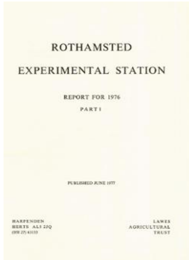
Report for 1976 - Part 1


ROTHAMSTED

EXPERIMENTAL STATION

REPORT FOR 1976

PART 1

Nematology Department

F. G. W. Jones

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Introduction

Nematodes are small translucent round-worms averaging about 1 mm long and barely visible to the naked eye. The Department is concerned only with those that harm crops or play a part in the economy of the soil. Because of their small size and obscure mode of life special techniques are necessary to study them (page 206). The mechanics of nematode feeding on or within roots or other plant parts (page 200) are important as this is how plant growth is stunted, usually by large numbers that have multiplied on some preceding crop. Because there are many different kinds of nematodes it is essential to be able to identify and classify them (page 202) and also to understand host ranges and other details of their biology. Often races or pathotypes of the same species (page 203) are important because some of these breed on resistant varieties of crops. The plant breeder must know how these races are interrelated and the farmer also needs to know what races are in his fields so that the correct resistant variety may be chosen. Details of morphology are also important in trying to understand how the bodies of nematodes work during movement, feeding, reproduction and invasion of tissues (page 205). The way in which populations fluctuate when resistant, susceptible and other crops are grown greatly affects the incidence of crop damage. For this reason we have for several years studied nematode population dynamics (page 207). Damage to crops by nematode

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populations of various kinds has also been studied, especially that caused by cyst-nematodes to potatoes and attempts are being made to relate maximum yields to irrigation, application of a nematicide and enhanced farm practice on heavily infested land (page 210). Work on the control of nematodes by nematicides continues. Besides evaluating a number of potential nematicides (page 214), we are especially interested in finding the best ways of incorporating granular nematicides to plough depth and below (page 216), and in testing nematicides against cyst-nematodes and stem nematodes on a range of crops (pages 216–219) and in a rotation (page 215).

Feeding and hatching

Feeding. We have studied how three related nematodes of similar size and shape and with overlapping food sources ingest food through their hollow, needle-like mouth stylets and how they defaecate. They represent three steps on a scale from high internal body pressure, active feeding and elaborately controlled defaecation at one end to low body pressure, passive feeding and feeble defaecation at the other. The most active nematode is *Aphelenchoides blastophthorus*, a species injurious to scabious and other ornamentals which also feeds on fungi. A less active nematode but more important economically is the stem nematode, *Ditylenchus dipsaci*, races of which attack several field crops and ornamentals. *Hexatylus viviparus* is least active of the three and feeds on fungi. It needs to keep its body pressure low because it is force-fed by its host, the cell contents of which are at high pressure initially. This species has a simple method of defaecation mainly concerned with pumping out the excess water it receives. Table 1 summarises the similarities and differences between these three plant-feeding nematodes.

TABLE 1

Food ingestion and defaecation in three contrasted nematodes

	H. viviparus	*D. dipsaci*	*A. blastophthorus*
Size and shape	All vermiform and about 1 mm long		
Food	fungi	higher plants	higher plants and fungi
Feeding	passive	pumping/passive	active pumping
Defaecation	slow and inconspicuous		forceful, quick
	no functional prerectum or rectal valve	no prerectal valve	functional prerectum and rectal valve
	slight movements only, round rectum	hind gut partly closes when the extreme hind body shortens	posterior half of body muscle active as body shortens
Rectal pump	present	absent	absent
Body pressure	low	variable	high

To understand the mechanism of feeding, the action of the oesophageal pump of *Ditylenchus dipsaci* was studied. Ciné film and working models of the sclerotised pump lining were made. The pump lining is small in relation to the pump as a whole, is strongly thickened and opens from a triradiate form to at least a triangular one. It may operate as a 'click mechanism'. Such an arrangement, as in insect wings, can be very efficient, and could result in rapid intake of food. (Seymour and Doncaster)

Directions of stresses (induced in the pump lining when it is opened by the radial muscles) that tend to close the pump, have been determined photoelastically, using Perspex models of sections of the pump lining viewed in polarised light. The stress pattern is complex and symmetrical. The cuticle around both the outer and inner hinge regions is thought to act as integral springs to close the pump lining. Young's elastic

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modulus E was estimated as 3×10^7 Nm^{-2}, comparable with that of some tanned ligaments of bivalve molluscs. (Seymour)

Using short-interval, time-lapse cinematography the effects of saliva injected into cells of bean leaves (*Vicia faba*) by *D. dipsaci* were compared with those of other tylenchid plant parasites. When *D. dipsaci* pierces a plant cell wall it injects a globule of saliva from the dorsal gland which appears more homogeneous than the contents of the gland ducts. Salivation lasts about 70 s and is followed immediately by ingestion when most of the visible saliva is withdrawn from the cell. Cytoplasmic changes in the food cell follow: inclusions, brought to the site by cyclosis, tend to accumulate there and streaming away from the site is retarded, suggesting that the cytoplasm matrix gels around the penetration site. Globular inclusions are not ingested by the nematode but remain immobile close to the stylet aperture.

D. dipsaci can feed passively without pumping. Such behaviour may be because a pressure gradient develops between the food cell and the nematode, or because some differentially permeable structure forms between the stylet tip and the cell cytoplasm and establishes a local gradient. No such structure has been identified nor is there evidence that cell pressure rises in response to injected saliva. When a flaccid guard cell of a closed stoma was pierced, the cell neither changed shape nor opened the stoma, suggesting that pressure did not increase. For solutes to be transferred to the nematode a living, differentially permeable structure is more likely to be involved than a dead one. Consistent with this is the fact that aggregations of host cytoplasm at the penetration site remained immobile only while the nematode held its stylet in the penetration hole; cytoplasm dispersed and the cell took up external liquid once the nematode withdrew. When the stylet was quickly re-inserted the cytoplasm aggregated again.

Hatching. The stylet thrusting during hatching, invasion of plant parts and passage through the cell walls of tissues is basically the same as that made in the initial stages of feeding. Second-stage *D. dipsaci* larvae made perforations with the stylet at random at the pole of the egg from which they later hatched. At first, the eggshell was stiff, with a distinct, inner lipid layer, but later the lipid layer disappeared and the shell was deformed and wrinkled when the larva moved inside it. In one egg, the pierced end of the shell burst open under impact from the head of the larva, suggesting it had been weakened by enzymes.

Although secretions filled the subventral salivary gland ducts in unhatched larvae, they could not be seen issuing from the stylet. The oesophageal pump pulsated before the larvae hatched, sometimes even before the first moult was completed. Young second-stage larvae were the thinnest, they had most liquid between them and the eggshell and their bodies were deeply kinked at each bend. Second stage larvae ingest egg fluid by pumping and their body volume and turgor increase while the liquid around them diminishes. Subventral gland secretions may be swallowed and excreted from the anus. Enzymes therein and locomotory movements may break down the lipid layer of the eggshell.

Unlike *D. dipsaci* larvae, those of *Meloidogyne hapla* were not kinked where their bodies were bent in the egg and they appeared more turgid, but the eggshell was always rather flexible. Many larvae moved vigorously in the eggs and probed with their stylets but became quiescent again. However, although *Meloidogyne* spp. can hatch without slitting the eggshell, stylet thrusts, gland secretions and body movements combine to weaken the eggshell (Dropkin *et al.*, *Nematologica* (1958) **3,** 115–126).

This work on hatching ties in with that reported last year on larvae of *G. rostochiensis* (Clarke & Hennessy, *Rothamsted Report for 1975*, Pt 1, 200) and with earlier work on hatching factors. (Doncaster)

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Taxonomy of cyst-nematodes

Punctodera chalcoensis is a new species in the *punctata*-group widespread in the central highlands of Mexico where it is injurious to maize, causing severe stunting and chlorosis, especially in badly nourished crops. Damage is more severe when rains occur early in the growing season, permitting heavy invasion of young plants. *Zea mays* and the Chalco race of teosinte, *Z. mexicana*, are the only known hosts. The nematode fails to develop on grasses from a range of other genera. *Z. mexicana* is a putative ancestor of maize and the Chalco race is similar to maize. The hypothesis that *P. chalcoensis* has co-evolved with maize-like plants is being tested. (Stone, with Dr. C. Sosa Moss, Escuela Nacional de Agricultura Chapingo, Mexico, and Mr. R. H. Mulvey, Biosystematics Research Institute, Department of Agriculture, Ottawa, Canada)

Heterodera mani was identified from pasture in Lincolnshire and is the first record of this species in England. Although typical in other respects, this population lacks the prominent forward development on the second-stage juvenile stylet knobs formerly regarded as a reliable character distinguishing *H. mani* from other species in the *H. avenae* group. (Stone, with Mr. J. M. Holliday, ADAS, Shardlow)

