

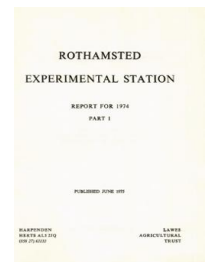
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Nematology Department

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NEMATOTOLOGY DEPARTMENT

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Introduction

Nematodes or eelworms are worm-like, translucent creatures mostly about 1 mm long but varying from 0.3 to 6 mm. Those that feed on plants have hollow, needle-like stylets with which they puncture plant cells to extract sap. Most feed on or in roots but some invade stem and leaf structures in the soil surface and get carried above ground when plants grow. Others climb plants while they are covered with moisture. When they occur in great numbers or transmit viruses, nematodes stunt growth and greatly decrease yields, and some persist for many years. The Department studies harmful species and seeks ways of preventing the injury they do.

After a comment on an exceptional year, this year's report contains summaries of work done during the last six.

The nematode year

The spring and summer of 1974 reversed the usual weather pattern which favours nematodes in spring and is against them in mid-summer. The drought at planting time continued into May and greatly decreased the activities of soil nematodes. At Pitstone, Bucks, in a cereal trial on light soil overlying chalk where an attack by the cereal cyst-nematode was anticipated it failed to materialise. The infestation of beans at Rothamsted by stem nematode was less than expected. The dry spell was followed by a prolonged wet one; consequently damage to potatoes in the ley/arable experiment from two kinds of root ectoparasitic nematode, one favoured by moist conditions in spring, the other

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causing losses only when summer rainfall is slight, did not occur. In land heavily infested with potato cyst-nematodes, nematocides were helped by the drought, root invasion was diminished and the better root systems took advantage of the summer moisture to give phenomenal increases in potato yields; as much as 42 t/ha, which is greatly in excess of the previous record, 27.5 t/ha.

Progress in nematode taxonomy

Microscope slide collection. The department is an internationally recognised centre for the identification and description of plant and soil nematodes and has one of the largest collections of specimens. Type specimens of described species are kept and information and specimens exchanged with workers throughout the world. The collections of longidorid and trichodorid spp. (which include plant-virus-vector nematodes) and of cyst-nematodes are especially noteworthy. (Hooper and Stone)

Although the species studied are usually preserved or mounted on slides, they are supplemented by observations on living specimens. Cultures of various rhabditid, aphelenchoid, *Neotylenchus*, *Ditylenchus*, *Pratylenchus* and especially *Heterodera* spp., are maintained to study variation within and between populations, their biology and, when appropriate, their host ranges amongst crops and weeds. (Hooper, Stone and Corbett)

Heteroderidae. Work on potato cyst-nematodes resulted in the recognition of a new species, *H. pallida*, which occurs in many potato growing areas of the United Kingdom and also in South America, Europe, Iceland, India and New Zealand. Both *H. rostochiensis* and *H. pallida* have pathotypes distinguished by their ability to multiply on potatoes with different genes for resistance (see page 177). To understand the pathotypes of *H. rostochiensis* and *H. pallida* and their relationships with other *Heterodera* species parasitising Solanaceae, extensive collections of round-cyst nematodes were made from the Eastern United States and Central and South America. *Heterodera avenae* also has pathotypes. Pathotypes 1 and 2 exhibit none of the differences which led to the recognition that there were two species of potato cyst-nematode, but pathotype 3 is now recognised as a distinct species. (Stone, Course, Matthews, S. L. Jenkinson, Williams and Beane)

Longidoridae and Trichodoridae. Accurate identification of nematodes in these groups is imperative because some transmit harmful viruses which are peculiar to individual species. Since 1961 seven new species of *Longidorus* and six of *Trichodorus* have been described; these include *Longidorus euonymus* thought to transmit euonymus mosaic virus to spindle trees in Czechoslovakia. When numerous enough some species cause severe damage to plant roots by feeding without transmitting virus. In work on Docking disorder of sugar beet (with A. G. Whitehead), five species of *Trichodorus*, *Longidorus attenuatus* and *L. elongatus* were found to stunt beet seedlings by injuring their roots. *Trichodorus velatus* also stunts seedlings of Sitka spruce.

Aphelenchoidea. This large group contains many poorly described species especially within the genus *Aphelenchoides sensu lato*. Progeny from cultures of several species including *Aphelenchoides blastophthorus*, *A. sacchari*, *A. rutgersi* and an undescribed species from West Africa were studied in detail to establish the range of variability within and between species, which is important to determine the value of the characters normally used to distinguish members of the group. Nutrition and age affect body shape and size, especially the size of the gonad and the tail shape. (Hooper and Brown)

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Scanning electron microscopy. Many structures used to identify and describe nematodes are near the limits of resolution of ordinary light microscopes under which surface details are difficult to discern. The scanning electron microscope solves this problem and is used increasingly. However, before nematodes can be viewed and their surfaces photographed, they must be carefully prepared. Methods were developed and refined that avoid shrinkage and distortion (with C. D. Green and R. Turner, Plant Pathology Department). Especially valuable is one recently devised using epoxy resin. (Clark)

Photographs of the lip structures of 35 species of *Heterodera* and related genera taken with the scanning electron microscope have demonstrated hitherto unsuspected differences and provided new ideas of the ancestry and interrelations of the Heteroderidae (Stone and Course). Similarly, hitherto unsuspected lip features have been observed in species of Aphelenchoidea which may help in the separation of genera and species in this amorphous group. (Clark and Hooper)

Under the light microscope species of *Pratylenchus* are separated on characters that include the number of head annules, tail crenulation and the structure of the lateral field. The scanning electron microscope has shown that some of these characters are unreliable. The surface structure of the fused lips and the first body annule indicates that the species fall into three groups: *P. brachyurus*, *P. coffeae*, *P. crenatus*, *P. goodeyi*, *P. loosi*, *P. sefaensis* and *P. zaei* in which it is undivided; *P. neglectus* and *P. thornei*, where it is divided into subdorsal and subventral segments separated by lateral segments; and *P. fallax*, *P. penetrans*, *P. pinguicaudatus*, *P. pratensis* and *P. vulnus*, where it is similar to that of the second group except that the subdorsal and subventral segments have more angular outlines. In all species the oval mouth is surrounded by six papillae and flanked on each side by the amphid apertures. (Clark and Corbett)

Ultrastructure

Sections of nematodes viewed at very great magnifications in the transmission electron microscope reveal characters which help to establish phylogenetic relationships and to explain the function of cells and organs previously unclear or unknown.

