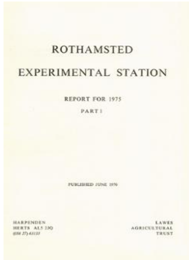
Report for 1975 - Part 1

Full Table of Content


ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1975
PART 1

Nematology Department

F. G. W. Jones

F. G. W. Jones (1976) *Nematology Department ;* Report For 1975 - Part 1, pp 191 - 212 **- DOI: https://doi.org/10.23637/ERADOC-1-132**

NEMATOLOGY DEPARTMENT

F. G. W. JONES

Staff

Head of Department F. G. W. Jones, SC.D.

Principal Scientific Officers
A. J. Clarke, PH.D.
C. C. Doncaster, B.SC.
D. J. Hooper, M.I.BIOL.
Audrey M. Shepherd, PH.D.
A. G. Whitehead, PH.D.
T. D. Williams, PH.D.

Senior Scientific Officers
R. H. Bromilow, PH.D.
K. Evans, PH.D.
M. K. Seymour, PH.D.
A. R. Stone, PH.D.

Higher Scientific Officers
Mrs. Sybil A. Clark, B.SC.
D. N. Greet, B.SC.
B. R. Kerry, PH.D.
Diana M. Parrott, B.SC.
D. J. Tite, N.D.A.
R. M. Webb, B.SC.

Scientific Officers
Mrs. Margaret M. Berry
A. J. Callewaert
D. H. Crump, H.N.C.
P. H. Finch, C.D.A.
Mrs. Janet E. Fraser
Mrs. Eileen M. French

Assistant Scientific Officers
J. Beane
Mrs. Janet A. Cowland
Jean E. Firth
Carole A. Grant
Judith A. Hennessy
P. Humphrey
Susan L. Jenkinson
Mrs. Lynne C. Hingston
M. A. Lane
Clare Osbond
Mrs. Janet A. Rowe
Lesley Swain

Temporary Workers
M. R. Bridgeman, B.SC.
J. Franco, ING.AGR.
W. J. C. Oswald, B.SC.
P. A. Roberts, B.SC.
Mrs. Jean M. Welbank, M.A.

Personal Secretary
Mrs. Elizabeth M. Brall

Shorthand Typist
Mrs. Helena M. Cairns

Laboratory Attendants
A. Duffus
Mrs. Phoebe M. Smith

Introduction

The Department studies nematodes, minute unsegmented round worms, that are common in soils and are often called eelworms. Some species attack crops, principally their root systems, stunt growth and diminish yield. Usually great numbers are required to do harm but small numbers of those species that transmit important viruses may do much damage. It is essential that the Department should be able to identify harmful species for which slide and other collections are maintained. In this and in other work we collaborate with the Agricultural Development and Advisory Service (ADAS), with the Commonwealth Institute of Helminthology and with nematologists abroad. Ability to identify is based on detailed studies of particular groups, for example the economically important cyst-nematodes (p. 192). To understand nematodes better their internal structures and the way they function are also studied (p. 193). All nematode problems in crops are related to the numbers present. Hence populations, their composition in terms of closely allied species (sibling species) and races (pathotypes) which behave differently on resistant cultivars are important parts of our work (p. 195). For the most part we study model systems such as potato cyst-nematodes and the potato crop with the intention of probing deeper than would be possible if we worked on all nematode pests of all crops. The greater understanding of one or a few systems can then be transferred to other situations. Nevertheless we also investigate the nematodes of particular crops, for example cyst-nematodes in cereals (p. 200), stem nematodes in field beans (p. 202) and root-

https://doi.org/10.23637/ERADOC-1-132

lesion nematodes in cereals and in maize (page 203). Lastly the Department has a powerful team working on the control of nematode populations by nematicides (page 203). The section on this work contains tables useful to farmers, ADAS and manufacturers of nematicides. Joint work with the Chemical Liaison Unit, which includes a member of our staff, concerns the fate and distribution of nematicides in soil. One object of this cooperation is to improve kill and decrease the amount of nematicide applied by securing better distribution (page 174).

Taxonomy

Identification and classification of cyst-nematodes. Cyst-nematodes are important pests of a number of British crops, of crops in temperate regions generally and also in tropical and sub-tropical areas where the climate is moderated by altitude. Distinguishing and classifying them is a difficult task because they are all similar in all stages and diagnostic characters are few.

Scanning electron microscope studies of second-stage juveniles in five of the genera of Heteroderidae showed that *Meloidodera*, *Atalodera* and the round-cyst members of the genus *Globodera* (formerly *Heterodera* (*Globodera*)) all have the basic hexaradiate lip pattern of the Tylenchida with distinct sub-median and lateral lip sectors surrounding a central oral disc or plate. *Meloidodera* is the most primitive. The female retains the cuticular annulation of the larvae, has an equatorial vulva and does not form a cyst. *Atalodera* also does not form cysts but has other more advanced characters. This suggests that in their head characters round-cyst nematodes are the most primitive of cyst-nematodes. The other non-cyst forming genus examined, *Cryphodera*, has a lip pattern which can be derived from the basic hexaradiate form while *Sarisodera*, a cyst-forming genus distinct from *Heterodera* and *Globodera* also has a distinct pattern which can be derived from the basic form. *Globodera punctata* and allied species have a similarly distinct lip pattern. Phylogenetically *Meloidodera* represents the stem form from which the *Cryphodera–Zelandodera* line, the *Globodera–Heterodera* line, *Sarisodera* and the *punctata* group have all evolved independently. Earlier work (*Rothamsted Report for 1974*, Part 1, 175) showed there are a number of distinct lip patterns among *Heterodera* species, in which the oral plate is extended dorso-ventrally and carries different types of ornamentation, whereas the sub-median lips are lost as distinct structures. When *Heterodera* species are classified according to lip pattern the groups conform to those derived from other characters. One group, the *H. cacti* group, has a lip pattern intermediate between the basic hexaradiate pattern and those of the other *Heterodera* spp. The cysts of this group are also intermediate in having circular fenestration and sometimes also have a small vulval cone. This group may represent or be derived from species linking *Globodera* and *Heterodera*. (Stone and Rowe)

Because of these differences and other morphological and biological ones, the sub-genus *Globodera* is elevated to generic rank. It now contains all the round cyst-nematodes, except *H.* (*G.*) *punctata* and related species which will be assigned to a new genus distinguished by spherical to pear-shaped cysts with a circular fenestra surrounding the anus. Species with lemon-shaped cysts remain in the redefined genus *Heterodera*. A new *punctata* group species is being described from permanent grassland in Canada. (Stone, with Dr. R. H. Mulvey, Biosystematics Research Institute, Ottawa, Canada)

During the year, *H. cruciferae* was redescribed and a lectotype designated. A new species injurious to a maize in Mexico was found and work was begun on a new species of *Heterodera* parasitising sugar cane in Lucknow (with Dr. S. R. Misra, Indian National Sugarcane Research Institute). Another *Heterodera* species, remarkable for its large carrot-shaped cysts and the very short tail of second stage juvenile may

https://doi.org/10.23637/ERADOC-1-132

prove to be the rare and inadequately described *H. 'methwoldensis'*. (Stone, with Mr. G. Murdoch and Mr. L. J. Coppock, ADAS)

Form and function

Laimaphelenchus penardi. Although *Laimaphelenchus* spp. are thought to be predaceous nematodes, two parthenogenetic populations of *L. penardi* reproduced slowly in cultures of the fungus *Botrytis cinerea*. Progeny from the cultures did not attack or feed on *Aphelenchoides blastophthorus* or *Caenorhabditis* spp. They reproduced parthenogenetically because males were absent.

In *Laimaphelenchus* spp. the ventrally curled tail has four caudal tubercules each bearing a rosette of 12–15 finger-like processes about 1 μm long and 0·2 μm in diameter. Because the processes are small and delicate, their preparation for scanning electron microscopy is difficult but by depositing on specimens infiltrated with epoxy resin a gold layer ten times the thickness of that conventionally used, micrographs magnified up to 40 000 times were obtained. Particles become attached to the tubercules which do not move independently of each other. The tubercules and their rosettes are not prehensile and the rosettes are not suckers: they do not adhere to glass fibres as do the caudal suckers of some Plectids. Nevertheless, once they are attached to objects the worms have difficulty in freeing their tails. Presumably the curled tail and its tubercules with their rosettes serve to anchor the worms in their natural habitat. (Hooper and Stone)

Ultrastructure of a passively-ingesting nematode, *Hexatylus viviparus*. Electron microscopy has revealed unusual features in the structure of the anterior alimentary tract of this nematode which ingests food passively from fungal hyphae (*Rothamsted Report for 1974*, Part 1, 179). The oesophagus is a straight tube with a very narrow, oval-shaped, cuticle-lined lumen, of the same cross-sectional area as the stylet lumen (about 0·02–0·03 μm^2). At no point is the lumen triradiate, and so it cannot enlarge to form a pumping mechanism. The oesophagus leads, via the oesophago–intestinal valve, into an anterior intestinal region which also has a narrow lumen (about 1 μm in diameter) lined with short microvilli. This region was previously described as a posterior oesophagus until Nickle (*Proceedings of the Helminthological Society of Washington* (1968) **35**, 154) postulated that it might be intestinal. The anterior intestine leads into the mid-intestine, which has a much wider lumen lined with microvilli that, unlike those of the anterior intestine, have a sculptured outer coat. The oesophageal glands lie alongside the anterior intestine and the gland ducts pass up through the oesophageal tissue. The two subventral gland ducts enter the oesophageal lumen just in front of the oesophago-intestinal valve and the dorsal gland duct enters just behind the stylet base. There is no musculature or other contractile tissue associated with the oesophagus.