Heterodera schachtii was identified from cabbage crops at Iquiqui, Chile, the first record for beet cyst-nematode in that country. The region where the nematode was found is isolated and unimportant agriculturally but was a loading port for ships carrying nitrate to Europe. The infestation may have arisen from soil carried as ballast on the voyages to Chile. (Stone, with Miss A. Valenzuela, Universidad de Chile)

***Globodera* spp.** Populations of *Globodera rostochiensis* from Vancouver Island, Canada, and Steuben County, New York State, were re-tested on the full range of differential clones used in the new international pathotyping scheme (*Rothamsted Report for 1975*, Part 1, 195–6) and proved to be Ro1, but a population from Botwood, Newfoundland, is *G. pallida*, the first record of this species in North America. A population of *G. pallida* from eastern England was typed as Pa2 in the international scheme, a pathotype previously unrecorded from Great Britain. Until recently clones differentiating Pa2 from Pa3 were unavailable in the United Kingdom and the detection of Pa2, which occurs in the Netherlands, is not unexpected. However, this population differs from Dutch Pa2 in its behaviour on a line of experimental clones developed at the Plant Breeding Institute, Cambridge and so may eventually be recognised as a new pathotype. (Stone, Rowe and Blindell)

Two samples of *Globodera* cysts found by the MAFF Plant Health Inspectorate in ware potatoes from the Netherlands and the Canary Islands were identified as *G. pallida*. The Dutch cysts were from cv. Saturna, resistant to pathotype Ro1 but susceptible to *G. pallida* pathotypes. Previous reports of potato cyst-nematode from the Canary Islands have been of *G. rostochiensis sensu lato*. (Stone)

An infestation of potato cyst-nematode from Coquimbo, Chile, was confirmed as *G. rostochiensis* and is a pathotype able to develop on resistant potatoes with gene H_1. (Stone, Rowe and Blindell)

Biology of cyst-nematodes

Host ranges of *Globodera* spp. on spiny solanums. The six species of *Globodera* parasiting Solanaceae are believed to have co-evolved with their hosts in Central and South America. Thirty populations, representing the six species, were tested on sixteen

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species of spiny *Solanum*. *S. prinophyllum*, *S. platense* and *S. citrullifolium*, which evidently lack resistance genes, were hosts for all populations and *S. quitoense*, *S. hispidum* and *S. capsicoides*, which possess them, were non-hosts for all populations. Neither group belong to botanically recognised sub-groupings of the genus. Ten *Solanum* species differentiated one or more nematode populations. Of these, *S. fructo-tecto*, *S. rostratum*, *S. tequilense*, *S. sodomaeum*, *S. indicum* and *S. carolinsene* were hosts for all populations except *G. rostochiensis* Ro1. A population from Bolivia which is *G. rostochiensis* Ro2, Ro3 or Ro5, was able to reproduce on all these plants. It seems probable therefore that all these plants possess a resistance gene identical to H_1 or similar in effect. Populations of *G. solanacearum* behaved differently on *S. sisymbrifolium*, indicating heterogeneity in ability to circumvent resistance genes within this species. Although some plants were hosts and some non-hosts of the *G. tabacum* populations tested, all behaved the same. Grouping the plant species that differentiated between nematode species according to host range did not produce arrangements corresponding to the classical taxonomic subdivision within the spiny solanums. This tends to confirm that the solanums have had a long association with the round-cyst nematodes. (Roberts, Stone, Lane, Rowe and Blindell)

Behaviour of populations on hybrid potato clones with gene H_3. Thirteen hybrid potato clones with various combinations of resistance genes H_1, H_2 and H_3 were tested against *G. rostochiensis* Ro1 (one population), *G. pallida* Pa1 (two), Pa2 (one) and Pa3 (six). On average, the combination H_1H_3 decreased significantly the number of cysts per plant produced by Pa3 populations. The effect of gene H_2 could not be assessed as it is masked by gene H_3. Unlike the effect of gene H_1 which confers almost 100% resistance to *G. rostochiensis* Ro1 that of gene H_3 on *G. pallida* is only partial and can be modified by other genes such as H_1 which are not always inherited with it. There were no significant differences in the number of cysts produced by the six *G. pallida* Pa3 populations on ten clones, suggesting a uniformity in the frequency of genes able to circumvent resistance in them. However, there were differences between populations on three clones possibly due to differences in genes modifying the effect of gene H_3. (Stone, Lane and Rowe)

Effect of temperature on development. The development of *G. rostochiensis* Ro1 and *G. pallida* Pa3 on potato was studied at temperatures ranging from 13 to 25°C. Juveniles of the second generation of *G. rostochiensis* appeared in the soil after 12 weeks at 16°, ten weeks at 19°C, eight weeks at 22°C and 11 weeks at 25°C but development was not completed at 13°C. Juveniles of *G. pallida* appeared only at 19°C after ten weeks and at 22°C after nine weeks. Maximum numbers of juveniles of both species were produced at 22°C, so the optimum temperature for both species lies between 16 and 22°C. The numbers of females produced after 12 weeks were greatest at 19°C for *G. rostochiensis* and 16°C for *G. pallida* and the numbers of eggs per cyst greatest at 22 and 16°C respectively. Although many eggs were produced at 13°C few contained fully formed embryos, probably because development was slower than at 22°C. The lower optimum temperature for development of *G. pallida* agrees with the lower optimum for hatching of this species (*Rothamsted Report for 1975*, Part 1, 198). (Berry, Stone, Parrott and Edwards)

Pathotypes. Features which could be used to characterise males and larvae of different *H. avenae* pathotypes and any changes which might be caused by development on resistant and susceptible cereals have been studied.

Males of pathotype 2 produced on a resistant oat had longer stylets than those from a susceptible oat. This differs from *G. rostochiensis* and *G. pallida* where males developing on resistant potatoes tend to have shorter bodies and stylets. Pathotype 1 males from susceptible and resistant cereals did not differ in body, stylet or spicule length when

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processed to glycerine by Baker's method but again the stylets were longer in males from resistant plants when processed by Seinhorst's method. The position of the hemizonid was not affected. Body and stylet lengths of males of an Australian *H. avenae* population were unaffected by development on susceptible Sun II oats or Barley var. No. 191.

Pathotype 2 eggs hatched somewhat more freely than those of pathotype 1 in root diffusates of Drost barley (host for 2) compared with those of Sun II oats (a host of both). The best hatching regime was pre-storage of cysts at 5°C and hatching at 10°C, although initially eggs hatched faster at 15°C. In water agar cultures and in small pots larvae of pathotypes 1 and 2 invaded roots of Zephyr barley (host of both) in the presence of roots of Drost barley (host of 2) equally. These results confirm earlier ideas that there are scarcely any differences that can be used to separate the two pathotypes other than reproductive behaviour on differential hosts such as Drost barley. (Williams, Beane and Wisden)

Sex ratios. The sex ratio (male/female) of species in the Heteroderidae and some other nematode groups tends to increase with an increase in population density. This may be because sex is determined by the environment, juveniles being able to become male or female according to circumstances. Alternatively sex may be determined genetically and changes in the sex ratio may be the result of a differential death rate, or some other selective process, diminishing the proportion of females that survive to adulthood. A better understanding of this process might lead to novel methods of control and it is of interest in connection with resistant crop varieties; on some of these only males develop.

In a test with the cereal cyst-nematode, no significant differences in sex ratio were detected when they developed on wheat, barley or oats. Of juveniles that invaded plants, 85 to 99% could be traced to sexual maturity. When 100 juveniles were added to plants in pots, 37% invaded the root system of which about three quarters became male and one quarter female (sex ratio 3.3). When 4000 were added, only 9% established themselves in the roots and most of these became males (sex ratio 11.1). In tests where only 1 larva was added, i.e. where there was no intraspecific competition, 60% invaded the roots, 40% became 4th stage male juveniles, 14% 4th stage female juveniles; the remaining 7% were 2nd stage juveniles of undetermined sex. Even if the last eventually became females, the juvenile sex ratio would have been 2. Genetically determined sex ratios are usually but not invariably 1. If sex is genetically determined, it is possible that female juveniles are less successful in invading and establishing themselves in roots than male juveniles, and that some actually leave the roots when competition is intense. Initially all larvae seem to behave identically and probably feed in exactly the same way. By the 4th stage females feed vigorously whereas 4th stage males may not feed. Somehow, possibly during the 3rd stage, the future feeding pattern and the syncytial transfer-cell system must be established if females are to enlarge greatly and produce many eggs. Their ultimate food requirement is several hundred times that of males. (Bridgeman)