Sperm. A study of sperm of four groups of nematodes shows that in all the nucleus lacks a membrane, and that all lack a flagellum and are more or less amoeboid. Rhabditid, aphelenchoid, ascaroid, strongyloid and oxyuroid sperm have organelles called membrane specialisations of unknown function which are absent from sperm of *Heterodera* and *Meloidogyne* (Heteroderoidea) and *Pratylenchus* (Tylenchoidea). Instead, sperm of these nematodes usually have a sheath of microtubules lining their outer coat which is absent in sperms of *Xiphinema* (Dorylaimoidea). The state of chromatin in the nuclei of testicular sperm differs in species with round cysts (s.g. *Globodera*) from that in species with lemon-shaped cysts (s.g. *Heterodera*).

During the formation of sperm by cyst-nematodes cell divisions are complete before the male becomes adult when the testis contains only late spermatids and fully-formed spermatozoa. Thus, the quantity of sperm produced by the adult male *Heterodera* is fixed at the final moult. Nevertheless, *in vitro* experiments show that males are efficient and can fertilise several females. (Shepherd and Clark)

Copulatory spicules. Female nematodes are impregnated with sperm via a pair of small, sclerotised copulatory spicules in the male tail. In *Heterodera* spp. these have two minute pores at their tip and a large nerve internally which ends in two dendritic processes just beneath the pore apertures. The spicular tips are pointed in s.g. *Globodera* and cusped in s.g. *Heterodera* and in both are so shaped that when extended they form

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a tube through which sperm are transferred efficiently into the female. In *Rhabditis oxycerca* and *Aphelenchoides blastophthorus* the shape of the spicules is different and they fit together less well but, as in *Heterodera*, they have a large central nerve and are clearly sensory. In *Heterodera* the spicules appear to be the only specialised sensory structures to aid copulation, whereas *R. oxycerca* and *A. blastophthorus* have other sensory structures on the tail. (Shepherd and Clark)

Valves. Serial sections of the rectal valve in *A. blastophthorus* and the oesophago-intestinal valve of *Thornenema wickeni* failed to reveal a clearly defined lumen although food passes through to the intestine of *T. wickeni*, and the rectal valve of *A. blastophthorus* opens and closes during defaecation. In both nematodes the closed valves appear in section as convoluted pathways of closely apposed pairs of membranes like specialised cell wall junctions. Presumably these are held tightly together by inter-molecular forces when closed and open only under pressure. (Shepherd and Seymour)

Cuticle, subcrystalline layer and cement. Cuticle structure is of interest because it helps to maintain body shape and turgor, has a skeletal function and is a route through which nematicides must pass. In dead females of cyst-nematodes, it also persists as the cyst wall enclosing and protecting the brood of 2nd stage larvae still within the eggs. The electron microscope showed that in females the outer and inner cuticular layers of the larva are modified and additional inner layers laid down. In females of lemon-shaped species (s.g. *Heterodera*), one coarsely fibrous layer is added and in those with round cysts (s.g. *Globodera*) two are added. In the first of these additional layers the fibres are laid down randomly whereas in the second, innermost layer they are arranged helicoidally. The inner cuticle of larvae and males is crystalloid and consists of two blocks per annule. In the female it breaks between blocks when she enlarges. When intact, this layer is thought to be impermeable. It breaks at the stage when young females become attractive to males and it seems possible that the cuticle then becomes permeable releasing the attractant substance all over the body surface. Also, in species with lemon-shaped females the body is encrusted with a subcrystalline layer which develops soon after the inner cuticle disrupts. This layer is composed of a saturated, long-chain fatty acid and its calcium salt (tetracosanoic acid mixed with homologues). Nematode cuticle contains no waxes or wax glands and so it is improbable that the sub-crystalline layer is derived from the nematode itself. Sections through cuticle and its accretion of wax revealed a layer of fungal hyphae between wax and cuticle. The fungus, whose hyphae contain many secretion globules, has not been identified but is thought to produce the wax from unwanted sugars excreted through the cuticle while the female feeds copiously from the syncytial transfer cell it has induced in the host root. The subcrystalline layer is not produced when the nematodes are cultured on roots in a water medium, presumably because the substrate cannot accumulate or because the fungus is absent. (Shepherd, Williams, Green and Jones, with others in the Insecticides and Fungicides, Pedology and Soil Microbiology Departments)

Behind the 'head' of female cyst-nematodes embedded in host roots are globules of a tanned, viscous secretion thought to act as cement and once thought to be produced by cement glands. However, electron microscope sections suggest the cement is a fluid protein which exudes through ruptures in the outermost layer of the cuticle and then rapidly tans and hardens. (Shepherd and Green)

Endoparasites. Thin sections of cyst-nematodes revealed another unknown micro-organism endoparasitic mainly within the cells of the reproductive system. Infested populations were widely separated geographically. The organism resembles rickettsias

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and is otherwise similar to symbionts found in leaf hoppers. It appears to pass from one generation to the next via the egg and seems not to harm the tissues in which it is found. Whether it decreases the fecundity of infested populations is unknown. (Shepherd)