The position of the nerve ring in this nematode is unusual in being circum-intestinal, encircling the anterior intestine just behind the oesophago–intestinal valve. There are four cephalic papillae at the tip of the head which is flattened and has only a delicate head skeleton. The six labial papillae surround the stoma. The two amphids are slightly dorso-lateral in position and each has a large amphidial gland associated with it. There is a well-developed enteric nervous system.

At the front end of the nematode the excretory system consists of a single canal running up the left side and opening to the exterior at the excretory pore which lies ventrally behind the nerve ring. The canal extends forward to just behind the base of the amphidial gland, about 15–20 μm from the tip of the head. Behind the excretory pore the canal leads into a much enlarged excretory gland which occupies about a third of the volume of the body cavity in this area. The gland is spindle-shaped, about 70–80 μm long and 20 μm in

https://doi.org/10.23637/ERADOC-1-132

diameter at its widest point, with a very vacuolated cytoplasm, some rough endoplasmic reticulum, and a large nucleus. The excretory canal passes through the gland and continues backwards. The wall of the canal contains smooth endoplasmic reticulum, and the duct itself is cuticularised from the pore to the middle of the excretory gland. (Shepherd and Clark)

Accessory reproductive structures of *Aphelenchoides blastophthorus* and *Rhabditis oxycerca*. The accessory reproductive structures on the male tails of *Aphelenchoides blastophthorus* and *Rhabditis oxycerca* were examined using the transmission and scanning electron microscopes. *A. blastophthorus*, with no copulatory bursa, has three pairs of papillae. The adanal and mid-tail papillae are similar, each having a nerve supply which opens to the exterior through a pore. The pore is formed in a mound of cuticle the surface pattern of which is disordered. The third pair near the tail tip have a different structure.

In *R. oxycerca* the papillae are on the small bursa. Their structure is similar to that in *A. blastophthorus* with a nerve crossing the thickened cuticle of the bursa and surfacing on a small papilla pierced by a pore which, however, is not surrounded by disordered cuticle. Below and in front of the cloaca, in the mid-body line, is a larger disc-shaped papilla.

The paired spicules of both *A. blastophthorus* and *R. oxycerca* are similar to those of other nematodes with a central nerve surrounded by a scleroprotein sheath. In *A. blastophthorus* each thorn-shaped spicule has a longer dorsal and a shorter ventral limb and dendrites come to the surface on the inner and outer edges of the last third of the dorsal limb. There is no gubernaculum. The spicules are separated by a cuticular guiding bar which extends from the dorsal wall of the cloaca and serves to guide them in and out of the cloaca. When the spicules are protruded it pushes the dorsal limbs apart so that the spicules do not form an enclosed tube. Although the ventral limbs are closely applied seminal fluid escapes through the gap between the dorsal wings. Two innervated cuticular processes project from the lateral walls of the cloaca.

The spicules of *R. oxycerca* are long and slender with slightly incurved limbs; each ends in a fine point. The sclero-protein sheath is thin and extends only half way along the dorsal and ventral limbs. The spicule nerve is large and central. It divides and the branches travel up the dorsal limb to the tip. The tip has at least one pore but whether it connects with the nerve is uncertain.

The spicules are widely separated at their base but come closer together and are separated, as in *A. blastophthorus*, by a cuticular guiding bar projecting from the dorsal wall of the cloaca. The gubernaculum is a large 'U'-shaped structure which follows the shape of the spicules. The gubernaculum and guiding bar ensure that the spicules move smoothly in and out of the cloaca. When the spicules are protruded they fit together in the mid region but the ends spring apart. Also protruded with the spicules and dorsal to them is a cuticular structure bearing two innervated processes. (Shepherd and Clark)

Feeding and defaecation of *Ditylenchus dipsaci*. When *Ditylenchus dipsaci* feeds on bean-leaf epidermis, saliva is first injected into the food cell. Pressure in the cell then forces injected saliva, cell sap and any products of extra-oral digestion into the nematode. Passive feeding in this manner lasted between half a minute and half an hour by when pressures in the cell and nematode presumably became equal. The nematode then usually extended its feed by pumping, so reducing pressure in the food cell, for when *D. dipsaci* stopped feeding and withdrew, the cell took up liquid from its surroundings through the hole made by the nematode stylet. A cell could be fed on a second time within a few minutes and again generate enough pressure to 'force feed' the nematode but, about an hour after a cell was first attacked, the nucleus became rounded and enlarged

https://doi.org/10.23637/ERADOC-1-132

and no cell with such a nucleus was seen to be fed on. As in *Hexatylus viviparus*, the other nematode we have studied which feeds passively, the body of *D. dipsaci* was prone to kinking, suggesting that its pressure could drop considerably; nevertheless, feeding nematodes were not kinked and measurements of body length showed that a nematode was often shorter while it fed than afterwards. (Doncaster)

Changes of body length associated with defaecation were recorded on film and analysed. During feeding regular shortenings of the hind end of the body were accompanied by groups of a few defaecation periods. Each period began as the shortened hind body elongated, and consisted of several defaecation cycles. In each cycle the posterior rectum became dorsally bowed and, as it straightened, the rectal valve, rectum and anus opened. Faeces passed out irregularly while the rectum remained open and were forcibly expelled as it closed. Defaecation in *D. dipsaci* was intermediate between that of the high-pressure nematode, *Aphelenchoides blastophthorus* and the low-pressure passive feeder, *H. viviparus*. The main function of defaecation in plant nematodes is probably to excrete water. (Doncaster and Seymour)

Population studies

Pathotypes of cyst-nematodes. Populations of nematodes exist as a series of races or closely allied (sibling) species and mixed populations occur in many fields. The existence of allied species and races can sometimes be detected by differences of form discernible under the microscope. Often, however, the differences only become apparent because races (pathotypes) react differently to host plants with genes for resistance, i.e. some can multiply upon them and some cannot. For the present our work has concentrated mainly on pathotypes of potato cyst-nematodes and of cereal cyst-nematodes. This is because both groups are economically important pests and because plant breeders are engaged in the production of resistant varieties. Some are already on the market and it is

TABLE 1.

		Old nomenclature							
		British A, Dutch A, Hiltrup	Dutch B, Obersteinbach	Dutch C	Dutch F	Harmerz	British B	Dutch D	Frenswegen, Chavorney, Dutch E, British E
		New nomenclature							
		G. rostochiensis					*G. pallida*		
Differential host	Designation of host resistance	RO_1	RO_2	RO_3	RO_4	RO_5	PA_1	PA_2	PA_3
S. tuberosum tuberosum		*+	+	+	+	+	+	+	+
S. tuberosum andigena CPC 1673	$RO_{1,4}$	−	+	+	−	+	+	+	+
S. kurtzianum hybr. KTT 60-21-19	$RO_{1,2}$	−	−	+	+	+	+	+	+
S. vernei hybr. G-LKS 58.1642/4	$RO_{1,2,3}$	−	−	−	+	+	+	+	+
S. vernei hybr. $(VT^n)^2$ 62.33.3	$RO_{1,2,3,4}$ $PA_{1,2}$	−	−	−	−	±	−	−	+
S. vernei hybr. 65.346/19	$RO_{1,2,3,4,5}$	−	−	−	−	−	+	+	+
S. multidissectum P. 55/7	PA_1	+	+	+	+	+	−	+	+
S. vernei hybr. 69.1377/94	$RO_{1,2,3,4,5}$ $PA_{1,2,3}$	−	−	−	−	−	−	−	−

* +, able to reproduce −, unable to reproduce

https://doi.org/10.23637/ERADOC-1-132

important to know how their resistance will perform in different places and against what races of nematodes new resistance should be sought.

International collaboration on nomenclature. In the past confusion has arisen because the pathotypes found in different countries have been named either according to different systems or by the locality from which they came. Some of our effort has been directed to testing foreign populations so that the different nomenclatures could be equated, and for the last three or four years we have collaborated with Ir. J. Kort, the Netherlands, Prof. H. Ross and Dr. H. J. Rumpenhorst, West Germany, to secure an internationally-recognised scheme. The following was proposed at a meeting held in November 1975 at the Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Hackfrucht-krankheiten und Nematodenforschung, Münster, West Germany, and will be fully documented in Nematologica and in Potato Research (Table 1). In future pathotypes of *G. rostochiensis* are to be designated RO_1, RO_2, RO_3, . . . and those of *G. pallida* PA_1, PA_2, PA_3, . . . according to ability to multiply on chosen differential *Solanum* hosts. The resistance in the hosts is also designated in the same way. The scheme can be extended if new sibling species or new pathotypes of existing species are found. Six of the 11 resistant clones tested distinguished clearly between *G. rostochiensis* and *G. pallida*, providing further evidence of fundamental differences between the two species:

	G. rostochiensis	*G. pallida*
S. tuberosum ssp. *andigena* with gene H_3	+	–
S. vernei hybr. 65.346/19	+	–
S. vernei hybr. C 8099	+	–
S. vernei hybr. C 8087	+	–
S. spegazzinii hybr. 66.1044/112	–	+
S. oplocense hybr. J 7886	–	+

To keep the number of test clones small only one of these clones is included in the pathotyping scheme in Table 1.