Electrophoresis of soluble proteins. We have continued attempts to separate species and pathotypes by gel electrophoresis. Suspensions of freshly hatched larvae of round cyst-nematodes were cleaned by filtration, concentrated by centrifuging, frozen in liquid nitrogen, crushed and the resulting macerate immediately freeze-dried. This method enables stocks of material from freshly hatched larvae to be accumulated until there is enough for gel electrophoresis. The method also aids standardisation of procedures in that protein extracts can be made from starting material of known dry weight. Protein bands in gels from larvae are entirely of nematode origin and free from contamination with plant proteins ingested as food which complicate the interpretation of gels from young females: all protein patterns from larvae of *G. rostochiensis* Ro1 populations from Puno

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(Peru) and Feltwell (England) were identical but different from those of larvae of *G. pallida* populations from Otuzco (Peru) and Cadishead (England) which were similar but not identical. Differences were also demonstrated in protein patterns from larvae of *G. solanacearum* and *G. virginiae*, although *G. mexicana* was very similar to *G. virginiae*. No such differences could be demonstrated between their females which contain host proteins. (Greet and Firth)

Lipids of *Globodera rostochiensis*. The second stage larvae of cyst-nematodes contain many large lipid globules in the intestinal cells which are probably reserves of energy. Whole cysts (females) of *G. rostochiensis* contained on a dry weight basis about 14% lipid and juveniles isolated from them at least 20%. In the cyst lipids, octadecenoic (19%), eicosatetraenoic (22%) and eicosenoic (28%) acids predominated. Hexadecanoic, eicosanoic and eicosatrienoic acids together accounted for another 19% and small amounts of six other fatty acids made up the remaining 12%. In *Meloidogyne* spp. Krusberg, Hussey and Fletcher (*Comparative Biochemistry and Physiology* (1973) **45** B, 335–341) found that octadecenoic acid (75%), octadecanoic acid (5–8%) and hexadecanoic acid (6–7%) were the three most prevalent acids. The substantial amounts of the highly unsaturated low m.p. eicosatetraenoic acid in *G. rostochiensis* may be related to the ability of the nematode to survive low soil temperatures (e.g. of — 33° in Finnish Lapland). Higher m.p. fatty acids predominate in *Meloidogyne* spp. which are adapted to higher temperatures.

The innermost layer of the egg shell is believed to be a lipid membrane which may control the passage of water and solutes and be concerned with the hatching process. In some nematodes the major constituents of the lipid membrane is a group of related glyco-lipids, the ascarosides, but *G. rostochiensis* hydrolysates of the unsaponifiable fraction of the lipid extracts did not contain the characteristic dideoxy-sugar or the long-chain fatty alcohol portion of the ascaroside molecule. Lipids extracted from *G. rostochiensis* egg shells were separated by thin-layer chromatography into three components. The major component, obtained in crystalline form, is under investigation. (Clarke and Hennessy)

Stem nematode

Stem nematode on field beans. Infestations on the Rothamsted and Woburn farms were least for some years due to the planting of uninfested seed on uninfested fields. Even on infested sites, beans were only lightly infested, probably because of late sowing and the exceptional dry weather. Consequently more clean seed was produced than for several years.

Thirty-one selections of *V. faba* supplied by the Plant Breeding Institute, Cambridge and Welsh Plant Breeding Station were tested in pots inoculated with the giant race of *D. dipsaci;* most of the plants became well infested. No selection showed any marked degree of resistance. These selections are in addition to 44 tested in 1975 (*Rothamsted Report for 1975*, Part 1, 203). (Hooper)

Nematode morphology

The oesophagus of *Aphelenchoides blastophthorus*. The musculature of the oesophagus of *A. blastophthorus*, which has a powerful pumping system, is more complex than that of any other tylenchid yet described. The median bulb contains the usual radial musculature which operates the pump mechanism. In addition there is a large sphincter complex surrounding the circular lumen at the front of the bulb and a valve between the dorsal gland orifice and the heavily cuticularised pump chamber. The hind end of the

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bulb almost completely surrounds a narrow tubular region, possibly equivalent to the isthmus of most tylenchids, which is very short and also contains a valve. The front and rear valves are tri-radiate and supplied with radial muscles which open and close the lumen. Associated with the rear valve are three longitudinal and three circular muscles. The oesophago-intestinal junction is just behind the base of the median bulb, and is itself a third valve similar to that of other nematodes (Seymour & Shepherd, *Journal of Zoology* (1974), **173,** 517–523), in which naked cell membranes lining the lumen are closely apposed when closed. The intestine is lined with smooth-coated microvilli which are constricted where they join the intestinal epithelium. The oesophageal glands, one dorsal and two subventral, overlap the intestine but are quite distinct from it. Each gland has a single large nucleus associated with it and there is also a group which is probably nerve cell bodies. All three gland ducts join the oesophageal lumen in the median bulb, the two subventral ducts just behind and the dorsal duct just in front of the pump chamber. Each duct has an ampulla within which a small, perforated, sclerotised collecting duct arises and connects with the oesophageal lumen. The nerve ring encircles the intestine about 3μm behind the oesophago-intestinal junction. (Shepherd and Clark)

Sperm and male reproductive tract of *Rhabditis oxycerca*. Under the light microscope, the gonad of *R. oxycerca* is short and broad, with several distinct regions. The reflexed tip contains many small spermatogonial cells. Half way along the tract is a marked constriction, where the cells are indistinct. Thin sections in the electron microscope show that the spermatogonia are closely packed, have large nuclei, and cytoplasm full of ribosomes. There is a small central rachis. At the meiotic division, when the chromosomes are clearly distinguishable, spermatids are produced, and residual bodies are cast off which rid the cells of excess cytoplasm and ribosomes. Double membranes associated with 'fibrous bodies' become separated from them and form membrane specialisations which are almost spherical. These have long microvilli, electron-dense boundary membranes and inclusions. Each specialisation has a secondary, spherical, smooth-walled clear vesicle attached. This secondary vesicle is absent from *R. pellio*, the only other rhabditid sperm described. After the meiotic division the nuclear membrane is not reconstituted. The sperm are cuboidal, with few pseudopodia and some mitochondria, and with the membrane specialisations arranged around the periphery but not opening to the outside at this stage. There are no thin-walled, translucent vesicles as in the sperm of *Aphelenchoides blastophthorus* (Shepherd & Clark, *Nematologica* (1976) **22,** 1–9), nor are there any microtubules lining the outer membrane of the sperm as in *Heterodera* spp. (Shepherd, Clark & Kempton, *Nematologica* (1973) **19,** 551–560). The sperms are stored in the thin-walled seminal vesicle, demarcated by the constriction in the tract. The vas deferens, a glandular region of the tract, is initially thick-walled, with an occluded lumen, but then becomes thinner-walled, although still secretory, with a wide lumen. At the junction of this region with the cloaca there is a thick fringe of long microvilli which almost fills the lumen. (Shepherd and Clark)

Special techniques

A new intervalometer was made, that permits a wider range of filming speeds for cine-micrography of nematodes.

A film consists of separate photographs, so high-speed phenomena can be missed. To overcome this an image of the nematode is projected on a television monitor screen and a photocell placed over the area of interest. The output from the photocell is amplified and displayed on a recorder chart. The television camera enables low light intensities to be used, so that the nematodes are not disturbed. Brightness and contrast can be boosted to give light intensities on the screen suitable for the photocell to measure. Other advantages

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over cinematography are that recordings can be continued during long periods, expensive film is not used, results are obtained immediately and rapid pulsations can be monitored easily by increasing chart speed. First records of pump pulsation in *D. dipsaci* feeding on bean leaf epidermal cells are promising. (Seymour and Doncaster, with Minter, Electronics Workshop)

To study variations of internal pressure in nematodes and the cells of their host plants, glass microcannulae rigidly coupled to sensitive low-displacement electronic pressure transducers, were inserted into developing females of *Globodera rostochiensis* attached to potato roots. Initially body contents enter the cannula when the body wall is pierced which is counteracted by forcing body contents back into the body with a micrometer syringe. Possible osmotic interactions between body contents and the air-free distilled water that filled the recording system were avoided by filling the tip of the cannula with inert silicone oil. In this way realistic pressure records were obtained. The maximum pressure recorded was $9{\cdot}4 \times 10^4 Nm^{-2}$ (940 cm water) which was developed almost isometrically. The cyst wall withstands a tensile stress of about $5 \times 10^8 Nm^{-2}$ which is only 1% of the stress that collagen can endure. (Seymour)

When dilute ammonia solution (0·3 — 0·4 N) is added to some male nematodes in a drop of water the copulatory spicules are protruded. Once these are fully protruded the specimens can be killed, fixed and processed to glycerol in the usual way. The technique is especially useful for obtaining specimens with protruded spicules for observation with the scanning electron microscope. The dilute ammonia solution caused temporary protrusion of the mouth stylet of second stage juveniles and males of *Heterodera* and *Globodera* species. The stylet retracted if specimens were killed by heat but not if they were killed with iodine solution (0·1% iodine in 4% aqueous potassium iodide). This effect is useful because stylet length is used in separating some *Globodera* species and a protruded stylet is much more easily measured because its tip is not obscured by the head skeleton. (Hooper)

Population dynamics and population models

General. Nematodes are relatively immobile. Consequently nematode populations large enough to inflict economic injury on crops are usually slow to build up, much inbred and difficult to dislodge. Their life strategies vary greatly. Some complete several generations in a year and multiply more than a thousand times within a growing season. However, this is a far smaller rate of increase than that of viral, bacterial or fungal pathogens and of some insects. Populations of this kind of nematode, which may be described as exploiters, fluctuate greatly. They tend to survive the interval between outbursts upon weeds and other marginal hosts but some seem able to survive in soil for long periods without hosts. Other nematode species pass only one or two generations a year, often only one because of the short vegetative life of their host crops from planting to harvest. The observed increase is usually much less than 100 times and in cyst-forming species population fluctuations are limited largely because not all eggs hatch when a host crop is grown and even fewer hatch when it is withheld. Yet other nematode species have even longer generation times which may exceed 12 months and their numbers increase less than ten times a year.