Pathotypes: progress in understanding

Potato cyst-nematodes. Detailed studies of many British and foreign populations of potato cyst-nematodes during the last six years support the separation of *H. pallida* as a species distinct from *H. rostochiensis*, and enable the pathotypes of both to be related to those occurring in Europe and elsewhere. All known pathotypes of *H. rostochiensis* have yellow females. British pathotype A is equivalent to Dutch A and is unable to multiply on potato hybrids with resistance gene H_1 (e.g., the variety Maris Piper, now grown increasingly). In the Netherlands three other pathotypes of *H. rostochiensis*, B, C and F are distinguished by resistance genes derived from *Solanum kurtzianum* (KTT 60-21-19) and *S. vernei* (G-LKS 58.1642/4). All three pathotypes, which are rare or absent in the UK, and all known pathotypes of *H. pallida* multiply on potatoes with resistance H_1 . In Britain two pathotypes of *H. pallida* are recognised, pathotype B with pale cream females unable to multiply on plants with gene H_2 derived from *Solanum multidissectum*, and pathotype E with white females which can multiply on these plants. On the continent populations of *H. pallida* are classified as Dutch pathotype E which is able to multiply on *S. vernei* ((VTⁿ)²⁶²⁻³³⁻³) and Dutch D which is not. Tests in Britain, the Netherlands and Germany suggest Dutch E and British E are equivalent. With minor deviations, test populations used in West Germany fit the above scheme but are called by their place of origin. As more resistance genes are found and tested it seems probable that more pathotypes will be described. (Stone, Evans, Parrott, Course, Matthews and Berry)

When the variety Maris Piper was grown repeatedly in soil infested with British or Dutch populations of *H. rostochiensis*, some remained unable to multiply suggesting that they were virtually pure pathotype A. Other *H. rostochiensis* and *H. pallida* populations tested were unable to multiply fully on plants with resistance genes H_1 or H_2 at first but reproduced almost equally as well as on a susceptible variety after several generations. This suggests that these were originally mixtures of pathotypes. (Parrott and Berry)

Controlled matings between pathotypes indicate that there is a gene-for-gene relationship between potato plants with genes for resistance and the pathotypes able or unable to multiply upon their root systems. In 1973 the best evidence yet that this is so was obtained from crossing British pathotype A (unable to multiply on plants with gene H_1) and a population from Bolivia (able to multiply). Tests of F_1 and F_2 supported the hypothesis that females able to develop on the roots of plants bearing gene H_1 are double recessives. The all-or-nothing response of both populations to plants with gene H_1 suggests that pathotype A consists almost wholly of homozygous dominants whereas the Bolivian population is almost wholly homozygous recessives. Pathotypes which give a less clear cut response to resistance genes may be mixtures of these types and of heterozygotes. Presumably, in such a complementary gene system, the dominant gene in the resistant host codes for a substance H which is incompatible with the products of the complementary gene N in nematodes unable to multiply upon it and the absence of gene H or gene N or both is essential for multiplication to occur. Ability to induce syncytial transfer cells essential for the nourishment of female nematodes is probably common to all members of the genus *Heterodera* but whether induction can proceed may depend on the compatibility of host cell contents and nematode saliva determined by the complementary gene system. (Parrott and Jones)

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Competition between pathotypes. Competition between *H. rostochiensis* and *H. pallida* is important as many fields contain both and there is always the risk of introducing *H. pallida* into fields infested only with *H. rostochiensis* pathotype A, where varieties with gene H_1 can be grown successfully. When Maris Piper and Pentland Dell (a susceptible variety) were grown each year on land that initially seemed only to be infested with *H. rostochiensis* pathotype A, *H. pallida* pathotype E was detected in one plot when it had grown Maris Piper four years running. Pathotype E has since spread to other 'continuous Maris Piper' plots and subsequently to plots growing the resistant and susceptible varieties in alternate years. Growing susceptible Pentland Dell every year has delayed but not entirely prevented the spread and establishment of *H. pallida*. A computer program is being developed to simulate competition between the two species in different crop rotations, with and without an applied nematicide. The program allows for different frequencies of the species initially, different maximum multiplication rates and different responses to the hatching factor exuded by potato roots. Attempts to quantify other ways in which the species differ and in which they may compete are being studied. (Parrott and Jones, with Ross, Statistics Department).

Cereal cyst-nematodes. In collaboration with ADAS, populations from fields in many localities in England and Wales have been typed, providing a picture of the pathotype distribution of *H. avenae* in Britain. At Rothamsted the population on Pennell's Piece is pure pathotype 1, unable to reproduce on Drost Barley, at Woburn Farm the population is 40% pathotype 2, able to reproduce on Drost, and 60% pathotype 1. Experimentally the Woburn population was converted to almost pure pathotype 2 by planting Drost repeatedly. The life cycles of both pathotypes under cool greenhouse conditions and the development times of males and females are similar. We have collaborated with nematologists from 14 countries in screening populations of *H. avenae* using a test assortment of 24–35 oat, wheat, barley and rye varieties. So far, throughout the world, though not in Britain, at least 15 pathotypes of *H. avenae* (or closely allied undescribed species) have been identified. These studies, as yet far from complete, should assist cereal plant breeders in all countries.