In Britain both species of potato cyst-nematode *G. rostochiensis* and *G. pallida* occur. Currently available British resistant potato cultivars contain a major gene which confers resistance to *G. rostochiensis* RO_1 (formerly pathotype A) only. New varieties incorporating other forms of resistance are being bred in Britain and some are already available elsewhere. The other pathotype common in Britain is *G. pallida* PA_3 (formerly pathotype E). Populations of pathotype PA_1 (formerly British pathotype B) of the same species are widely scattered but uncommon. (Stone)

South American potato cyst-nematodes. Potatoes and their parasitic cyst-nematodes originated in South America. The populations and pathotypes now known in Europe are probably only part of the range of types existing in South America. We need to know more about populations there because, when cultivars resistant to European populations have been bred, new pathotypes may arise or may be imported which can multiply on the resistant cultivars. To study South American populations further, the typing of Andean populations from Colombia, Ecuador, Peru, Bolivia and elsewhere continues. In the Andes, north of 15·6° S only *G. pallida* seems to occur, but south of this latitude most populations are *G. rostochiensis* or a mixture of both. In that part of the Andes where they overlap the natural barriers (high mountain ridges, Lake Titicaca and the boundary between territories of the two main Indian tribes), which have only recently been breached by commerce, formerly restricted movement of tubers and nematodes and may have allowed the two species to develop in genetic isolation, but from a common ancestor.

However, distribution may also have been influenced by the reaction of potato cultivars

https://doi.org/10.23637/ERADOC-1-132

to day-length which seems to influence suitability as a host for potato cyst-nematodes. To test this effect the varieties Arran Banner (main crop) and Arran Pilot (second early) were grown in pots subject to day-lengths of 8, 12 and 16 h after inoculation with potato cyst-nematodes from three British populations (*G. rostochiensis* RO_1, *G. pallida* PA_1 and PA_3) and two Peruvian populations (*G. rostochiensis* from Puno and *G. pallida* from Otuzco). The plants grew very differently in different day-lengths, producing more roots and senescing later in longer days; Arran Pilot being an earlier variety senesced before Arran Banner. All populations produced more cysts on Arran Banner, although both varieties produced equal weights of root and Arran Pilot root systems contained more nematodes than Arran Banner 17 days after inoculation. The difference in numbers of cysts produced was probably influenced by changes in the sex ratio (males to females) which, on Arran Pilot, increased with day-length. The Peruvian *G. pallida* population produced many more cysts than all the others, under all conditions, and had the smallest sex ratio.

Clearly the day-length influences development of the nematodes in the roots of host plants, but it is not obvious from results obtained so far that the shorter day-lengths experienced north of latitude 15·6° S in Peru are *per se* responsible for the dominance of *G. pallida* in that region. (Evans and Franco)

Competition between *G. rostochiensis* RO_1 and *G. pallida* PA_3. Earlier work begun at Rothamsted and continued by ADAS through its Working Party for Potato Nematodes, showed that *G. rostochiensis* RO_1 is dominant in Scotland and south-eastern England and that *G. pallida* PA_3 is dominant in the Humber basin. Elsewhere the two occur together in varying proportions but in a manner which suggests that they cannot coexist. Both are now so widespread that fields infested mainly by one must be repeatedly challenged by chance introductions of cysts of the other.

Preliminary tests in pots containing a wide range of mixtures of the two types suggest that, in pots at least, *G. pallida* always out-competes *G. rostochiensis*. Evidence from a long-term field trial at Woburn where resistant and susceptible potatoes have been grown repeatedly on the same plots and where *G. pallida* PA_3 has established itself on those planted with the resistant cultivar Maris Piper, suggest the same outcome, for *G. pallida* has now invaded plots of susceptible potatoes where *G. rostochiensis* RO_1 was previously dominant. Whether *G. pallida* PA_3 is replacing *G. rostochiensis* PA_1 in Britain generally is unknown, but the increase in the acreage planted with Maris Piper, e.g. in the Fens, could hasten the switch from one species to the other.

Little is known of the mechanics of competition. *G. pallida* may hatch less freely and be adapted to somewhat lower soil temperatures (see p. 198) which would tend to make it more persistent. *G. rostochiensis* may be able to pass more generations but effectively it succeeds in passing only one and sometimes a partial second before potato crops mature.

Males of *G. rostochiensis* and *G. pallida* are known to be attracted to the females of both species. In tests on agar plates females attracted similar numbers of males of both species. However, time lapse photography showed that when the males were not of the same species as the females, the males, having reached them, moved away more frequently and further before being re-attracted than if the males and females were of the same species. In both situations the distance moved increased with time. Hence when females from both species were equally attractive and lying within the range of circling males, the males congregated around females of their own species. No differences were detected between the behaviour of populations of pathotypes of the same species. Unfortunately, this work threw no light on competition: it tends to confirm that selection of the correct mate occurs and is based on stimuli that arise when the male is in close proximity to the

https://doi.org/10.23637/ERADOC-1-132

female. It also confirms the separation of *G. rostochiensis* and *G. pallida* as distinct species. (Parrott and Berry, with Mr. K. M. Farrell, University of the West Indies, Trinidad)

Hatching of encysted eggs. Hatching tests were done on 12 *G. rostochiensis* and 14 *G. pallida* populations at 10, 15, 20, 25 and 30°C to determine whether they behaved consistently and whether there were any substantial differences between the two species which might help to account for differences in distribution. Seven *G. rostochiensis* and 12 *G. pallida* populations hatched most juveniles at 20°C but the remaining five of *G. rostochiensis* hatched best at 25°C whereas the remaining two of *G. pallida* did so at 15°C. At 25°C all but one of the *G. rostochiensis* population hatched more than 65% of their maximum hatches: only one of the *G. pallida* populations did so. This confirms that *G. pallida* hatches less freely than *G. rostochiensis* at higher temperatures and suggests that it is adapted to slightly lower temperatures. (Parrott and Berry)

Canonical variate analysis of juvenile and cyst measurements of 15 European populations. Eight populations of *G. rostochiensis*, six of *G. pallida* and a mixture of both, obtained from the United Kingdom, the Netherlands, Germany and Switzerland which include all of the recognised pathotypes were raised in standard conditions. The stylet knob shape of second stage juveniles and female colour were the most reliable characters for species identification, other characters gave an incorrect diagnosis of at least one population. This difficulty was overcome when more than one measured character was used.

Measurements of cysts and juveniles were first submitted to separate canonical variate analyses to choose axes (linear functions of the original variates) which maximised the between species variation compared with that within species. When positions of the populations on the first two axes were plotted *G. rostochiensis* and *G. pallida* were clearly separated on measurements of juveniles and cysts.

For juveniles, the first axis accounted for 80% of variation between groups, the main component being stylet length. The *G. rostochiensis* populations and *G. pallida* populations formed two separate groups with one *G. pallida* population, one *G. rostochiensis* and the mixed population lying between them.

For cysts, the first axis accounted for 64% of variation between groups. The two species were again well separated, the atypical *G. rostochiensis* population now clearly lying in the *rostochiensis* group, although the atypical *G. pallida* population still lay closest to the *rostochiensis* group but within the *pallida* group. The analysis was repeated on log cyst measurements when similar but better separation was achieved. The first axis could be equated with log $(abc^{-1}d^{-1})$ where a is fenestral width, b fenestral length, c anus to fenestra distance, and d number of cuticular ridges. Since c and d were strongly correlated, equally good separation of the populations and the species would be achieved using the variate log (abc^{-1}) which is similar to Granek's ratio bc^{-1}. The ratio (expressed as a percentage) of the between to the within population sum of squares for different measures were:

Measurement	Variance ratio %
Juvenile stylet length	71
Fenestral width a	43
Fenestral length b	40
log $(abc^{-1}d^{-1})$	56
log (abc^{-1})	55
bc^{-1} (Granek's ratio)	47

Mixed populations would be expected to vary more than pure ones. Except for the population known to be a mixture, which had the largest variance, all others had similar variances whether they lay near the centre of clusters or near the extreme. This tends to

https://doi.org/10.23637/ERADOC-1-132

confirm that populations other than the mixture were substantially pure. (Stone and Rowe, with Kempton, Statistics Department)

Effects of nematodes on plant growth and potassium uptake

Ten potato varieties (nine susceptible to potato cyst-nematodes and one—Maris Piper—resistant to *G. rostochiensis* RO_1) were grown on each of two sites, one free of and the other infested with *G. rostochiensis* RO_1. On the infested site, Maris Piper quickly grew away from all other varieties whereas the early variety Maris Peer grew poorly and died within 12 weeks of planting. Of the other susceptible varieties Pentland Crown tolerated the nematode best. Its haulms persisted as long as those of Maris Piper although never attaining the same ground cover. On the uninfested site, all varieties grew much better, with Maris Piper and Pentland Dell developing the best leaf cover. However, under the exceptionally dry conditions, no variety grew as well as expected. Maris Peer grew much better on the clean site, but again was the first to die.