Our knowledge of the population structure of most plant-parasitic nematodes is imperfect. Most sampling methods are subject to large errors and not all nematodes are extracted. Only in those species in which all or most of the eggs are retained in cysts or in those with recoverable egg masses, are resonably accurate estimates of egg population densities obtainable with present-day techniques. For no species do we have accurate assessments of age-specific mortality and its causes. Yet these might provide clues indicating why some species are serious pests and others not.

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Field experiments on larger, mobile pests (insects, mammals, birds) are complicated by emigration and immigration. Consequently many fundamental studies can be done only in artificially closed systems or in very large plots. With nematodes, meaningful population studies are possible in pots and small field plots outdoors. Large plots are inappropriate because populations are usually patchy and the multiplication rate decreases as the population density increases. The average rate for the field as a whole gives no indication what is happening in its parts. If, for example, the infestation overall is slight, but made up of a few patches of high density, the average may suggest that the multiplication rate is small, which is misleading.

Agriculturally, the most convenient time scale in population work is one year. For many species one year is equivalent to one generation but the general form of the population curve is unaltered when there are more.

The observed multiplication rate per generation or per year is usually far less than the reproductive potential of the species because eggs fail to hatch, larvae fail to find their hosts and enemies, parasites and competitors take their toll at each stage. Because of the pyramidal age structure of populations, with many juveniles at the base and few adults at the apex, enemies that kill or competitors that eliminate a proportion of juveniles tend merely to remove individuals surplus to the carrying capacity of their hosts. In contrast, enemies and competitors that kill the few surviving females or seriously decrease the number of eggs they produce have, relatively, a much greater impact.

In practice multiplication at high densities is restricted by the limited food supply. The most familiar mathematical description of such density dependent regulation is the logistic equation. From this we may derive the difference equation relating final to initial egg densities.

$$P_f = \frac{aP_i}{1 + (a-1)\, P_i/E_l} = amP_i \qquad \ldots\ldots\ (1)$$

where P_i is the population density at planting and P_f that after harvest, a is the maximum rate of increase, E_l is the equilibrium population density and $m = 1/(1 + (a - 1)\, P_i/E_l)$. For cyst-nematodes we need to take into account the fraction of eggs that does not hatch, C_p, i.e.

$$P_f = amP_i\,(1 - C_p) + C_pP_i$$

Computer models. Most nematodes attack roots and their main effect is to decrease the size of the root systems. Only in crops like sugar beet is yield related directly to root size. In other crops the yield of leaf tissue, grain or tubers is affected indirectly or is the result of climatic and other stresses, mostly operating after root size is determined. Similarly, for nematodes attacking plant parts other than roots, yield of harvestable produce is often only indirectly related to the severity of attack. The minimum yield found at high nematode densities is likely to consist of parts of the plant which cannot be utilised by the nematode. In our modelling, which mainly concerns roots, this is of no interest and the minimum root size is taken as zero.

In an early computer model (Jones, Parrott & Ross, *Annals of Applied Biology* (1967) **60,** 151–171) we tried to predict population changes of *G. rostochiensis* under different rotations when susceptible potatoes, resistant potatoes or crops other than potatoes were grown, and to simulate the increase in frequency of a resistance-breaking gene when resistant potatoes were grown. This model did not allow for the damage done to the root system, i.e. to the food supply as nematode density increases. Equation (1) has been derived from first principles and the effects of nematode damage incorporated (Jones & Kempton (1977) In: *Plant nematology* Ed. J. F. Southey, *Ministry of Agriculture, Fisheries*

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and Food Technical Bulletin No. 7, 3rd edition revised). The term m in equation (1) now becomes:

$$m' = \frac{1}{1 + (a' - 1)\, P_i z^{-P_i/cE_l}}$$

where a' is the observed maximum increase rate, c is a constant representing the tendency for the root to compensate damage done and z is another constant representing the fraction of resources left after one nematode has fed. The value of c ranges from 1·05 to 1·15, and that of z is slightly less than 1 (see Seinhorst 1965, *Nematologica*, **11**, 137–154). At equilibrium $z_l = z^{E}{}_l = (E/c)^{1/E}$ where the observed equilibrium density E is now expressed as a fraction of E_l, i.e. represents the root size at equilibrium expressed as a fraction of maximum root size. If for example $E = 1/4$, $c = 1$, then $z_l = 1/256$.

The model has also been extended to include the effects of nematicides applied at or before planting and of competition between *G. rostochiensis* and *G. pallida*, which do not interbreed. It is also being extended to apply to other species of cyst-nematode and to include the effects of enemies that attack females. The last is to take into account fungi such as the one that limits numbers of *H. avenae*. Methods of stochasticising the model are being explored so that it will more nearly represent results from fields rather than small plots. (Jones, with Kempton, Perry and Ross, Statistics Department)

Competition between species of root-lesion nematode. Populations of *Pratylenchus* spp. usually consist of a mixture of species. To study competition between them preliminary experiments were done on sweet corn roots in sterile culture. Different ratios of pairs of species, each obtained from single female cultures, were incubated at 25°C for 12 weeks when final ratios were determined.

When pairs of parthenogenetic species were put together: *P. pinguicaudatus* with *P. neglectus* and *P. pinguicaudatus* with *P. thornei*, the population balance always moved towards *P. pinguicaudatus*. When *P. pinguicaudatus* was mixed with bisexual *P. penetrans* or *P. fallax*, the last two took over when they comprised more than 30 to 40% of the initial mixture. *P. pinguicaudatus* maintained itself only when it greatly predominated. It seems that none of these pairs are able to coexist in the cultures. (Webb)

Disappearance of females of *Heterodera avenae* from cereal roots. The development of females of *Heterodera avenae* was followed on cereal roots. At 13°C, females ruptured the root cortex 21–56 days after planting and were liable to attack by the *Entomophthora*-like fungus (ELF) in the following 2–25 days (*Rothamsted Report for 1975*, Part 1, 185). Four days after infection, the nematode cuticle was destroyed and the body filled with resting spores; by the 7th day attacked females had disintegrated and disappeared. A time-lapse ciné film showed that the females and the mass of resting spores produced from them had probably been eaten by enchytraeid worms.

Initially, infection of nematode females seems to arise from resting spores the abundance of which depends on conditions in the previous year. Thereafter, the fungus is spread by infective spores produced on diseased nematodes (*Rothamsted Report for 1975*, Part 1, 202). Resting spores were killed by formalin at 2988 litres ha^{-1} after which no females became infected and none disappeared from roots. In soil from Butt Close, Woburn 61% of females were infected by the ELF but when the soil was mixed with formalin-treated soil, at 3:1, 1:1 or 1:3 by volume, the infection rate was halved, there being little difference between the mixtures. When diseased females were removed from roots before they produced infective spores, the rate of infection decreased from 61 to 17%. Newly-produced infective spores seem to kill more females than overwintered resting spores possibly because of their proximity to other females on the nematode-infested root system.

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As females infected by the ELF disappear rapidly from soil, attempts were made to assess infection rates in the field more accurately by collecting samples weekly or more often.