At Rothamsted and Woburn we have tested the agricultural worth of resistant barley and oat varieties. Resistant varieties significantly decrease the number of cereal cyst-nematodes after harvest and increase the yield of 'commercial' susceptible cereal varieties in the following year. Experimental spring oat varieties suffer badly from nematode invasion even though females of either pathotype do not develop on the roots. It seems desirable to incorporate in them a degree of tolerance to the damage done by invading larvae. (Williams and Beane, with Dr. R. Cook, Welsh Plant Breeding Station and ADAS Regional Entomologists)

Form and function

Methods. To study the functional morphology of plant nematodes, apparatus was developed to observe, manipulate and film living specimens under the microscope. One observation cell had variable depth and open sides for micromanipulation, another was designed to observe and photograph specimens over long periods under the high-power of an interference microscope, another was for use on the inverted microscope and yet another had a system of wicks to control the flow of perfusing liquid (Doncaster). Glass microdissection knives were developed and micro-cannulae made to hold or penetrate nematodes for observation and to record automatically internal pressures via electronic transducers. (Seymour)

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Feeding. Because plant nematodes have a high internal body pressure it was thought they needed a powerful pharyngeal pump to enable them to ingest food. However, observations on *Hexatylus viviparus* feeding on *Botrytis cinerea* show that food flows without pumping from the hypha, where pressure is high, into the nematode where it is lower. This is the first record of passive feeding in any plant nematode (Doncaster and Seymour). Observations on *Ditylenchus dipsaci* feeding on bean leaf tissue showed that passive ingestion occurred in this species also but was usually followed by active pumping. Ingestion started only after gland secretions were injected into the food cell. In aphelenchoid species no passive ingestion was seen nor were gland secretions injected into the host (Doncaster). We tried to culture the alkaline-fen nematode *Thornenema wickeni* but although it survived in the laboratory for 7 weeks it would not feed. It swallowed air which is the first record for a stylet-bearing nematode (Doncaster and Audrey M. Shepherd). Films of several tylenchid species showed the same basic pattern of behaviour leading to feeding. Simple sequences of searching behaviour (locomotion, head movements and probing with stylet) initiated in response to stimuli, led to rupture of the egg shell in hatching and penetration of host cells. (Doncaster and Seymour)

Defaecation. The mechanism of defaecation was studied in several nematodes by cinemicrography. In *A. blastophthorus* before defaecation the gut contents are displaced forward. During defaecation faeces are isolated in the prerectum by the closure of the prerectal valve. After passing the rectal valve they dilate the rectum, and are ejected when the anus opens. Following defaecation the posterior body re-elongates and the prerectal valve opens whereas the rectal valve and rectum remain closed until the next defaecation cycle (Seymour and Doncaster). In *H. viviparus* liquid and fungal globules were expelled, or liquid only, by a pumping action of the rectum, a process believed to aid passive feeding by keeping the intestinal pressure low (see above). (Seymour)

Eggs. In *Aphelenchoides blastophthorus* eggs move down the ovary and uterus by growth, by the kneading action of body-wall muscles and by transfer of fluid tissues forward and a corresponding backward displacement of the eggs. Eggs are forced through the vagina by contraction of the muscles in the body wall, which increases the internal pressure, and then out through the vulva which is opened by its own muscles. (Doncaster and Seymour)

In *Heterodera rostochiensis*, potato-root exudates stimulate second-stage larvae to use their mouth stylets to cut a slit in the egg shell. Stimulation by sodium metavanadate makes larvae move vigorously and thrust their stylets, but activity seems poorly coordinated and larvae emerge by pushing through the softened egg shell. (Shepherd and Doncaster)

Biomechanics. The mechanics of stylet action were studied after films of hatching and feeding suggested that the stylet was withdrawn by an elastic recoil mechanism involving the protractor muscles, anterior body-wall muscles and cuticle. To study the mechanics and design of the tylenchid stylet, stress-distributions were determined photoelastically in transparent plastic models representing longitudinal sections of the stylet of *H. cruciferae*. Models were loaded to represent natural stresses and viewed in a plane polariscope. Calculated compressive stress values and Young's modulus of stylet material suggested it was collagenous. (Seymour)

Analysis of films showed that cuticle can be stretched markedly along the body, but very little round it. When longitudinal muscles contract, they swell locally within this constraint and compress or displace nearby organs and their contents. This mechanism underlies defaecation, movement of sperms and eggs, the thrusting of the stylet, and pumping by the pharynx and intestine. (Seymour)

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Gel electrophoresis of soluble proteins

As electrophoresis of negatively charged soluble proteins in polyacrylamide gels has been found useful in separating species of bacteria, fungi and nematodes, it was tried on plant parasitic nematodes. Applied to several species of vermiform nematodes, including aphelenchoids, *Longidorus* and *Ditylenchus*, marked differences between protein bands were evident between genera, but those between species were smaller and tended to correspond to the degree of difference indicated by the traditional methods of taxonomy. The method did not separate pathotypes 1 and 2 of cereal cyst-nematode, which seem to be one species (Stone and Williams) but helped to separate *H. pallida* as a new species of potato cyst-nematode distinct from *H. rostochiensis*. The electrophoretic patterns of four American species of round-cyst nematodes were so similar as to suggest they were one species. Further experiments revealed slight differences between their patterns which were attributable to the host plant on which the females were raised. By using newly hatched larvae which have not fed the difficulty would be avoided and could be used to type cysts extracted from soil at any time of the year. Unfortunately larvae are very much smaller than females so that getting the necessary bulk of material is difficult. Also macerating them proved difficult but was successful when a frozen suspension was alternately crushed and thawed. Although the electrophoresis of all soluble proteins separates genera and sometimes species, provided interference from host proteins is avoided, it is too crude a tool to separate species within genera reliably. Attempts are being made to narrow the test to selected groups of enzymes and to apply it to smaller amounts of protein. (Greet and Firth)

Effects of nematodes on root systems

Nematodes shorten roots and often cause proliferation of lateral rootlets resulting in shallow, matted root systems unable to exploit fully the reservoir of nutrients and moisture in the soil. Stunted and debilitated root systems are also predisposed to attack by other disease organisms. Root weights obtained from attacked and unattacked plants are deceptive. Often, attacked plants appear to have larger root systems because they are lifted more or less intact, whereas healthy roots penetrate deeply, many break off and cannot be uprooted entirely. Nematodes that induce transfer cells from which they feed for as long as 3 months (e.g. cyst-nematodes) probably shunt back to the soil much water and many unwanted nutrients.