Potato cyst-nematodes decrease uptake of nutrients by potato plants, especially of potassium. They also induce water stress and, since potassium is necessary for efficient water use by potato plants, part of this stress may be due to potassium deficiency. Potato plants (both infested and uninfested) were grown in a medium which was short of potassium and extra potassium was added to some of the pots, either to the growing medium or as a foliar spray. Water usage by all plants was monitored over a three-month period. Nematode-free plants grew better than infested ones and all plants grew better when extra potassium was given, best growth being when the potassium was applied to the nutrient medium. Although plants given potassium used more water they used it more efficiently, requiring less water per unit increase in either fresh or dry weight. When potassium was applied to the foliage, the plants used almost as much water per unit weight gain as plants given none. In spite of marked responses to extra potassium and poorer growth when infested by nematodes, plants did not use water less efficiently when infested with nematodes, a result contrary to expectation. (Evans)

Chemical studies on *G. rostochiensis*

The action of hypochlorites. Hypochlorites have been used as cheap nematicides and as hatching agents for cyst-nematodes, but neither role has been clearly defined. Weak solutions (28mM) of hypochlorous acid killed all the juveniles in *G. rostochiensis* cysts within 16 h. Neither chemical destruction of the cysts or of the eggs and juveniles which occurs in strong solutions, nor hatching were essential to the toxic action. The hypochlorite ion was less toxic than free hypochlorous acid. The latter is also a weak hatching agent; at the optimum concentration of 14mM, about 8% of the cyst contents are hatched. Hatching in hypochlorites is of two types. One occurs at low concentrations ($<$28mM) when the extent of hatching varies with the hypochlorite concentration and that of the cation present, but it is largely independent of the pH. Live juveniles are released under these conditions, but the maximum hatches obtained are about 10% of the cyst contents. The second type of hatching occurs in hypochlorite concentrations of 28–282mM, requires a pH $>$12, is largely independent of the cation present, and can release almost all (90–100%) the juveniles from the cysts. Hypochlorite solutions at pH 11–12 dissolve the cyst walls and liberate the contents as free eggs (95–100%) containing juveniles. If left long enough the juveniles disappear from the eggs. The egg shells are dissolved last possibly because they contain chitin. The optimum concentration for these effects is 226mM. (Clarke and Hennessy)

The sex attractant. Crude material was partially purified by column chromatography.

https://doi.org/10.23637/ERADOC-1-132

Evidence, so far, indicates that the attractant is a non-volatile, very weakly basic, highly polar compound. It is soluble in water but not in most common organic solvents. The elution volume of the attractant when chromatographed on a calibrated molecular-sieve column, suggests that, in the absence of special bonding effects, the compound has a molecular weight of about 400. At the concentrations tested, the attractant absorbs little light in the visible or u.v. regions, is ninhydrin negative, and does not give the reactions of a reducing sugar, either before or after hydrolytic treatment. (Clarke, Firth and Greet)

Carbohydrates as food reserves. To obtain information on food and energy reserves and their possible role in the energy requirements of hatching juveniles, the carbohydrate content of the cysts, eggs and juveniles of *G. rostochiensis* were studied.

Alkaline digests of *G. rostochiensis* cysts containing eggs yielded glycogen (1·4%), oligosaccharides (2·3%) and trehalose (5·3%). Glycogen was confined to the juveniles within the eggs and to cyst walls, whereas trehalose predominated in the perivitelline fluid (at a concentration of about 12% w/v). Ethanol extracts of ground whole cysts, also yielded glucose (0·5%), fructose (0·01%) and a small amount (0·2%) of an unidentified trisaccharide.

As trehalose is confined to the egg, trehalose determinations might be used to estimate the egg content of cysts; similarly trehalose liberated from hatched eggs might be used as a measure of the numbers of hatched juveniles. (Clarke and Hennessy)

Observations on cereal cyst-nematodes

Effects of autumn and spring-sown cereals and a nematicide on numbers in soil. The effects of cereals, Maris Ranger wheat, Maris Otter barley and Peniarth oats sown in autumn and spring and of an oximecarbamate nematicide, oxamyl, on numbers of cereal cyst-nematode, *Heterodera avenae*, were tested in a field trial at Woburn. Results are summarised in Table 2. The exceptionally dry summer weather led to poor cereal yields. Nevertheless, oxamyl greatly improved growth, especially of the oats, Despite a heavy invasion of the seminal and crown roots, notably those of the oats, which was similar in the autumn and spring sowings and with and without oxamyl, few females survived to produce new cysts because of attacks by fungi (see p. 201). Consequently the numbers of eggs remaining in the soil were little different from those at planting. (Beane)

TABLE 2

Mean effects of sowing time, nematicide (oxamyl) and cereal species on eggs of cereal cyst-nematodes in soil and juveniles in root systems

	Sowing			Oxamyl			Cereal				
	Autumn		Spring	With		Without	Wheat		Barley		Oat
Pre-crop eggs, g^{-1}	16		17	17		16	17		19		14
Juveniles, g^{-1} seminal root	199	**	264	207	*	254	155	NS	168	***	459
Juveniles, g^{-1} crown root	153	*	121	124	NS	150	98	NS	100	***	256
Post-crop, eggs g^{-1} soil	11	NS	13	13	NS	11	9		12	*	16
									***		

Comparisons between pairs horizontally: NS, not significantly different; *, **, ***, significantly greater than untreated at $P<0·05$, 0·01, 0·001, respectively

Residual effects of varieties and aldicarb. In 1973, a susceptible oat (Mostyn) and two

https://doi.org/10.23637/ERADOC-1-132

resistant varieties Nelson and Wiebulls w. 16840 were sown with and without aldicarb. (*Rothamsted Report for 1973*, Part 1, 163). In 1974, the site was sown with the susceptible oat variety Manod; no further chemical treatments were applied. Results are in Table 3.

TABLE 3

Residual effects of cereal varieties and aldicarb (1973) on Manod oats grown in 1974 and on numbers of eggs of cereal cyst-nematode in soil

	aldicarb (1973)			No aldicarb (1973)		
	Mostyn †(S)	Nelson (R)	W 16840 (R)	Mostyn (S)	Nelson (R)	W 16840 (R)
Plots with *H. avenae*						
Pre-crop, eggs g^{-1}	0·9	0·6	0·1	9·4	1·5	0·9
Post-crop, eggs g^{-1}	3·6	1·8	2·8	8·1	2·4	2·5
Grain, t ha^{-1}	2·30	2·29	2·40 (Mean 2·33)	1·92	2·17	1·88 (Mean 1·99)
Plots 'without' *H. avenae*						
Pre-crop, eggs g^{-1}	0·0	0·0	0·0	0·6	0·1	0·2
Post-crop, eggs g^{-1}	0·0	0·0	0·1	1·7	0·2	0·0
Grain, t ha^{-1}	2·38	2·16	2·31 (Mean 2·28)	2·51	2·36	2·62 (Mean 2·50)

† S, susceptible; R, resistant
S.E. difference between means for grain yields = ± 0·240
S.E. difference between means for grain yields, aldicarb *v.* no aldicarb (1973) = ± 0·147

Manod yields were generally similar in plots treated with aldicarb (with or without *H. avenae* in 1973) and in plots which 'naturally' had no *H. avenae* in 1973. Yields were lowest in plots having *H. avenae* but no aldicarb 1973. The only plots having much *H. avenae* were those sown with Mostyn (no aldicarb, 1973). The population did not increase further during 1974 in these plots on the susceptible variety Manod. (Williams and Beane)

Rates of larval development of pathotypes 1 and 2. Previous studies (*Rothamsted Report for 1973*, Part 1, 158) failed to reveal any differences in morphology or protein band patterns between these two pathotypes. To eliminate host effects, Milford oats, a host of both populations, was sown in pots of soil containing each of both pathotypes. Roots were examined at weekly intervals. Both pathotypes developed at similar rates, second stage juveniles were present at two weeks, third stage males and females at three weeks, fourth stage males and females at four weeks. Mature males and females of both pathotypes appeared at similar times. (Williams and Beane)

Fungal parasites of cyst-nematodes. Populations of most animals have a pyramidal structure with many juveniles at the base and few surviving adults at the apex. Adults tend to produce eggs in such numbers that there are enough juveniles available in the next generation to bear the heavy mortality to which they are exposed. Fungal parasites of juveniles, e.g. the nematode trapping species, are abundant in all soils. Doubtless they and other agencies kill many juveniles but those removed are surplus to the carrying capacity of host roots and if not removed then they would be eliminated by competition later. Such fungal parasites appear to have little controlling effect on nematode numbers. However, fungi that kill females are more effective and may prevent the replacement of juveniles in the next generation. In recent years we have sought the agent which kills the females of the cereal cyst-nematode, *H. avenae*, and seems to prevent its multiplication when cereals are grown frequently. The principal if not the only agent seems to be an *Entomophthora*-like fungus common in many soils where cereals are grown intensively.

https://doi.org/10.23637/ERADOC-1-132

Observations were made on the fungal parasites of females and eggs of the cereal cyst-nematode in plots of oats, wheat and barley sown in autumn and spring at Woburn Farm (Table 2). Females and cysts were sampled at fortnightly intervals from May until September. Despite the large range of initial infestations in individual plots the nematode failed to increase, except in two plots of spring oats. There was a poor correlation ($r = 0.42$) between the number of females on roots and of new eggs in the soil after harvest. A large and significant correlation is expected unless many of the females have failed to form cysts or produced many fewer eggs than usual. In samples examined, parasitic fungi, mainly the *Entomophthora*-like fungus (*Rothamsted Report for 1973*, Part 1, 159), killed approximately 20, 40 and 50% of females on the roots of oats, wheat and barley respectively and fungi mainly *Verticillium chlamydosporium* (*Rothamsted Report for 1974*, Part 1, 185) parasitised 50% of the eggs in all plots by the end of June. There was a tendency for a greater degree of parasitism to be associated with poor egg production.

