controlled the nematode poorly when injected 9 in. deep into preformed ridges 5 weeks before planting, it greatly increased the yields of both varieties. Dazomet rotavated into the top 6 in. of soil, which was then formed into ridges 9 weeks before planting, controlled the nematode better and also greatly increased the yield of Majestic.

TABLE 23

Nematicides and potato cyst-nematode in silt soil, Terrington

Ware tubers ton/acre (larval invasion % untreated plots)

Treatment	Amount gal/acre (lb/acre)	Potato variety: Majestic (susceptible)		Maris Piper (resistant)
Untreated		0·3	1·0	2·6
Spring, 1969				
'D-D'	8 (95)	4·3*** (98)		8·5*** (93)
	16 (190)	5·2*** (64)		8·6*** (75)
	32 (380)	6·0*** (33)		8·0*** (76)
Dazomet	(100)		3·5*** (86)	
	(200)		7·4*** (57)	
	(400)		9·8*** (16)	

*, **, or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.

Applied during spring to the same plots and in the same amounts as in 1968, 'D-D', dazomet and aldicarb at Woburn and 'D-D' and aldicarb at Mepal killed a smaller percentage of the nematodes than in 1968, perhaps because the spring of 1969 was wetter. (Whitehead and Tite)

In Long Mead, Woburn, carbon disulphide, 'D-D' and methyl bromide applied under gas-tight sheeting in May significantly decreased the invasion of potato roots by larvae and greatly increased potato yields (Table 24). Dibromochloropropane ('Nemagon') injected 6 in. deep into soil, which was then covered with gas-tight sheeting for 3 weeks, also decreased larval invasion of potato roots but was toxic to potatoes planted in early

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TABLE 24

Assessing nematicidal activity of pesticides, Long Mead, Woburn

Treatment	Amount (a.i. lb/acre)	In field: Ware potatoes var. Majestic tons/acre	In field: Log larvae + 1/g root (4.7.69)	In pots: Change in viable larvae before planting (29.5.69) % before treatment (12.5.69)
Untreated		3·5	2·8	
Fumigants				
Aluminium phosphide (C)†	120	5·9*	2·9	13·5
Carbon disulphide (C)	400	10·5***	2·6	−50·3*
Carbon disulphide	400	5·3	2·7	−48·9
'D-D' (C)	400	10·4***	2·2*	−69·1*
Dibromochloropropane (C)	100	3·6	1·9**	8·6
Dibromochloropropane	100	2·6	2·7	−22·2
Ethyl bromide (C)	480	4·0	2·4	−7·7
Methyl bromide (C)	1000	14·8***	2·4	−91·3**
Methyl chloride (C)	500	2·8	3·0	44·5
Methylene dichloride (C)	440	5·9*	2·8	−20·8
Propylene oxide (C)	270	2·0	2·6	−33·0
Organo-phosphorus insecticides				
'Bidrin'	90	4·2	2·5	−58·5*
Chlorfenvinphos	90	9·6***	2·2*	−88·9**
Demeton-S-methyl	90	6·0*	2·8	−73·2*
Diazinon	90	10·1***	1·4***	−62·4*
Dimefox	110	5·5*	1·4***	−86·2**
'Dursban'	90	5·3	1·8***	−74·5*
Endothion	20	4·3	2·8	−1·8
'Folimat'	110	5·2	2·4	−26·5
Phosphamidon	90	8·7***	2·3*	−35·6
Schradan	100	5·2	2·1**	−18·4
Thionazin	90	9·4***	1·8***	—
Other pesticides				
Aldicarb	10	10·8**	1·6***	−79·0*
C14421	40	3·9	2·8	−40·8
Griseofulvin	20	4·3	2·6	−8·4
'Isolan'	90	7·5***	1·7***	−70·0*
Methomyl	5	6·4**	2·5	62·6

*, **, or ***, significantly different from the untreated at 5%, 1% or 0·1% levels of probability.
† (C) = covered with gas-tight sheeting.

June. Aldicarb, chlorfenvinphos, demeton-S-methyl, diazinon, dimefox, 'Isolan', phosphamidon and thionazin, applied to the soil surface and rotavated in just before potatoes were planted, greatly decreased the invasion of potato roots by larvae and greatly increased potato yields. Dimefox, thionazin, 'Isolan' and perhaps 'Dursban' and schradan, damaged potatoes at the amounts applied. (Whitehead and Storey)

Staff and visiting workers

A. R. Stone joined the staff in October and Miss J. B. Vincent (Liverpool Regional College of Technology), Miss Ljubica Rajicic (Yugoslavia), Mr. S. Gowen (Trinidad), Mr. O. O. Olowe (Nigeria), Dr. G. W. Yeates (New Zealand) and Dr. U. Wyss (Germany) worked in the Department.

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G. Storey (Liverpool Regional College of Technology) and M. Williams (Barking Regional College of Technology) worked as sandwich-course students. A. G. Whitehead organised sessions on the control of nematodes at the 5th British Insecticides and Fungicides Conference, Brighton, in November at which F. G. W. Jones and T. D. Williams gave papers.

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