The number of eggs with second-stage larvae indicates the number of healthy eggs in the population, for rarely do more than 15% of fully embryonated eggs contain fungal hyphae. However, eggs in all stages of embyronic development can be attacked by another fungus, *Verticillium chlamydosporium*. On water agar, eggs containing second-stage larvae were killed by *V. chlamydosporium* in four days at 19°C, leaving empty shells containing a few strands of hyphae. Hence, counts of eggs containing second-stage larvae may overestimate numbers if this fungus is in many cysts. Observations at laboratory temperatures on single cysts extracted from soil indicate that, when *V. chlamydosporium* is in a cyst, all the eggs it contains are eventually killed but how fast the fungus develops at soil temperatures overwinter is unknown. During the exceptionally dry summer of 1976, the ELF killed few females on roots of cereals at Woburn Farm and infection with *V. chlamydosporium* was rarer than in 1975. By early July when females would have been producing eggs, cereal crops were dead and consequently many cysts contained few eggs. Nevertheless in 1976 *H. avenae* populations increased (3·0 ×) compared with a decline (0·8 ×) in 1975 when fungal parasites were more active. (Kerry, Crump and Mullen)

Nematodes as enemies of insects and slugs. Nematodes that parasitise insects and debilitate, sterilise or kill their hosts, play a part in the regulation of numbers and are potential agents for biological control of pest species. In Britain, little is known of nematodes parasitising agricultural pests. Therefore a survey was begun of nematodes parasitising economically important soil invertebrates. Many samples of wireworms, leather-jackets, cutworms, slugs, the glasshouse fly (*Bradysia paupera*), carabid beetles and hibernating ladybirds were dissected. Perhaps because of the exceptionally dry conditions in 1975, the only parasitic nematodes found were *Tripius sciarae* (introduced into a Rothamsted greenhouse ten years previously) in *B. paupera*, and *Angiostoma limacis* in several species of slug.

Adults and post-infective stage larvae of *A. limacis*, previously known only as the adult in the crop of two species of *Arion*, were found in six species belonging to three genera. Previously infections were thought to be local but six out of nine samples of slugs from Scotland and England contained the nematode, and the average rate of infestation was 17%. Adults, usually found in the crop, lay eggs which pass out in the faeces. Development of eggs until hatching has been followed with time lapse photography. The rhabditiform larvae (apparently first stage) are bacterial feeders able to develop in slug faeces to the third stage, which is the earliest found in the gut of the slug. The third stage larvae seek or are passively ingested by slugs and develop to adults. The effect on the host is being studied. (Oswald)

Maximum yields of potatoes on land infested with potato cyst-nematodes

An opportunity was taken in 1976 to modify a long-term experiment and two others with the object of measuring some of the factors influencing yield of potatoes on land heavily infested with potato cyst-nematodes. Earlier unpublished work showed the great effect of extra nitrogen and the slight effect of extra P and K on the yield of potatoes in heavily infested land (Table 2). Other work on the effect of nematodes on potatoes is summarised in Table 3 and in Tables 8, 9 and 10 (pages 215 and 216).

Potatoes were grown continuously on the long-term site on light sandy soil at Woburn during the previous ten years. Before that the land was grass or lucerne for 15 years. When

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TABLE 2

Effects of FYM, nitrogen, phosphorus and potassium on potato yields: comparison of one site infested with potato cyst-nematode (G. rostochiensis *Ro1*) *with three uninfested sites*

	Total tubers t ha⁻¹ FYM t ha⁻¹ 0	12·6	25·1	50·2	SE	Mean	SE
	Infested (1 site)						
Mean	23·4	26·4	29·1	34·1	±0·92	28·2	
O	15·7	17·5	20·8	29·6	±1·31	20·9	
N	31·1	35·2	37·4	38·7		35·6	
OvN	+15·4	+17·7	+16·6	+9·1	±1·84	+14·7	±0·92
OvP	+1·6	+1·1	+0·4	−0·2		+0·7	
OvK	+2·9	−2·3	−0·2	−2·8		−0·6	
	Uninfested (3 sites)						
Mean	29·6	32·4	34·9	36·5	±0·60	33·3	
O	28·0	30·7	33·9	35·6	±0·85	32·1	
N	31·1	34·0	36·0	37·5		34·6	
OvN	+3·1	+3·3	+2·1	+1·9	±1·20	+2·5	±0·60
OvP	+2·2	+3·1	+2·6	+3·0		+2·7	
OvK	+4·1	+3·1	+1·7	+1·2		+2·5	

TABLE 3

Effect of Globodera rostochiensis *on the potato plant*

Roots	
Smaller, more branched	
Search smaller soil volume	
Take up water and nutrients less efficiently	
Water and nutrients shunted to exterior by female nematodes	
Haulms	
Fewer, shorter stems	
Same number of smaller leaves per stem	
Total N, P, K, Mg, Ca, Na	depressed
Concentrations	
N	unchanged
P, K, Mg	depressed, especially K
Ca, Na	increased
Dry matter	increased
Water usage	less efficient

potatoes were first grown, infestation with *G. rostochiensis* was sparse and patchy. Later it became apparent that *G. pallida* Pa3 was also present, perhaps confined initially to one plot or one row of plots. The yield of the first potato crop was large, averaging about 40 t ha^{-1}. In the second year the yield of the susceptible variety Pentland Dell on plots not treated with nematicide fell to less than half, and in the subsequent years the crop was usually a total failure. Yields of the resistant variety, Maris Piper, remained large for five years by which time *G. pallida* Pa3 had multiplied and begun to decrease yields of Maris Piper, though never so much as those of Pentland Dell, a variety very sensitive to attack. By the end of 1975 all plots were heavily infested with either *G. rostochiensis* Ro1 or *G. pallida* Pa3 except where aldicarb was applied. Plots receiving aldicarb in 1976 had the benefit of the residual effects of previous nematicides applied to the same plots. Also, aldicarb is a systemic aphicide and some small part of the yield increase may have come from controlling insects and nematodes other than the potato cyst-nematode.

During all previous years, the site was farmed according to standard farm practice for potatoes and the experiments on it tested the effects of irrigation, a nematicide and a resistant or a susceptible variety grown continuously or alternately. In 1976 the plots were split to test standard against enhanced farm practice according to the ADAS blue-

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print for potatoes (Evans, *Outlook on Agriculture*, (1975) **8**, 184–187). Details are in Table 4 and some results in Table 5. The variety Pentland Crown, which withstands

TABLE 4

Treatments applied to long-term site where components of yield were tested in the presence of potato cyst-nematodes

Irrigation	None	Full
Nematicide	None	Aldicarb 5·6 kg a.i.ha^{-1}
Variety	Pentland Crown (susceptible)	Maris Piper (resistant to *G. rostochiensis* Ro1 only)
Farm practice	Standard	Enhanced
Fertiliser to seed bed (13–13–20)	1883 kg ha^{-1}	1883 kg ha^{-1}
Top dressing	None	125 kg N ha^{-1} in May as 'Nitro-Chalk'
Seed	Normal size 50 cm apart	Large seed 25 cm apart
Burning off haulms	Mid-September	Late October

TABLE 5

Main effects of treatments on yield of potatoes on land infested with potato cyst-nematodes, means of Pentland Crown and Maris Piper

	†Ware tubers, t ha^{-1}					
	*SFP	EFP	0	Aldicarb	Means	SED
Unirrigated	13·4	18·1	7·5	24·0	15·7	±1·73
Irrigated	32·9	46·8	24·7	55·1	39·9	(48)
0	12·9	19·2				
Aldicarb	33·5	45·0				
Means	23·2	32·4	16·1	39·5		
SED	±1·31 (48)		±1·29 (48)			

		Irrigation Farm practice	Irrigation Aldicarb	Aldicarb Farm practice
SED (24)	Horizontal			1·58
	Vertical	±1·86	±1·83	1·60
	Horizontal and diagonal	±2·17	±2·16	
	Diagonal			1·84

† Retained by 3·8 cm riddle.
* SFP, standard farm practice; EFP, enhanced farm practice.

nematode attack far better than Pentland Dell, yielded on average one third more saleable potatoes than Maris Piper. Irrigation and aldicarb alone increased yields greatly: together they increased it by 47 t ha^{-1}, a remarkable result achieved in an exceptionally dry year. Enhanced farm practice resulted in a smaller yield increase. The best yields on plots receiving the benefits of irrigation, nematicides and enhanced farm practice were Pentland Crown 81·3 t ha^{-1} total tubers 94% ware, and Maris Piper 68·0 t ha^{-1} total tubers 93% ware, the averages for these plots being 76·3 and 93%, and 58·3 and 89% respectively. Plots receiving none of these treatments yielded only 7·2 t ha^{-1}. Crop sequence, i.e. planting after Pentland Dell (susceptible to both cyst-nematode species) or after Maris Piper (resistant to *G. rostochiensis*) only, had little effect, as plots are now infested with either or both species of potato cyst-nematode.