The effects of root infestation on nutrient uptake, water balance and plant growth were studied using potatoes and potato cyst-nematodes as the model system. Observations were made on nematode resistant (Maris Piper) and susceptible (Pentland Dell) potatoes growing on infested land. Root weights were estimated, internal leaf water stress and stomatal resistances were measured, growth was analysed and amounts of nutrients in the haulms, roots and tubers measured at intervals throughout the growing season.

Poor growth of haulms was allied with poorly developed root systems and accentuated because stomata were closed by failure to take up enough water. However, the plants adapted to an internal water deficit by opening their stomata when they would normally remain closed, so allowing some respiration, photosynthesis and growth. Early in the season, when plants were small and water plentiful, they made good during the night water lost during the day. Nevertheless, infested plants failed to take up enough nutrients and grew poorly compared with uninfested ones. Stems were fewer and individual leaf areas smaller although the numbers of leaves per stem were the same. The nitrogen concentration of infested plants was the same as that of uninfested ones, whereas amounts of potassium, phosphorus (especially in unfumigated plots), magnesium and sodium were appreciably smaller. Amounts of calcium increased.

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That plants were potassium deficient and not nitrogen deficient was partly because potassium is less mobile in soil. Thus, potassium uptake was proportional to root size and nematode-induced potassium deficiency could be partly corrected by applying extra potassium. Shortage of potassium tends to hasten senescence which is probably why nematode infested plants died early.

Plants in unfumigated plots were more phosphorus-deficient than those in fumigated even when post-treatment nematode populations were the same. Phosphorus, like potassium, is very immobile in soil and its uptake is proportional to root size. Plants in fumigated plots may have taken up more phosphorus because mycorrhiza increased after fumigation. Amounts of magnesium in infested plants were only slightly depressed, probably because the soil had recently received dolomitic limestone. However, in an adjacent field not so treated, magnesium was the growth-limiting factor. The effects of nematode infestation on sodium uptake were small, but the calcium content of infested plants increased greatly, presumably to maintain ionic balance within the plant when potassium and magnesium were deficient. Calcium enters plant roots easily, by mass flow rather than by active transport.

As the season advanced, water was less available in the soil and water stress increased, especially in infested plants. Infested root systems were shallower and began to die as secondary pathogens invaded them. The plants also became infested with *Verticillium*. Water stress in the infested plants was accentuated and, with potassium deficiency, caused early death from permanent wilting. Irrigating heavily-infested plots did not alleviate water stress but lightly-infested plots responded well. (Evans, with Parkinson, Physics Department)

Progress with work on hatching factors

Work on the hatching factors of the potato cyst-nematode has concentrated on purification. The bioassay of the factors remains unchanged but has been simplified, made more convenient and less time consuming. Initially the starting material was leachings collected laboriously from soil or sand in which potato plants were grown. Examination of the distribution of the hatching factor in the potato plant showed that most was in the roots with progressively less in stolons, stems, leaves and tubers. Also young actively growing roots contained more hatching factor than old. Convenience of extraction and concentration have led to the use of macerated young roots as the source of raw material rather than root leachings.

Root extracts are now purified in five stages. The initial step is by simple counter-current method followed by solvent extraction, and two successive fractionations by column chromatography to yield fractions which are then purified by thin-layer chromatography. There is evidence that several compounds with hatching activity can be obtained from the crude extracts, but so far attention has been focussed on the most readily isolated one.

As the purification procedures developed it became apparent that earlier attempts to isolate the hatching factor had not attained a sufficient degree of purity. The end-product obtained by previous workers at Rothamsted and elsewhere, appear to be at least 10–20 fold less pure than the material now obtained. The absence of physical criteria of purity, the instability of the hatching factor, the delays and vagaries of the bioassay, and the difficulties of the separations have all tended to obscure the degree of purification needed.

Now that the hatching factor is obtained in microgram quantities, attempts are being made to convert it into a volatile derivative suitable for gas chromatography and mass spectrometry. Attempts to esterify the acidic group of the hatching factor by a variety of procedures were unsuccessful, but other derivatives showed promise and fractions

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collected from gas chromatography columns have, after hydrolysis, given material with hatching activity. Present work is directed towards improving the results of gas chromatography, obtaining chemical evidence of the structure, and supplementing the existing analytical procedures by high-pressure liquid chromatography. (Clarke and Hennessy)

Root-lesion nematodes

A survey of wheat and barley crops showed that root-lesion nematodes *Pratylenchus* spp., were the commonest and most numerous migratory nematodes present. Five species were found in different soils, often more than one in the same soil. Two of the species (*P. thornei* and *P. pinguicaudatus*) occurred in heavy soils, two (*P. crenatus* and *P. fallax*) in light soils and the fifth and most widespread (*P. neglectus*) in all soils. Because root-lesion nematodes are all very similar, identifying them to species is difficult but essential to determine which are injurious. Reappraisal of the genus led to the description of one new species. Three more await description, and a valuable new feature was found enabling easy separation with the scanning electron microscope (see p. 175).

Monthly soil samples taken from long term experiments showed that, in winter wheat, the numbers of *Pratylenchus* spp. within roots increased through the winter, decreased during the period of rapid root growth in spring and increased again in summer. Numbers in Broadbalk decreased during the bare fallow and increased with successive wheat crops after fallow but less rapidly in the second and subsequent ones than in the first. Numbers in a wheat crop grown conventionally differed little from those in wheat drilled directly into stubble sprayed with paraquat.