Females developing on the roots of autumn- and spring-sown cereals seem to be infected by the *Entomophthora*-like fungus before or soon after the females are fertilised. Diseased females contain few eggs, the cuticle is disrupted and their body contents are rapidly replaced by a much branched, aseptate mycelium which eventually breaks up into a number of hyphal bodies producing thick walled resting spores. Hyphal bodies may also give rise to thin, non-branching hyphae which can penetrate the softened female cuticle. The cytoplasm in these hyphal bodies and in the filiform hyphae rounds off to form small, thin-walled spores which have access to the soil. These spores probably represent the infective stage in the life cycle although as yet they have not been germinated nor has infection been observed.

Two soils from Butt Close, Woburn and Pitstone, Bucks., infested with *H. avenae* and known to contain the *Entomophthora*-like fungus and *Verticillium chlamydosporium* were inoculated with eggs of *G. rostochiensis*, *H. schachtii*, *H. trifolii*, *H. cruciferae*, *H. goettingiana* and *H. carotae* and the appropriate hosts grown. Approximately 2000 females of each species were examined on three sampling occasions for the presence of fungal parasites. The *Entomophthora*-like fungus was found in *H. carotae*, *H. cruciferae* and *H. schachtii* from both soils whereas females of *H. trifolii* and *H. goettingiana* were infected only in soil from Butt Close; females of the latter species contained hyphae but resting spores failed to develop. *G. rostochiensis* was not attacked by the *Entomophthora*-like fungus but eggs of all species were susceptible to *V. chlamydosporium*. *Tarichium auxiliare* previously observed in females of *H. avenae* and *H. schachtii*, was recorded for the first time in females of *G. pallida* in a laboratory population. (Kerry, S. C. Jenkinson and Crump)

Stem eelworm (*Ditylenchus dipsaci*) on field beans (*Vicia faba*)

On our farms and elsewhere symptoms on infested plants were generally less severe than in previous years because of late sowing and the short, dry growing season. However, many well infested stems were found in spring bean crops on Broadbalk at Rothamsted and White Horse and Horsepool fields at Woburn. These originated from soil-borne infestations traceable to the sowing of infested bean seeds in 1972. This indicates the care with which seed and sites for experiments need to be chosen. On land at Rothamsted infested with the giant race of *D. dipsaci* and which last grew infested beans in 1970, 3–9% of bean stems were infested this year; at Woburn, where beans were well infested in 1972, 42–69% of bean stems were infested this year. Land at Rothamsted, which last grew beans infested with the oat race in 1972, had 58–66% infested stems this year. These observations support circumstantial evidence that both races of stem eelworm can

https://doi.org/10.23637/ERADOC-1-132

persist in soil for several years under non-host crops. When aldicarb granules at 0, 1, 2, 4 kg a.i. ha^{-1} were applied in the rows of spring beans sown in land heavily infested with the giant race of *D. dipsaci*, stem infestations of 87, 41, 15 and 1% respectively were observed. The corresponding seed yields were 1·08, 1·69, 1·87, 2·03 t ha^{-1} and, whereas 14% of the seed from untreated plots was infested, seed from plots treated with aldicarb were less than 1% infested. The same treatments also decreased the incidence of weevil transmitted viruses (see p. 262). A similar experiment last year (*Rothamsted Report for 1974*, Part 1, 183–184) in which aldicarb was applied in the rows with infested seed prevented infestation of the seed crops. In-row treatments use much less aldicarb than broadcast treatments and it therefore seems feasible to use them to produce eelworm-free seed from valuable seed stocks. The cost of treatment is probably too great to justify use on ordinary farm crops although some increase in yield might be obtained. (For aldicarb residues in seed, see p. 177.)

Pot tests of thiabendazole as a wettable powder and a water soluble formulation were made against the giant race of stem eelworm on spring beans. Beans were sown in 25-cm diameter pots (5·5 litre soil) and inoculated with 75 000 *D. dipsaci* per pot at sowing. Pots were covered with a 5 cm layer of soil containing either of the above formulations to give 0, 60, 120, 240 mg a.i. per pot. Stems in untreated pots became heavily infested and distorted, some stems in pots treated with 60 or 120 mg were lightly infested but none were infested in pots treated with 240 or 480 mg of either formulation.

Forty-four selections of *V. faba* hybrids/lines supplied by either the Plant Breeding Institute, Cambridge, or the 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 showing any marked degree of resistance. Two selections of *V. narbonensis* seemed to be resistant to infestation by the giant race of *D. dipsaci* but their general growth was poor. (Hooper)

Root-lesion nematodes on maize

Tests in aseptic root cultures showed that different species of root-lesion nematodes (*Pratylenchus* spp.) differed in their pathogenicity to sweet corn cv. Golden Bantam. Heavy penetrations of *P. fallax* were observed within three days of inoculation, browning was first observed within three days and was marked by the sixth day. Symptoms reached their peak in 21 days by which time the roots were in poor condition. Invasion and symptom expression was similar when cultures were inoculated with *P. pinguicaudatus* but browning took longer and roots were not quite so badly affected. *P. crenatus* and *P. neglectus* were less pathogenic. Heavy penetrations did not occur, browning was much less pronounced and roots were far less affected. These results agreed with previous ones (*Rothamsted Report for 1968*, Part 1, 166) which showed that *P. fallax* and *P. pinguicaudatus* were the species most injurious to wheat, barley and oats. In a survey of maize crops on farms at ARC Institutes, *P. pinguicaudatus* was not found. Most fields were infested with *P. neglectus*, with *P. crenatus* or with mixtures of both but, at one farm, mixtures of these two species with appreciable numbers of *P. fallax* (39–48%) were found associated with stunted maize plants and heavily infested weed hosts (see also p. 260). (Webb)

Trials with nematicides

The effectiveness of nematicides in preventing nematode damage to field crops and in controlling population increase is assessed in pot and field experiments. Most experiments are on potato cyst-nematodes but we test ideas further on other nematodes, e.g. pea cyst-, beet cyst-, cereal cyst-, stem, and root-knot nematodes. Because nematodes are

https://doi.org/10.23637/ERADOC-1-132

especially harmful to young plants, much effort is put into combating damage to early growth and into controlling populations in the top 20 cm of the soil. Crop yields may also be decreased by nematodes feeding on roots deeper down. Hence, we study their depth distribution and try to control them at greater depths.

In 27 infested potato soils in Cambridgeshire, Lincolnshire, Yorkshire and Lancashire potato cyst-nematodes were abundant down to 20–40 cm. In two they were abundant in the first ten only: few cyst-nematodes were found in the region 40–80 cm deep. Beet cyst-nematode may also be as abundant 20–40 cm as 0–20 cm deep, but in three fields, pea cyst-nematode was abundant only in the top 20 cm.

Because of the contrast between the weather patterns during 1974 and 1975, results of similar trials done in both years are compared where possible.

Potato cyst-nematodes

Tomatoes. In a glasshouse at Chawston, Bedfordshire, tomatoes (cv. Eurocross BB) grew and yielded poorly in 1974 in sandy clay loam heavily infested with *G. rostochiensis* RO_1. Where the soil had been 'sheet steamed' or fumigated with methyl bromide, dazomet and 'Di-Trapex CP', or dazomet and 'Telone' (1,3-dichloropropene mixture) under polythene sheeting, tomatoes grew and yielded much better. Where the soil had been fumigated with 'Telone' or 'Di-Trapex CP' and had then had oxamyl at 11·2 kg ha^{-1} incorporated in the top 15 cm soil before planting, the crop also grew and yielded well. There were fewer nematodes in the top 20 cm soil in all plots than before planting and fewest in plots fumigated with methyl bromide or treated with 'Di-Trapex CP' and oxamyl (Table 4). Below 20 cm there were usually fewer nematodes than in the soil above. Methyl bromide and dazomet plus 'Di-Trapex CP' killed all eggs of potato cyst-nematode recovered from soil 20–40 cm deep, dazomet plus 'Telone' and oxamyl (plus 'Telone' or 'Di-Trapex CP') killed nearly all (97·7–99·5%), but sheet steaming killed none.