Whether the plots which gave very large yields will leave larger populations of the nematodes than usual and whether aldicarb will have succeeded in controlling post harvest populations has still to be investigated. (Jones, Evans, Grant, Parrott and Berry)

Similar results were obtained in another 'blue print' experiment on a different infested field where the soil contained much more clay. Here too yields of Pentland Crown were

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increased greatly by the nematicide oxamyl at 11·2 kg ha^{-1}. Closer spacing of tubers and later destruction of haulms also increased the yield of plots that received oxamyl but extra fertiliser had little effect probably because of the exceptional drought: irrigation was not possible. (Whitehead, Tite and Finch)

In a further experiment on yet another infested field, the susceptible varieties Pentland Crown and Record were grown with and without aldicarb and with two rates of N, P and K fertilisers to represent standard and enhanced farm practice. Aldicarb doubled yields. Extra N increased yields of all plots as did extra K on plots not treated with aldicarb, supporting the hypothesis that K-uptake is important in plants heavily infested with nematodes. Extra P had no effect. (Evans and Grant)

The rotation-fumigation experiment

The aim of this experiment, now in its eighth year, was to see if a single fumigant treatment benefited succeeding crops in the rotation and to compare this with continuous treatments. At first 'D-D' (dichloropropene, dichloropropane mixture) at the rate of 448 kg ha^{-1} was the only soil fumigant, either applied before every crop in the rotation (potatoes, barley, sugar beet) or only once before a particular crop. Later, dazomet and benomyl were applied before every crop and in 1976 aldicarb was substituted for 'D-D'. Three nitrogen rates, appropriate to each crop, were applied. At the beginning, *H. avenae* nowhere exceeded 4 eggs g^{-1} soil and *G. rostochiensis* Ro1 averaged 27 eggs g^{-1}.

The annual application of dazomet has been the outstandingly successful (though expensive) treatment for yield improvement and nematode control. 'D-D' has often failed to benefit (particularly barley) in the year of application probably because it is somewhat phytotoxic. However, the beneficial residual effects of 'D-D' have been considerable for two years after application. Barley has responded best in this way, but potatoes have often been similarly improved. Benomyl has consistently improved potato yields by 50% but has had little effect on barley or sugar beet. On the whole, sugar beet has responded less favourably to treatments, perhaps because of the absence of nematodes harmful to the crop.

Both continuous dazomet and 'D-D' applications have most effectively controlled *G. rostochiensis* and *Pratylenchus* spp. *H. avenae* soon declined to almost undetectable numbers under the rotation alone. *G. rostochiensis* declines under successive non-host crops but recovers rapidly on potatoes planted in plots other than those treated every year with dazomet or 'D-D'. Even with these treatments three or four-fold increases occur though post-potato crop populations are much smaller than in untreated, single crop 'D-D', or benomyl plots. At the end of the experiment it should be possible to assess crop production and nematode control through three complete cropping cycles. (Williams, Beane, Parrott, Berry, Tite, Finch and Webb)

Trials with nematicides

Severe drought throughout the summer of 1976 not only stunted potato, sugar beet, onion and pea crops in our nematicide field trials but also greatly lessened nematode increase on them. As a result our trials were less informative than usual. Four potato trials at the Arthur Rickwood Experimental Husbandry Farm, Mepal, Cambridgeshire, using King Edward and Maris Piper potatoes were badly affected by drought and are not reported here. Our pea trial at Witham, Essex and one with spring-sown onions at Rothamsted were also badly affected. Five potato trials at Woburn using Pentland Crown potatoes and a sugar beet trial at Little Downham, Cambridgeshire, benefited from ample rain in September and October and yielded better than expected.

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Potato cyst-nematodes

Pot and field assessment of potential nematicides. Fifty-six pesticides were assessed as nematicides in pots of Kettering loam inoculated with *G. rostochiensis* Ro1. The potatoes grew well and potato cyst-nematode increased greatly on the roots of plants growing in untreated soil. The nematode also increased greatly in soil treated with compounds having proved or suspected activity against potato cyst-nematodes, probably because high soil temperatures accelerated their decomposition. However fensulphothion and 'AC 64475' (2-(diethoxyphosphinylimino)-1,3-dithietane) gave good control and thiabendazole and terbufos, previously known as 'AC 92100' gave outstanding control of the nematode (Table 6). Terbufos has not previously been reported as a nematicide.

TABLE 6

Effect of several pesticides on increase of potato cyst-nematode (G. rostochiensis *Ro1*) *on Arran Banner potatoes in pots of Kettering loam*

Pesticide	mg a.i. per 1500 ml soil	Solvent used	Nematode increase, times
Untreated	0	—	18·8
Aldicarb	7	water	17·1
Fensulphothion	7	acetone	3·7
'AC 64475'	7	acetone	2·9
Thiabendazole	7	water	0·8
Terbufos	7	acetone	0·3

'AC 64475', carbofuran and phoxim were further assessed as nematicides in a trial on Great Hill, Woburn. 'AC 64475' as 5% granules at 2·2 kg a.i. ha^{-1}, incorporated into the top 15 cm of the soil by rotavation, significantly increased the yield of Pentland Crown potatoes in soil heavily infested with *G. rostochiensis* Ro1 without increasing the nematode infestation of the soil (Table 7).

TABLE 7

Effect of three pesticides on yields of Pentland Crown potatoes and on potato cyst-nematode increase (G. rostochiensis *Ro1*)

Treatment	kg a.i.ha^{-1}	Tubers over. 3·8 cm diam t ha^{-1}	(nematode increase, times)
Untreated	0	7·7	(0·7)
'AC 64475'	1·1	12·0	(0·4)
	2·2	18·4***	(0·4)
	4·4	17·1**	(0·4)
Phoxim	5·6	10·7	(0·5)
	11·2	12·5	(0·5)
	22·4	15·2*	(0·4)
Carbofuran	1·4	10·4	(0·6)
	2·8	13·0	(0·6)
	5·6	17·8**	(0·5)
LSD (5%)		5·6	
(1%)		7·6	
(0·1%)		10·4	

*, **, *** Significantly greater than untreated at $P < 0·05, 0·01, 0·001$, respectively.

Control in successive susceptible main crop potatoes. In Butt Close, Woburn, in soil treated each year with Telone (dichloropropene) soil fumigant and oxamyl or oxamyl alone, potatoes susceptible to *G. rostochiensis* Ro1 were grown each year without in-

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creasing the nematode infestation in the top 20 cm of soil. Yields of tubers from treated plots were much greater than from untreated plots, which were severely damaged by the nematodes in 1975 and 1976. In all three years, fumigating the soil with 'Telone' in autumn increased yields of tubers obtained from plots treated in spring with oxamyl, probably by preventing nematode injury to roots in soil below 20 cm, which oxamyl does not usually penetrate (Table 8).

TABLE 8

Effect of oxamyl and oxamyl plus 'Telone' on yields of Pentland Crown potatoes (t ha^{-1}) and on nematode increase (times) when potatoes grown for three consecutive years on infested soil

Treatment	1974	1975	1976	Mean
Untreated	26·8 (4·0)	1·8 (0·7)	4·8 (0·5)	11·1
Oxamyl†	58·8 (0·8)	16·2 (0·9)	22·5 (0·6)	32·5
Oxamyl plus 'Telone'	68·8 (0·4)	21·7 (1·9)	32·4 (0·4)	41·0

† Oxamyl 5·6 kg ha^{-1}, 'Telone' 224 kg ha^{-1}

Integrated control of a potato cyst-nematode. An experiment to control *G. rostochiensis* Ro1 by a combination of nematicides, crop rotation and a resistant potato variety (Maris Piper) was started in 1972 on sandy loam in Stackyard, Woburn. The rotations are (a) resistant potatoes, sugar beet, barley, susceptible potatoes and (b) susceptible potatoes, sugar beet, barley, susceptible potatoes. The nematicides tested are the soil fumigants dazomet and 'Telone' applied in autumn or winter and the oximecarbamate oxamyl applied to the soil in spring before potatoes are planted. The rotations were completed on the second of the three series of the experiment in 1976 and the results show that nematicide treatment doubled the yield of tubers whether resistant or susceptible potatoes had been grown in 1973. Little nematode increase occurred in untreated plots and in treated plots nematode numbers decreased (Table 9).