To determine which species were responsible for injury to cereal roots, pure line cultures of all British species of *Pratylenchus* were established. Tests with *P. fallax*, associated with a stunted, chlorotic barley on Bunter sand soils, showed that it can cause necrosis of barley, wheat and sugar beet roots in the absence of other soil organisms. Root tips are invaded as are young lateral roots at their junction with the main root. Invasion stops growth, causes cavities in the cortex and thickening of cell walls in the endodermis. Weeds, especially grass weeds e.g. *Agrostis gigantea*, maintain numbers of *P. fallax* in patches of unthrifty barley. Nematicide treatments improved barley yields when *P. fallax* was the only species present, but when *P. neglectus* or *P. crenatus* were present alone or with *P. fallax* an improvement was not always seen. All five species of *Pratylenchus* from British cereal fields invade and reproduce well in maize roots, causing necrosis and eventually breakdown of the cortex. Symptoms appear sooner following invasion by *P. fallax* and *P. pinguicaudatus* than by *P. neglectus*, *P. crenatus* and *P. thornei*. In an experiment at Woburn where *P. neglectus* and *P. crenatus* were the most numerous nematodes, soil fumigation decreased nematode numbers and increased yields, even when much nitrogen was applied.

P. fallax and *P. pinguicaudatus* alone caused necrotic lesions on bean roots resembling the earliest stages of a root rot thought to be caused by a fungus. *P. neglectus* and *P. crenatus* also invade and reproduce in bean roots but cause necrosis only when very many are present. (Corbett and Webb)

The interaction between *Heterodera rostochiensis* and *Verticillium dahliae*

Pot experiments showed that plants infected with *Verticillium dahliae* died earlier when the soil in which they were growing was infested with more than 10 eggs/g of *H. rostochiensis* pathotype A, and the more eggs/g there were the sooner the onset of symptoms. Symptoms developed late in potted potato plants when their root systems were split and *H. rostochiensis* and *V. dahliae* were applied to different halves, but developed early when both organisms were together on one half. Yellowing began about 10 weeks after planting

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when swollen females were rupturing the root cortex and creating large gaps through which the fungus could penetrate. This interaction, therefore, is different from most others between nematodes and fungi in which the fungus penetrates through the far smaller holes made by vermiform adults and larvae.

Methyl bromide applied to field plots under gas tight sheets killed both organisms and increased yields for two years, doubling them in the first. Bromine residues in tubers were acceptable and mainly in the peel but residues in a succeeding wheat crop were so near the WHO tolerance limit that subsequent fumigation of the grain in store might have increased it unacceptably. Aldicarb controlled the nematode, and increased yields for two years after. Benomyl as a tuber treatment was ineffective but, when incorporated in soil, it controlled the fungus in the year of application and decreased nematode multiplication for four years thereafter. In the year of application the yields of tubers from benomyl and aldicarb treated plots were about 50 % more than the control, but in subsequent years yields of benomyl treated plots were best. Evidently benomyl has nematocidal properties. (Corbett, with Hide, Plant Pathology)

Stem nematode, *Ditylenchus dipsaci* on field beans

Since 1965 during July and August field beans (*Vicia faba*) at Rothamsted and Woburn farms were surveyed annually for stem nematode. Both the oat and giant race occur in many fields and have sometimes greatly reduced bean yields from some experiments. The nematode is seed-borne and has been spread in seed harvested from infested fields and also in purchased seed. Of 49 seed samples obtained from seed producers and farmers' crops, 26 were infested including the varieties Maris Bead, Maris Beagle, Maxime, Minden, Minor and Throws MS notwithstanding that some were basic or certified stocks. The oat race is polyphagous and potentially dangerous to onions, peas, sugar beet, carrots, strawberries and rhubarb as well as susceptible varieties of oats; it also reproduces on many weeds. The giant race seems not to have good alternative hosts except broad beans on which it is equally devastating.

Effect on yield. Seed-borne infestations usually have little effect on the yield of the first bean crop but are important in introducing and establishing *D. dipsaci* in uninfested land. In 1973 at Rothamsted spring beans with 80 % of the stems infested by the oat race had their seed yield decreased by 25 %, and 3 % of the seed was infested. Plots with 99 % of the stems infested with the giant race had their yield decreased by 50 %, and 67 % of the seed was infested. In 1974 on the same field, plots with 46 % of the stems infested with the oat race had 4 % of the seed infested and those with 81 % of the stems infested with the giant race had 60 %. Yields were again decreased compared with 'control' plots which themselves had become well infested with both races from adjacent plots having an average 25 % of the stems and 7 % of the seed infested. These results confirmed that the giant race is more devastating and produces more infested seed.

Survival in soil. On plots at Woburn well infested with giant race in 1972, all stems were infested in 1973 and 57 % in 1974: at Rothamsted where the land was well infested in 1970, 52 % of the stems were infested in 1973 but only 2 % in 1974. On other plots infested with the oat race in 1972, from 78–86 % of stems were infested in 1973 and 12–40 % in 1974. Although infestations seem to have declined from 1973 to 1974, this was probably due to the dry spring. Observations over eight years indicate that the oat race survives in soil under non-host crops for as many as five years and sometimes longer than seven.

Chemical control. At Rothamsted aldicarb granules broadcast at 11.2 kg a.i. per hectare

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and incorporated into the soil controlled soil-borne and to some extent seed-borne infestation, the latter decreasing from 56% to 6% on a demonstration plot. Row treatments of aldicarb granules at 0, 1.01, 2.02, 4.04 kg a.i./hectare, gave stem infestations after sowing infested seed, of 65, 41, 35, 12% respectively and 10, 3, 1, <1% of the harvested seed was infested.

Seed treatments. Attempts to eradicate *D. dipsaci* by heating infested seed for four days at 60°C or 1 h at 80°C were unsuccessful. Both treatments decreased seed germination (with Cockbain, Plant Pathology Department). Also, the dosage of the fumigant methyl bromide required to ensure eradication of *D. dipsaci* from heavily infested seed decreased germination markedly (with Mr. D. Powell, MAFF, Plant Pathology Laboratory).