TABLE 4

Effect of steam and chemical soil treatments on tomato yields and on potato cyst-nematode increase

Treatment	kg ha^{-1}	kg fruit per plant	Nematode increase
untreated	0	1·2	×0·8
steam	—	3·2***	×0·7
methyl bromide	977	3·3***	×0·2
'Telone' and oxamyl	448, 11·2 †	3·4***	×0·6
'Di-Trapex CP' and dazomet	448, 448 †	2·9***	×0·6
'Di-Trapex CP' and oxamyl	448, 11·2 †	3·2***	×0·3
'Telone' and dazomet	448, 448 †	3·4***	×0·8

LSD (5%) 0·8, (1%) 1·1, (0·1%) 1·6

† Treated with both compounds

*** Significantly greater than untreated at $P < 0{\cdot}001$

Potatoes

Effect of nematicides on resistant and susceptible potatoes grown in infested soil. In well infested sandy loam at Woburn in 1974, yields of resistant Maris Piper potatoes and susceptible Pentland Crown potatoes were very greatly increased by fumigating the top 30 cm of soil in winter with dazomet, 'Telone', dazomet and 'Telone', or by treating the

https://doi.org/10.23637/ERADOC-1-132

top 15 cm of soil with oxamyl in spring, especially where the soil had already been deeply fumigated with 'Telone' in winter. Oxamyl 5·6 kg ha^{-1} incorporated in the top 15 cm of soil in spring controlled the nematode better in the top 20 cm of soil than very large amounts of dazomet, 'Telone', or dazomet and 'Telone' combined (Table 5). At the

TABLE 5

Effect of nematicides on resistant and susceptible potatoes in sandy loam infested with G. rostochiensis *RO_1 in 1974*

Treatment	kg ha^{-1}	Pentland Crown (susceptible) Tubers † t ha^{-1}	Pentland Crown (susceptible) log (eggs g^{-1} soil) at harvest	Maris Piper (resistant) Tubers † t ha^{-1}	Maris Piper (resistant) log (eggs g^{-1} soil) at harvest
untreated	0	36·9	2·61	39·1	1·81
dazomet	224	58·0	1·96	62·2	1·04
	336	64·2	1·77	71·9	1·59
	448	63·3	1·70	75·2	1·92
	672	72·5	1·63	72·3	1·66
dazomet and 'Telone'	224 } * 224	59·7	2·10	68·2	1·91
'Telone'	448	50·9	2·41	57·1	1·58
oxamyl	5·6	61·4	1·26	61·8	1·42
oxamyl and 'Telone'	5·6 } * 224	67·6	1·43	68·4	1·42
LSD (tubers vertical comparisons only)	(5%)		9·2		
	(1%)		12·2		
	(0·1%)		16·0		
Mean		59·4		64·0	
LSD	(5%)		3·4		
	(1%)		4·5		
	(0·1%)		6·0		

* Treated with both compounds
† Tubers over 3·8 cm diameter

Arthur Rickwood EHF, Mepal, Isle of Ely, small amounts of aldicarb or oxamyl incorporated in heavily infested peaty loam greatly increased yields of susceptible King Edward and resistant Maris Piper potatoes in 1974 and 1975. In 1975 yields of King Edward potatoes increased with increasing nematicide dosage but in neither year did yields of Maris Piper tubers increase significantly with more than 2·2 kg aldicarb or 3·4 kg oxamyl ha^{-1} (Table 6).

Residual benefit of controlling a potato cyst-nematode population. On Great Hill, Woburn, plots of sandy loam were treated in spring 1971 or 1972 with small amounts of oxime-carbamate or organophosphate nematicides before planting Pentland Crown potatoes. The nematode population increased in untreated but not in treated plots and tuber yields were much larger in treated than in untreated ones. Following potatoes, sugar beet and then barley were grown on the plots but their yields were unaffected by previous nematicide treatments. The yields of Pentland Crown potatoes grown in 1974 were greatly increased on all plots previously treated in 1971. In 1975 yields were greatly reduced by severe drought and significant yield responses were detected only in plots which had previously received the largest amounts of aldicarb or oxamyl in 1972.

Integrated control of a potato cyst-nematode. An experiment to control potato cyst-nematode by a combination of nematicides, crop rotation and a resistant potato

https://doi.org/10.23637/ERADOC-1-132

TABLE 6

Effect of oximecarbamate nematicides on resistant (Maris Piper) and susceptible (King Edward) potatoes in peaty loam infested with G. rostochiensis *RO_1, Arthur Rickwood EHF, Mepal*

Treatment		kg ha⁻¹	1974 King Edward †t ha⁻¹	1974 Maris Piper †t ha⁻¹	1975 King Edward †t ha⁻¹	1975 Maris Piper †t ha⁻¹
untreated		0	23·5	26·7	17·5	34·2
aldicarb		2·2	38·9**	46·5**	26·0***	41·6**
		3·4	50·9***	39·9*	29·2***	41·1**
		5·6	58·0***	47·0**	27·8***	45·0***
oxamyl		2·2	32·9	35·2	22·8*	41·7**
		3·4	43·5**	43·5**	21·1	43·0***
		5·6	53·5***	46·1**	25·9***	41·8**
LSD	(5%)		10·6		4·2	
(Vertical	(1%)		14·7		5·9	
comparisons only)	(0·1%)		20·4		8·2	
Mean			43·0	40·7	24·3	41·2
LSD	(5%)		5·2		1·3	
	(1%)				1·8	
	(0·1%)				2·6	
Eggs g⁻¹ soil before treatment (average of 42 plots)			257		277	

*, **, *** Significantly greater than untreated at $P < 0{\cdot}05$, 0·01, 0·001, respectively
† Tubers over 3·8 cm diameter

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 oxime-carbamate oxamyl applied to the soil in spring before potatoes are planted. The rotations were completed on the first of the three series of this experiment in 1975 and the results show that nematode population increase was prevented by growing Maris Piper potatoes or by growing Pentland Crown potatoes in soil treated with an effective nematicide. Where Pentland Crown potatoes in 1975 followed Pentland Crown potatoes in 1972 the nematode population was controlled best by 5·6 kg oxamyl or the larger amounts of dazomet and worst by 'Telone'. Except for oxamyl applied in 1972, which did not increase Maris Piper yields, yields of Maris Piper and Pentland Crown were greatly increased where the soil had been treated with a nematicide in 1972 and 1975 (Table 7).

Methods of incorporating granular nematicides in infested soil. An experiment in Butt Close, Woburn, in 1974 and 1975 tested the effectiveness of fumigating sandy loam with 'Telone' and smaller amounts of dazomet incorporated in the top 7·5 or 15 cm of the soil, compared with incorporating a small amount of oxamyl in the top 15 cm of the soil in spring. In 1974 all treatments very greatly increased yields of Arran Pilot and Pentland Crown potatoes but in 1975, when Pentland Crown potatoes were grown on all the plots after retreatment, tuber yields were increased significantly only by oxamyl or oxamyl plus 'Telone'. Yields of Pentland Crown tubers were greater following oxamyl plus 'Telone' than following oxamyl alone, probably because nematode damage was prevented to a greater depth by the 'Telone'. This effect was not produced in the Arran Pilot plots, which were more shallowly injected with 'Telone'. None of the 'Telone' plus dazomet treatments affected nematode increase in 1974 and equally large numbers of

https://doi.org/10.23637/ERADOC-1-132

TABLE 7

Integrated control of G. rostochiensis *RO_1, Stackyard Field, Woburn 1972–75. Effects on nematode numbers of nematicides and of a three-course rotation beginning with resistant or susceptible potatoes in 1972. A test crop of susceptible potatoes was grown in 1975. Nematicides applied before planting to the same plots in 1972 and 1975*

		Eggs g^{-1} soil		
	kg ha^{-1}	Before treatment, 1972	Before treatment, 1975	After harvest, 1975
Rotation: Resistant potatoes (1972), sugar beet (1973), barley (1974), susceptible potatoes (1975)				
untreated	0	51	12	56
dazomet	224	26	8	13
	336	41	12	26
	448	51	10	13
	672	100	29	25
dazomet and 'Telone'	224 / 224 †	79	24	26
'Telone'	448	76	19	18
oxamyl	5·6	37	7	5
oxamyl and 'Telone'	5·6 / 224 †	98	17	13
Rotation: Susceptible potatoes (1972), sugar beet (1973), barley (1974), susceptible potatoes (1975)				
untreated	0	47	41	97
dazomet	224	65	35	39
	336	58	12	20
	448	38	11	12
	672	30	6	11
dazomet and 'Telone'	224 / 224 †	30	6	15
'Telone'	448	37	26	74
oxamyl	5·6	62	9	8
oxamyl and 'Telone'	5·6 / 224 †	68	17	10

† Treated with both compounds

nematodes were found in the same, retreated plots, after harvest in 1975. In contrast, plots treated with oxamyl, or oxamyl plus 'Telone', remained much less infested (Table 8).