TABLE 9

Yields of Pentland Crown potatoes and increase of potato cyst-nematode in soil treated with different amounts of three nematicides, following a three-course rotation beginning with resistant or susceptible potatoes in 1973

		Tubers over 3·8 cm diam. (t ha^{-1}) in 1976 (nematode increase, times)	
		Potato variety in 1973	
Treatment	kg ha^{-1}	Maris Piper (resistant)	Pentland Crown (susceptible)
Untreated	0	22·6 (1·4)	18·0 (1·3)
Dazomet	224	37·2 (0·9)	37·0 (0·3)
	336	37·9 (0·8)	39·0 (0·6)
	448	38·4 (0·5)	35·7 (0·7)
	672	40·5 (0·6)	41·8 (0·5)
Dazomet and Telone	224, 224	37·2 (1·2)	39·4 (0·4)
'Telone'	448	38·7 (1·1)	32·6 (0·8)
Oxamyl	5·6	40·0 (0·8)	38·1 (0·8)
Oxamyl and 'Telone'	5·6, 224	42·2 (0·8)	40·4 (0·9)
	Mean	37·2	35·8

LSD (5%)	vertical comparisons of yields only	4·5
(1%)		6·0
(0·1%)		7·9

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Methods of incorporating granular nematicides in soil. The effect of dosage and method of incorporating oximecarbamate nematicides in the soil on the control of *G. rostochiensis* Ro1 was further studied in Butt Close, Woburn, using 10% granules of aldicarb or oxamyl. Tuber yields were reduced by late planting with unsprouted potato setts and by severe drought. Yields of tubers were much larger in aldicarb or oxamyl treated soil but this is due in part to the fact that untreated plots were untreated plots in the 1975 experiment, whereas the treated plots had received some aldicarb treatment in 1975. Tuber yields were significantly larger following soil treatment with 6 or 12 kg a.i. aldicarb or oxamyl ha^{-1} than 3 kg a.i. ha^{-1}. Neither tuber yields nor nematode control differed significantly between the different methods used to incorporate the granules in the soil. There was no significant difference in tuber yields from aldicarb and oxamyl treated plots. Nematode numbers decreased slightly in untreated and treated plots the effect of aldicarb being slightly greater than oxamyl (Table 10).

TABLE 10

Effect of incorporating granules containing 10% aldicarb or oxamyl on yields of Pentland Crown potatoes and on potato cyst-nematode increase (G. rostochiensis *Ro1*); *means of plots receiving* 3, 6 *or* 12 *kg a.i. ha*$^{-1}$

Treatment: Where granules placed	Treatment: How incorporated in soil	Tubers over 3·8 cm diam. t ha^{-1}	Nematode increase, times
Untreated	Roterra to 10 cm deep	7·4	(0·7)
Soil surface	Roterra to 10 cm deep	24·9	(0·8)
Half to soil surface, half 5 cm deep	Roterra to 10 cm deep	22·8	(0·7)
Third to soil surface, third 5 cm deep, third 10 cm deep	Roterra to 10 cm deep	25·2	(0·8)
Half to soil surface, half 10 cm deep	Duck-foot tine harrow	26·5	(0·6)
Soil surface	Rotavator to 15 cm deep	27·3	(0·7)

Pea cyst-nematode (*Heterodera goettingiana*). In a multifactorial experiment at Witham, Essex, pea yields and pea cyst-nematode control were affected by date of sowing, dosage and method of incorporating oxamyl in the soil. Yields were largest and nematode increase least where peas were sown rather late and where oxamyl was incorporated in the top 15 cm soil by rotavation. Incorporating oxamyl granules in the soil by Lely 'Roterra' or applying them in the seed furrows during sowing had much less effect. Gas-liquid chromatographic analyses of soil cores showed that the L-bladed rotavator incorporated the granules fairly evenly to the nominal working depth of 15 cm, whereas the 'Roterra' left 60% of the granules in the top 5 cm of the soil. Rainfall from February to May was slight and chemical analyses of soil cores collected over this period showed that very little leaching of oxamyl occurred. It is not surprising, therefore, that rotavation of oxamyl into the soil increased pea yields more and controlled pea cyst-nematode better than either the 'Roterra' or seed furrow application. Degradation of oxamyl in this soil followed approximately first order kinetics with a half-life of 3–4 weeks. Oxamyl residues on peas at harvest were less than 0·01 $\mu g\ g^{-1}$, the limit of detection of the analytical method.

At Evesham, Worcestershire and Bidford-on-Avon, Warwickshire peas were grown for a second year in untreated plots and in plots treated with oxamyl or aldicarb as in 1975. As in that year, pea yields were very greatly increased by treating the soil with either

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TABLE 11

Control of pea cyst-nematode by granules containing 10% oxamyl or aldicarb applied to the soil in different ways

Treatment	kg a.i.ha^{-1}	Evesham Fresh peas (t ha^{-1})	Evesham Increase of nematode, times (1974–76)	Bidford Fresh peas (t ha^{-1})	Bidford Increase of nematode, times (1974–76)
Untreated	0	0·70	14·1	0·10	4·0
Oxamyl rotavated into seedbed	2·4	6·18	2·6	4·46	3·4
	4·9	8·20	3·0	5·77	2·6
	9·8	9·66	1·5	6·19	1·2
Oxamyl in seed furrows	2·4	4·78	8·6	3·60	12·0
	4·9	5·45	5·1	4·53	1·5
	9·8	5·29	3·5	5·37	1·9
Oxamyl (at sowing depth, 5 cm)	2·4	—	—	2·62	2·0
	4·9	—	—	3·07	1·9
	9·8	—	—	4·14	1·7
Aldicarb rotavated into seedbed	2·4	5·97	4·9	4·40	2·9
	4·9	8·10	1·2	5·48	2·5
	9·8	9·77	1·2	6·77	1·8
LSD (5%) Excluding untreated		1·11		0·85	
(1%)		1·52		1·15	
(0·1%)		2·05		1·53	

of these nematicides (Table 11). Pea cyst-nematode increase on peas was much reduced over the two years of this experiment by most treatments. Oxamyl or aldicarb increased pea yields more when rotavated into the top 15 cm of the soil than when placed in the seed furrows during sowing. At Bidford oxamyl at 4·9 or 9·8 kg a.i. ha^{-1} controlled the nematode as well when it was placed in the seed furrows as when it was rotavated in but at 2·4 kg the nematode population after harvest increased when it was placed in the seed furrows. At Evesham seed furrow application of oxamyl was inferior to rotavation, there being ten times as many pea cyst-nematode eggs in soil 10–20 cm deep after harvest following application of 4·9 kg a.i. oxamyl ha^{-1} in the seed furrows than following rotavation of the same amount into the seedbed.

These and earlier experiments lead us to conclude that pea cyst-nematode can be so well controlled by oxamyl or aldicarb that peas could be grown in much shorter rotations than at present without significant yield losses due to the nematode.

Peas usually follow a cereal crop in the rotation. With the help of fieldmen of several Pea Processing Companies in eastern England soil was collected from 17 fields which had grown a cereal crop in 1975 and which were due to grow peas in 1976. Treatment of these soils with oxamyl (which was watered in) increased the haulm weight of peas in pots on average by 20%. Sometimes the yield increases were much greater than this but sometimes yields were decreased. The increase in pea haulm weight following treatment of the soil with oxamyl was not related to the initial numbers of nematodes in the soil. The nematodes present were mainly *Pratylenchus* (on average 4000 litre^{-1} soil), *Tylenchorhynchus* and other tylenchid nematodes. Pea cyst-nematode was rare or absent.

Beet cyst-nematode (*Heterodera schachtii*). A good crop of sugar beet was grown in peaty loam lightly infested with beet cyst-nematode at Little Downham, Cambridgeshire. In untreated soil the nematode increased only a little on sugar beet roots but, in soil in which aldicarb or oxamyl had been rotavated in, its numbers decreased significantly. Severe drought in the spring and summer stunted growth and probably prevented many female nematodes being fertilised by males. Heavy rain in September and October benefited the

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crop and may have allowed nematodes to increase a little. The larger amounts of aldicarb increased sugar yield more than corresponding amounts of oxamyl, possibly because aldicarb is a better systemic aphicide (Table 12).

TABLE 12

Effect of rotavating granules containing 10% aldicarb or oxamyl into the top 15 cm of soil infested with beet cyst-nematode on sugar yield and on nematode increase

Treatment	kg a.i.ha^{-1}	Sugar (t ha^{-1})	Increase of nematodes, times
Untreated	0	6·84	1·4
Aldicarb	2·2	7·19	0·8**
	4·5	7·28	0·4***
	9·0	7·80**	0·4***
	17·9	7·86**	0·4***
Oxamyl	2·2	7·11	1·0
	4·5	7·17	0·8**
	9·0	7·72*	0·6***
	17·9	7·41	0·4**
LSD (5%)		0·66	0·5
(1%)		0·90	0·6
(0·1%)		1·21	0·8

*, **, *** Significantly greater or less than untreated at $P < 0{\cdot}05$, 0·01, 0·001, respectively.