Seed stocks. Seed stocks are easily checked by soaking seed in water overnight and examining the water extract. Cooperating with the National Institute of Agricultural Botany (NIAB), some basic and prebasic stocks were found infested. As a result the NIAB is now encouraging, and sometimes insisting that seed stocks and seed producing land is examined for *D. dipsaci* in the hope that it can gradually be eliminated from seed stocks. Although all common bean varieties seem susceptible, these and other lines are being tested for resistance to stem nematode (with Welsh Plant Breeding Station, Plant Breeding Institute and NIAB). (Hooper and Brown)

Nematode problems in the ley-arable rotation experiment, Woburn

In the Woburn ley-arable rotation experiment (*Details of the classical and long term experiments up to 1967*, 105–114; *Rothamsted Report for 1970*, 155) frequent cropping with potatoes led to heavy infestations of potato cyst-nematodes on certain plots and almost total crop failures in 1955. A survey in 1956 showed that *Heterodera rostochiensis* was present in all plots, with a concentration in the continuous arable and alternating rotations of Block 4. After 1955 potatoes were grown once every five years and in 1966 the variety was changed to Maris Piper, a variety resistant to *H. rostochiensis*, pathotype A. By 1970 large populations remained only in the continuous arable plots of block 4.

Despite the introduction of Maris Piper and the few potato cyst-nematodes in blocks 1 and 2, potato yields from the continuous arable plots were small in 1966 and 1967. Examination of the crop in 1967 showed that 38% of stems in the continuous arable series of rotations were infested with *Verticillium* but only 6% in the alternating arable/ley rotations. To study the effects of *Verticillium* infestation and a possible interaction between other fungi and nematodes, chloropicrin was applied to half the area of the 1968 potato crop. Growth and yield improved strikingly particularly on plots that were continuously arable, but as only traces of *Verticillium* were found in either treated or untreated plots, and *Rhizoctonia solani* and other genera of plant parasitic fungi (except *Pythium* and *Cylindrocarpon*) were favoured in fumigated plots, fungi were probably not responsible. Estimates of cyst-nematode populations showed that they might account for some of the differences between arable and ley rotations, and release of nutrients in the soil after fumigation undoubtedly improved growth, but neither effect could account for the very large yield differences, sometimes as great as 27.5 t/ha.

Since the only other likely pathogen was a free-living ectoparasitic nematode, the treatments for the rotation potatoes in 1969 included the nematicide aldicarb. There were yield responses in all the sequences of ley and arable crops to both chloropicrin and aldicarb with the largest responses again in the plots that were continuously arable. The response to aldicarb suggested that nematode pathogens had been controlled, but the numbers of potato cyst-nematodes and migratory ectoparasitic nematodes were small

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and seemed not to account for the poor yield of untreated plots. Numbers of *Pratylenchus*, *Tylenchorhynchus* and *Longidorus* approached those sometimes found pathogenic but were not great enough to cause appreciable yield losses.

Repeating the tests with chloropicrin and aldicarb in 1970 on potatoes grown in block 4 again resulted in large yield increases, although these could be accounted for in the continuous arable plots by control of large residual populations of potato cyst-nematodes. Responses in the plots where ley and arable rotations alternated could not be explained either by control of cyst-nematodes or root ectoparasitic nematodes, all of which were few in the top 20 cm of soil. However, samples taken 30–60 cm deep revealed about 200 *Longidorus leptocephalus* per litre of soil in untreated plots, whereas this nematode was virtually absent from plots treated with chloropicrin.

The absence of *L. leptocephalus* from the top 20 cm of soil under potatoes is probably due to the cultivations peculiar to potatoes as they are distributed more or less uniformly down to 60 cm under barley. The distribution under potatoes means that only deeper-growing roots are affected, so symptoms only appear in the tops as the crop becomes dependent on deep roots when the soil moisture deficiency mounts in July. Plants in unfumigated soil begin to wilt sooner than those in fumigated soil, but only after a considerable dry spell. If the weather continues dry wilting is rapidly followed by early senescence, cessation of tuber formation and consequent loss of yield.

When, in 1971, potatoes were grown as a test crop over all rotations the resistant variety Maris Piper was compared with susceptible Pentland Crown. This confirmed that cyst-nematodes were too few to affect yield. Nevertheless, the chloropicrin applied previously in autumn 1967 increased yields, supporting the hypothesis that *L. leptocephalus* is injurious. This nematode multiplies only slowly and had not recovered its numbers in the plots treated some four years earlier.

Partly because of insufficient replication and the complexity of the layout, correlations between yield and numbers of *L. leptocephalus* are not always good and there are indications that *Tylenchorhynchus*, another root ectoparasite, may have decreased yields in some seasons. This species occurs only in the top 20 cm of the sandy soil on which the experiment is sited, and is active and damaging only when the March to May rainfall is plentiful. In years when this rainfall is slight there may be a correlation between yield and numbers of *L. leptocephalus*, especially if there is summer drought. In 1974 when spring drought was followed by summer rain neither nematode was favoured: yields of potatoes after arable and ley sequences were similar and nematicides had no effect. Thus, the yield of potatoes in any one year may depend on seasonal rainfall as well as on the relative abundance of these two root ectoparasitic nematodes. (Evans)

Fungal pathogens of the cereal cyst-nematode

A natural enemy possibly specific to the cereal cyst-nematode appears to prevent it from multiplying in many fields where cereals are grown repeatedly (*Rothamsted Report for 1967*, 143). In 1973 an *Entomophthora*-like fungus killed females of *H. avenae* on continuous wheat in Broadbalk and continuous barley in Hoosfield, and in two fields at Bridgets Experimental Husbandry Farm.