Eleven experiments at sites in eastern and central England showed that 5·6 kg aldicarb or oxamyl usually controlled potato cyst-nematodes better when rotavated into the top 15 cm than when rotavated into the top 7·5 cm of the soil. At 3·4 kg, aldicarb or oxamyl controlled the nematodes less effectively and there was little to choose between the two depths of incorporation.

Rotavating the soil incorporates granules, spread on the soil surface, fairly uniformly to the working depth of the machine, but it is slow and the L-shaped tines may 'glaze' moist soils with appreciable clay contents. An alternative method is to place the granules at different depths in the soil and incorporate them with a rotary harrow (Roterra). These techniques were compared in 1974 and 1975 on heavily infested sandy loam at Woburn and on heavily infested peaty loam at the Arthur Rickwood EHF, Mepal. Results in 1974 suggested that the incorporation of aldicarb was more critical in the peaty loam than in the sandy loam. At Woburn aldicarb controlled potato cyst-nematodes equally well, whichever dosage was applied and however it was incorporated in the soil, whereas in peaty loam at Mepal 6 or 12 kg aldicarb controlled the nematodes better than 3 kg ha^{-1}. Control at Mepal was also better when aldicarb was incorporated by rotavation than when it was incorporated by Roterra. Similarly, tuber yields were influenced

https://doi.org/10.23637/ERADOC-1-132

TABLE 8

Effect of combined nematicide treatments on yields of susceptible potatoes and potato cyst-nematode (G. rostochiensis RO_1)

			1974				1975			
			Arran Pilot		Pentland Crown		Pentland Crown after Arran Pilot		Pentland Crown after Pentland Crown	
Treatment 1974 and 1975	Depth incorporated (cm)	kg ha⁻¹	†Tubers t ha⁻¹	‡Nematode increase	†Tubers t ha⁻¹	‡Nematode increase	†Tubers t ha⁻¹	§Nematode numbers	†Tubers t ha⁻¹	§Nematode numbers
untreated	—	0	8·6	(2·6)	26·8	(5·7)	0·9	(2·33)	1·8	(2·29)
'Telone' and dazomet	— / 7·5	224 / 112	25·2	(2·9)	58·1	(6·6)	11·9	(2·23)	5·8	(2·45)
'Telone' and dazomet	— / 15	224 / 112	21·5	(2·0)	49·5	(7·4)	8·2	(2·13)	2·5	(2·34)
'Telone' and dazomet	— / 7·5	224 / 224	29·0	(2·2)	53·3	(5·9)	12·2	(2·10)	11·7	(2·31)
'Telone' and dazomet	— / 15	224 / 224	29·6	(2·3)	56·2	(5·8)	11·0	(2·03)	8·5	(2·59)
'Telone' and oxamyl	— / 15	224 / 5·6	35·3	(0·3)	68·8	(0·5)	23·5**	(1·30)	21·7**	(1·76)
oxamyl	15	5·6	34·6	(0·8)	58·8	(0·7)	19·1**	(1·83)	16·2*	(1·69)
			All treatments significantly increased yields in 1974 at $P < 0{\cdot}001$							
LSD (5%)			3·5		7·3		11·3		10·6	
(1%)			5·0		10·2		17·2		16·0	
(0·1%)			7·1		14·4		27·6		25·7	

*, ** Significantly greater than untreated at $P < 0{\cdot}05$ and $0{\cdot}01$, respectively

† Tubers over 3·8 cm diameter, t ha⁻¹; ‡ Nematode increase, times; § log (eggs g⁻¹ soil), after harvest

https://doi.org/10.23637/ERADOC-1-132

more by incorporation technique and by dosage of aldicarb in the peaty loam than in the sandy loam. In 1975 tuber yields were much smaller and at Mepal aldicarb dosage had less effect than in 1974 but yields were increased rather more by rotavating the granules into the soil than by placing them at different depths in the soil and incorporating them by Roterra (Table 9).

TABLE 9

Effect of incorporating 10% aldicarb granules on yields of Pentland Crown or King Edward tubers and on potato cyst-nematode increase (G. rostochiensis RO_1) (*means of plots receiving 3, 6, 12 kg a.i. ha^{-1}*)

Treatment: Where granules placed	Treatment: How incorporated in soil	Total tubers, t ha^{-1} (nematode increase, times): Woburn (Pentland Crown) 1974	Woburn (Pentland Crown) 1975	Mepal (King Edward) 1974	Mepal (King Edward) 1975
Untreated	Roterra to 20 cm	30·3 (4·2)	7·7 (1·0)	37·2 (6·1)	10·2 (3·6)
Soil surface	Rotavator to 10 cm	60·9 (0·6)	21·9 (0·3)	67·1 (1·4)	26·6 (0·9)
Soil surface	Rotavator to 20 cm	62·9 (0·7)	23·5 (0·6)	63·6 (1·6)	25·1 (1·1)
Soil surface	Roterra to 20 cm	58·1 (0·7)	19·9 (0·5)	61·8 (2·5)	20·5 (1·5)
Half to soil surface, half 5 cm deep	Roterra to 20 cm	58·3 (0·8)	21·6 (0·6)	60·9 (2·2)	21·2 (1·6)
Third to soil surface, third 5 cm, third 10 cm deep	Roterra to 20 cm	59·4 (0·8)	17·6 (0·6)	57·5 (2·6)	22·6 (0·9)
LSD (5%)	Untreated *v.* any other treatment	4·6 (0·6)	5·1 (0·5)	5·4 (1·3)	4·2 (1·0)
(1%)		6·2 (0·8)	6·8 (0·6)	7·2 (1·8)	5·6 (1·4)
(0·1%)		8·1 (1·1)	9·0 (0·8)	9·6 (2·4)	7·5 (1·8)
LSD (5%)	Excluding untreated	3·3 (0·4)	3·5 (0·3)	3·8 (0·9)	3·0 (0·7)
(1%)		4·4	4·8	5·1 (1·3)	4·0
(0·1%)		5·7	6·3	6·8	5·3

Potato cyst-nematodes attacking potato roots deep in the soil may cause yield loss. Deep fumigation with 'Telone' is feasible only in sandy or silty soils and oxamyl or aldicarb granules incorporated in the top 10–15 cm of the soil do not control the nematodes in soil 20–40 cm deep. An experiment was therefore set up in 1975 at the Arthur Rickwood EHF to assess the effectiveness of different ways of dealing with this problem. The soil is a heavily infested peaty loam about 30 cm deep overlying a silty loam. Techniques being tested are (i) rotavating oxamyl granules to 25 cm rather than 13 cm deep, (ii) using resistant Maris Piper potatoes with or without oxamyl incorporated in the top 15 cm soil, and (iii) inverting the top 30 cm of the soil and reapplying oxamyl to the top 15 cm of the infested soil. Rotavating oxamyl to 25 cm deep did not increase tuber yields in 1975 compared with rotavating half that amount of oxamyl to 13 cm deep. The other treatments are due for assessment in 1976.

We conclude that to control potato cyst-nematodes sufficiently an adequate dose of an effective nematicide must be well mixed in the soil from which the ridges are formed and, where the soil is infested to a depth greater than 20 cm, additional control measures may be necessary.

Pea cyst-nematode. Pea cyst-nematode can be controlled by incorporating small amounts of oxamyl or aldicarb in the seed bed just before peas are sown. Alternative application techniques to rotavating the soil 15 cm deep were assessed at Spalding in 1974 and at Bidford-on-Avon, Warwickshire and Evesham, Worcestershire, in 1975. At Spalding, aldicarb or oxamyl incorporated in the seed bed by rotavation 15 or 7·5 cm deep greatly increased pea yields but aldicarb applied in the seed furrows did not. At Bidford, oxamyl applied in the seed furrows or in a layer at sowing depth (5 cm) in-

https://doi.org/10.23637/ERADOC-1-132

creased pea yields as much and controlled pea cyst-nematode as well as when incorporated in the top 15 cm of the soil. At Evesham, oxamyl in the seed furrows controlled pea cyst-nematode as well and increased yields more than did oxamyl incorporated in the top 10 cm of the soil (Table 10).