Stem nematode. The control, by granules containing 10% aldicarb, of 'bloat' disease in onions, caused by stem nematode (*Ditylenchus dipsaci*) was further studied in autumn- and spring-sown onions on Great Field, Rothamsted. In autumn-sown onions (var. Imai Early Yellow) aldicarb granules applied in the seed furrows during sowing prevented serious loss of seedlings by 'bloat', whereas in untreated soil few seedlings survived. Yield of onions did not increase with increasing amounts of aldicarb nor did split application (half at sowing, half in early March) boost yields further. Five or 10 kg aldicarb ha^{-1}, whether applied all at sowing or half at sowing and half in March left unacceptably large aldicarb residues in the harvested bulbs (0·22–0·44 ppm). This year the number of stem nematodes left in the soil after harvest bore no clear relationship to treatment. There

TABLE 13

Effect of granules containing 10% aldicarb in onion rows on yields of autumn- and spring-sown onions

		Healthy onions (t ha^{-1})	
Treatment	kg a.i.ha^{-1}	Autumn-sown onions	Spring-sown onions
Seed furrows only	2·5	18·9	14·6
	5	18·1	13·5
	10	22·6	8·8
Seed furrows and top dressing	1·25 + 1·25	20·0	14·2
	2·5 + 2·5	20·1	14·5
	5 + 5	24·8	13·8
Untreated		2·0	8·4
LSD (5%) Untreated *v.* any other		7·1	1·6
(1%)		9·6	2·2
(0·1%)		13·0	3·1
LSD (5%) Treated only		6·7	1·6
(1%)		9·5	2·2
(0·1%)		13·7	3·1

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was little sign of 'bloat' in spring sown onions (var. Robusta) but aldicarb applied in the seed furrows or half in the seed furrows and half in early summer significantly increased onion yields, probably by preventing early attacks of stem nematode which may have killed seedlings before emergence. The largest dose of aldicarb applied in the seed furrows was probably phytotoxic for it did not increase the yield of bulbs. Again the larger amounts of aldicarb (5 or 10 kg in the seed furrows or 2·5 kg as a split application) left unacceptable residues in the harvested bulbs (0·24–0·86 ppm) (Table 13). (Whitehead, Tite, Finch, Bromilow, Webb, Humphrey, Fraser and French)

Thiabendazole as a wettable powder or granular formulation (240 mg a.i. in 5·5 litres soil) controlled stem eelworm on field beans when applied at planting time to soil inoculated with *D. dipsaci*, confirming last year's results (*Rothamsted Report for 1975*, Part 1, 203). When the same dose was applied as a soil drench to pots containing heavily infested 5-week-old bean seedlings, many of the plants recovered and were freed from infestation: evidently thiabendazole is a systemic nematicide. (Hooper)

Conjoint and other work

R. H. Bromilow worked in the Chemical Liaison Unit on the fate and distribution of nematicides in soil (page 183), M. A. Quigley, Open University, studied climatic factors and the distribution of cyst-nematodes. Several members of the Department lectured to post-graduate students at Imperial College Field Station and elsewhere.

Visits and visitors

Jane Anderson, G. C. Edwards, G. Innes, T. McBurney and D. Wisden were sandwich course students: Rosemary Brind, M. Hanoman, J. Smeathers and P. Walpole were vacation workers. F. G. W. Jones visited Cyprus, Turkey and the USA. Four members of the Department attended the 13th International Symposium of the European Society of Nematologists, Dublin in September. Dr. A. E. Steele, USA, Dr. B. C. Narayanaswamy, Bangalore, India, Miss D. A. Richardson, Chesterford Park Research Station, Dr. T. Alphey, Scottish Horticultural Research Institute, and Mr. G. B. Sykes, ADAS, Leeds, spent varying periods in the Department.

Publications

General Papers

1 Corbett, D. C. M. (1976) *Pratylenchus brachyurus*. *Commonwealth Institute of Helminthology Descriptions of Plant-Parasitic Nematodes*, Set 6, No. 89.

2 Hooper, D. J. (1976) *Trichodorus viruliferus*. *Commonwealth Institute of Helminthology Descriptions of Plant-Parasitic Nematodes*, Set 6, No. 90.

3 Jones, F. G. W. (1977) Pests, resistance and fertilizers. *Proceedings 13th Colloquium International Potash Institute, Izmir, Turkey*, 1976, pp. 111–135.

4 Jones, F. G. W. (1977) *Report on the golden nematode of potatoes in Cyprus*. Rome: FAO, 21 pp.

5 Jones, F. G. W. (1977) The environment and the nematode. *Proceedings of the Association of Applied Biologists. Annals of Applied Biology* **86,** 6 pp.

6 (Evans, A. A. F.) & Perry, R. N. (1976) Survival strategies in nematodes. In: *The organisation of nematodes*, Ed. N. A. Croll. London: Academic Press, pp. 383–424.

https://doi.org/10.23637/ERADOC-1-133

RESEARCH PAPERS

7 (BURDEN, D. J.), WHITEHEAD, A. G., (GREEN, E. A., MCFADZEAN, J. A. & BEER, R. J. S.) (1976) The treatment of soil infested with human whipworm, *Trichiurus trichiura*. *Journal of Hygiene, Cambridge* **77,** 377–382.

8 CLARK, S. A. & SHEPHERD, A. M. (1977) Structure of the spicules and caudal sensory equipment in the male of *Aphelenchoides blastophthorus* (Nematoda: Tylenchida, Aphelenchina). *Nematologica* **23,** 103–111.

9 CLARKE, A. J. & HENNESSY, J. (1976) The distribution of carbohydrates in cysts of *Heterodera rostochiensis*. *Nematologica* **22,** 190–195.

10 DONCASTER, C. C. (1976) Feeding of the stem nematode, *Ditylenchus dipsaci* on leaf tissue of field bean, *Vicia faba*. *Journal of Zoology, London* **180,** 139–153.

11 DONCASTER, C. C. & SEYMOUR, M. K. (1976) Defaecation in the stem nematode, *Ditylenchus dipsaci*. *Journal of Zoology, London* **180,** 9–14.

12 EVANS, K., TRUDGILL, D. L. & BROWN, N. J. (1977) Effects of potato cyst-nematodes on potato plants. V. Root system development in lightly and heavily infested susceptible and resistant varieties, and its importance in nutrient and water uptake. *Nematologica* **23,** 145–156.

13 EVANS, K. & FORDER, D. (1977) An automatic nematode counter. *Nematologica* **22,** 475–476.

14 GREEN, C. D.† (1977) Simulation of nematode attraction to a point source in a flat field. *Behaviour, Leiden* **61,** 1–17.

15 GREEN, C. D.† (1975) The vulval cone and associated structures of some cyst-nematodes (genus *Heterodera*). *Nematologica* **21,** 134–144.

16 GREEN, C. D.† (1976) Mechanical factors affecting the shape of round-cyst nematode females. *Nematologica* **22,** 71–78.

17 HOOPER, D. J. (1977) Spicule and stylet protrusion induced by ammonia solution in some plant and soil nematodes. *Nematologica* **23,** 126–127.

18 JONES, F. G. W. (1977) Temperature and development of *Mononchus aquaticus*. *Nematologica* **23,** 123–125.

19 JONES, F. G. W. & THOMASSON, A. J. (1976) Bulk density as an indicator of pore space in soils usable by nematodes. *Nematologica* **22,** 133–137.

20 KERRY, B. R. & JENKINSON, S. C. (1976) Observations on emergence, survival and root invasion of second-stage larvae of the cereal cyst-nematode, *Heterodera avenae* Woll. *Nematologica* **22,** 467–474.

21 MOSS, S. R., CRUMP, D. & WHITEHEAD, A. G. (1976) Control of potato cyst-nematodes, *Globodera rostochiensis* and *G. pallida*, in different soils by small amounts of oxamyl or aldicarb. *Annals of Applied Biology* **84,** 355–359.

22 MULVEY, R. H. & STONE, A. R. (1976) Description of *Punctodera metadorensis* n. gen., n. sp. (Nematoda: Heteroderidae) from Saskatchewan with list of species and generic diagnoses of *Globodera* (n. rank), *Heterodera*, and *Sarisodera*. *Canadian Journal of Zoology* **54,** 772–785

23 SEYMOUR, M. K. (1976) Pressure differences in adjacent segments and movement of septa in earthworm locomotion. *Journal of Experimental Biology* **64,** 743–750.

24 SHEPHERD, A. M. & CLARK, S. A. (1976) Structure of the anterior alimentary tract of the passively feeding nematode *Hexatylus viviparus* (Neotylenchidae: Tylenchida). *Nematologica* **22,** 332–342.

https://doi.org/10.23637/ERADOC-1-133

25 STONE, A. R., SOSA-MOSS, C. & MULVEY, R. H. (1976) *Punctodera chalcoensis* n. sp. (Nematoda: Heteroderidae, a cyst-nematode from Mexico parasitising *Zea mays*. *Nematologica* **22**, 381–389.

26 WHITEHEAD, A. G. (1976) The effect of formalin on potato cyst-nematode, *Heterodera rostochiensis*. *Annals of Applied Biology* **84**, 97–99.

† Now at National Vegetable Research Station, Wellesbourne. Warwick.

https://doi.org/10.23637/ERADOC-1-133