Beet cyst-nematode. Good crops of sugar beet were grown in a peaty clay 'beet-sick' field at Mepal in 1973, where aldicarb or oxamyl had been incorporated in the top 15 cm of the soil before the seeds were sown. Not surprisingly, nematode numbers did not

TABLE 10

Control of pea cyst-nematode by 10% granules of 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	Bidford Fresh peas (t ha^{-1})	Bidford Increase of nematode
untreated	0	0·90	×2·6	0·17	×2·2
oxamyl rotavated into seedbed	2·4	2·02	×2·8	1·52*	×1·6
	4·9	2·27*	×4·0	3·26***	×1·7
	9·8	4·33***	×1·0	4·35***	×1·4
oxamyl in seed furrows	2·4	2·68**	×2·5	1·85**	×4·6
	4·9	4·74***	×2·2	3·34***	×0·9
	9·8	7·47***	×1·4	4·35***	×1·3
oxamyl (at sowing depth, 5 cm)	2·4	—	—	2·11***	×1·9
	4·9	—	—	3·45***	×1·3
	9·8	—	—	4·73***	×1·0
aldicarb rotavated into seedbed	2·4	2·36**	×4·0	1·93**	×1·8
	4·9	3·90***	×1·1	4·09***	×1·6
	9·8	7·64***	×0·7	6·73***	×1·8
LSD (5%) Excluding untreated		1·36		1·21	
LSD (1%) Excluding untreated		1·85		1·63	
LSD (0·1%) Excluding untreated		2·49		2·17	
Eggs g^{-1} soil before treatments applied		14		55	

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

TABLE 11

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

Treatment	Mepal 1973 (peaty clay) kg a.i. ha^{-1}	Sugar (t ha^{-1})	Increase of nematode	Pyemoor, Ely 1974 (peaty loam) kg a.i. ha^{-1}	Sugar (t ha^{-1})	Increase of nematode	Oxlode, Ely 1975 (peaty loam) Sugar (t ha^{-1})	Increase of nematode
untreated	0	3·4	×1·0	0	6·9	×1·0	6·8	×1·0
aldicarb	2·7	7·1***	×1·0	2·2	7·8**	×0·6	7·2	×0·4
	5·3	7·7***	×0·8	4·5	8·2***	×0·5	7·6**	×0·3
	10·7	7·5***	×0·5	9·0	8·3***	×0·5	7·8**	×0·5
				17·9	8·1***	×0·7	7·9**	×0·5
oxamyl	3·0	6·2***	×1·3	2·2	7·0	×0·5	6·8	×0·3
	5·9	7·0***	×1·8	4·5	7·8**	×0·5	6·7	×0·5
	11·9	7·0***	×1·5	9·0	7·8**	×0·6	7·4*	×0·3
				17·9	7·9	×0·8	7·4*	×0·4
Eggs g^{-1} soil before treatment		110			108		51	
(Range)		(14–232)			(19–286)		(19–88)	

*, **, *** Significantly greater (yields) or less (nematode increase) than untreated at $P < 0·05$, 0·01, 0·001, respectively

https://doi.org/10.23637/ERADOC-1-132

increase on the stunted crop that grew in the untreated soil, so it was difficult to assess how effective the treatments had been in terms of nematode population control. Similar experiments were made in 1974 and 1975 in moderately infested peaty loam soils to assess population control further. In neither year did the nematodes increase on sugar beet grown in untreated soil, despite the large root systems available to the nematodes and the possibility of a second generation in autumn. Early drought in 1974 delayed invasion of the roots by the nematode larvae and prolonged summer drought in 1975 may have prevented mating. Yields of beet were larger after aldicarb than after oxamyl probably because aldicarb is a better systemic aphicide (Table 11). (Whitehead, Tite, Finch, Bromilow, Fraser, French, Humphrey and Moss)

Other work

Work not reported this year includes yields and nematode population changes in the rotation-fumigation experiment and the experiment on fumigation, irrigation, resistant and susceptible potato varieties, both at Woburn Experimental Farm. Work on computer models to simulate population changes and competition between species of potato cyst-nematode is continuing in collaboration with R. Kempton, Statistics.

Staff changes, visitors and visits abroad

In October, M. R. Bridgeman, W. J. C. Oswald and P. A. Roberts joined us to work on host–parasite relations, insect-parasitic nematodes and the coevolution of round-cyst nematodes and their solanaceous hosts (a CASE project jointly with the Botany Department, Birmingham University). The following left during the year: Christine J. Brown, Sarah Coupar, Stephanie C. Jenkinson and Juliet C. Richards. T. J. Ahmad, Pamela Eaton, R. S. Chawla, P. Cowley and Clare Hunter were sandwich course students for periods of six months and the following worked in the Department briefly, R. J. Milsted, Wendy Nicholls and P. Walpole. Visitors and visiting workers included Dr. S. R. Misra, Sugarcane Research Institute, Lucknow, India, and Mr. K. Farrell, University of West Indies, Trinidad, who worked in the department for six months. Mr. M. Holliday and Dr. D. Alford, ADAS, spent short periods learning to identify nematodes.

In June, A. G. Whitehead visited nematology laboratories in the Netherlands, Belgium and France to discuss nematode control, and B. R. Kerry attended an EPPO conference in Gembloux, Belgium, on 'Pathological factors of the monoculture of cereals'. In November, A. R. Stone attended a meeting in Münster, West Germany, to consider an internationally agreed nomenclature for pathotypes and species of potato cyst-nematodes, and collected *Globodera* spp. nematodes in Mexico under the auspices of the Royal Society Latin America Programme in August/September.

Publications

General Papers

1 Hooper, D. J. (1975) *Aphelenchoides blastophthorus*. *Commonwealth Institute of Helminthology*. *Descriptions of Plant-Parasitic Nematodes*, Set 5, No. 73, 3 pp.

2 Kerry, B. R. (1976) Fungi and the decrease of cereal nematode populations in cereal monoculture. *EPPO Bulletin* **6**, 18–24.

3 Stone, A. R. (1975) Taxonomy of potato cyst-nematodes. *EPPO Bulletin* **5**, 79–86.

4 Stone, A. R. & Rowe, J. A. (1976) *Heterodera cruciferae*. *Commonwealth Institute of Helminthology*. *Descriptions of Plant-Parasitic Nematodes*, Set 6, No. 90, 4 pp.

https://doi.org/10.23637/ERADOC-1-132

5 WHITEHEAD, A. G. (1975) Chemical control of potato cyst-nematodes. *ARC Research Review* **1**, 17–23.

FILMS

6 DONCASTER, C. C. (1976) *Halichoerus grypus* (Phocidae). Parturition. Goettingen; Encyclopaedia Cinematographica. Film E 2180.

7 (NAAKTGEBOREN, C.) & DONCASTER, C. C. (1976) *Halichoerus grypus* (Phocidae). Parturition. Goettingen: Encyclopaedia Cinematographica. Companion publication to E 2180.

RESEARCH PAPERS

8 CLARK, S. A. & STONE, A. R. (1975) A simple method of preparing nematodes for scanning electron microscopy using Spurr's low-viscosity epoxy resin. *Nematologica* **21**, 256–257.

9 EVANS, K., FRANCO, J. (DE SCURRAH, MARIA M.) (1975) Distribution of species of potato cyst-nematodes in South America. *Nematologica* **21**, 365–369.

10 EVANS, K., PARKINSON, K. J. & TRUDGILL, D. L. (1975) Effects of potato cyst-nematodes on potato plants. III. Effects on the water relations and growth of a resistant and a susceptible variety. *Nematologica* **21**, 273–280.

11 KERRY, B. R. (1975) The extraction of cysts of the cereal cyst-nematode, *Heterodera avenae*, from soil. *Nematologica* **21**, 163–168.

12 MOSS, S. R., CRUMP, D. H. & WHITEHEAD, A. G. (1974) Control of potato cyst-nematodes *Heterodera rostochiensis* and *H. pallida*, in sandy, peaty and silt loam soils by oximecarbamate and organophosphate nematicides. *Annals of Applied Biology* **81**, 359–365.

13 SEYMOUR, M. K. (1975) Photoelastic stress analysis of a nematode stylet. *Nematologica* **21**, 117–128.

14 SHEPHERD, A. M. & CLARK, S. A. (1976) Spermatogenesis and the ultrastructure of sperm and of the male reproductive tract of *Aphelenchoides blastophthorus* (Nematoda: Tylenchida, Aphelenchina). *Nematologica* **22**, 1–9.

15 (SMITH, J.) & WHITEHEAD, A. G. (1975) The effects of dazomet on potato cyst-nematode (*H. rostochiensis* Woll.) and on King Edward potatoes grown in severely infested peaty loam. *Experimental Husbandry* **29**, 89–96.

16 TRUDGILL, D. L., EVANS, K. & PARROTT, D. M. (1975) Effects of potato cyst-nematodes on potato plants. I. Effects in a trial with irrigation and fumigation on the growth and nitrogen and potassium contents of a resistant and a susceptible variety. *Nematologica* **21**, 169–182.

17 TRUDGILL, D. L., EVANS, K. & PARROTT, D. M. (1975) Effects of potato cyst-nematodes on potato plants. II. Effects on haulm size, concentration of nutrients in haulm tissue and tuber yield of a nematode resistant and a nematode susceptible potato variety. *Nematologica* **21**, 183–191.

18 TRUDGILL, D. L., PARROTT, D. M., EVANS, K. & WIDDOWSON, F. V. (1975) Effects of potato cyst-nematodes on potato plants. IV. Effects of fertilisers and *Heterodera rostochiensis* on the yield of two susceptible varieties. *Nematologica* **21**, 281–286.

19 WEBB, R. M. (1975) A modified apparatus for the extraction of nematodes from sterile culture. *Nematologica* **21**, 408–409.

20 WHITEHEAD, A. G., BROMILOW, R. H., LORD, K. A., MOSS, S. R. & (SMITH, J.) (1975) Incorporating granular nematicides in soil. *Proceedings of the 8th British Insecticide and Fungicide Conference (1975)* **1**, 133–144.

https://doi.org/10.23637/ERADOC-1-132