In 1974 in cooperation with ADAS, 31 infested cereal fields were tested to see whether this and other fungal parasites were widespread in southern England. Soil samples were collected in spring, potted and sown with barley and female nematodes on the roots examined during June and July. Four parasites were identified. The *Entomophthora*-like fungus occurred in 97% of the fields but the average rate of infection never exceeded 17% at any sampling, the greatest being 44%, which was hardly sufficient to prevent population increase. However, conditions in pot tests are not those in fields and the numbers

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of nematodes and fungal spores present initially must have varied widely. In a field trial at Pitstone, Bucks., where '*Entomophthora*' and other fungal pathogens were present, formalin doubled the number of females on roots without decreasing the rate of invasion by the nematode or diminishing the rate of infection of females by '*Entomophthora*'. The method of extracting pot and field soils failed to recover immature females less than 250 μ wide or heavily infected females in which '*Entomophthora*' had destroyed the body wall as the latter disintegrates when washed. Better methods of recovering infected females are required and these may reveal that the rate of attack is greater than current estimates suggest.

Attempts to culture resting spores and hyphal fragments were unsuccessful and spores placed on sterile females on water agar did not germinate. The conditions for germination are being studied (with Wilding, Entomology Department and Gregory, Plant Pathology Department).

In fields, females are infected during late May and June even when numbers are fewer than 10 per root system. A third or more of females not infected by *Entomophthora* contained eggs infected by other fungi, e.g. *Verticillium chlamydosporium* and *Cylindrocarpon destructans*, which were present in 71 and 52 % of the fields examined, respectively. Both fungi occur in cysts of *H. schachtii* (Bursnall, L. A. & Tribe, *H. Transactions of the British Mycological Society* (1974) 62, 595–601) and therefore may not be specific factors responsible for the decline of *H. avenae* populations. However, as many as 91 % of females were infected at Pitstone and, when females were kept moist on agar, most of the eggs were killed by *V. chlamydosporium*. Although the fungus is thought to be only weakly parasitic, it is frequently found attacking eggs in females infected with the *Entomophthora*-like fungus. A fungus with reticulate spores was also found in females and eggs from 14 % of the fields. (Kerry and S. C. Jenkinson)

Chemical control

Root ectoparasitic nematodes and Docking disorder. Much exploratory work, done between 1964 and 1967 showed that root ectoparasitic nematodes, especially *Trichodorus* spp. (stubbyroot nematodes) and *Longidorus* spp. (needle nematodes) feed on and injure the root tips of sugar beet and other crops in sandy soils. The poor growth of sugar beet seedlings resulting from this primary damage is called 'Docking disorder', which is severe only in years with abundant rain in May e.g. 1969, when 8000 ha were reported affected and 50 000 t of sugar beet was estimated lost. Experiments from 1965 to 1967 showed that the disease is prevented if the soil is fumigated to kill the nematodes. It is not prevented by crop rotation because the nematodes feed on many different crops and weeds. Different soil fumigation techniques were tested in many field experiments from 1966 to 1969. The cheapest and most convenient was injection of 1-3-dichloropropene mixture (67.4 litres 'D-D' or 44.9 litres 'Telone'/ha) under the rows in which the sugar beet seeds are sown one day to two weeks later. This killed 80–90 % of the nematodes in the rows enabling the seedlings to grow quickly and yield good crops of sugar beet. Experiments with very large plots in 1970 showed that in some infested fields such treatments were profitable, even when Docking disorder did not occur. Row fumigation has been adopted commercially on many farms at risk from Docking disorder. Later work at Broom's Barn Experimental Station showed that granular nematicides applied in the seed furrow at sowing also control Docking disorder and will probably replace row fumigation as a means of control.

Cyst-nematodes. Cyst-nematodes (*Heterodera* spp.) are more difficult to control than root ectoparasitic nematodes. The females lay many more eggs than female ectoparasitic

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nematodes, most of them being retained in the toughened, protective, dead body wall (the 'cyst'), so a greater proportion of infective larvae must be killed or immobilised if population control is to be achieved. Many field experiments have been made with soil fumigants, organophosphorus and oximecarbamate nematicides since 1967 to control cyst-nematodes. Most have used potato cyst-nematodes (*H. rostochiensis*, *H. pallida*) as the model, because field populations are common, because they lack effective enemies and all the eggs are retained within the round cysts, and because the cysts are readily extracted from air-dried soil by flotation and more easily recognised than lemon-shaped ones. Chemical control of cereal cyst-nematode (*H. avenae*), beet cyst-nematode (*H. schachtii*) and pea cyst-nematode (*H. goettingiana*) was also attempted in replicated field experiments to test our ideas on other cyst-nematodes damaging to British field crops. Controlling *H. schachtii* is beset with problems arising from a second generation in autumn: other cyst-nematodes mostly have only one.

Fumigating soil with large amounts (300–1000 kg/ha) of methyl bromide, chloropicrin, methyl isothiocyanate mixture, dazomet or dichloropropene mixtures ('D-D' and 'Telone') often lessened or prevented damage to crops of potatoes and glasshouse tomatoes and sometimes lessened or prevented nematode increase. Only dazomet and the dichloropropene mixtures are suitable for field use. Dazomet is expensive and was unreliable on peaty soils and the dichloropropene mixtures worked well only in moist, well drained sandy soils. As all these nematicides are phytotoxic, crops cannot be planted in treated soil until the toxic gases have escaped from the soil into the atmosphere which takes from several days (methyl bromide) to several weeks or months (dazomet).

Smaller amounts (10 kg a.i. or less/ha) of non-phytotoxic granular nematicides can be applied more conveniently just before planting. Most organophosphorus compounds that are effective against potato cyst-nematodes are diethyl phosphorothioates or diethyl phosphates. Several organophosphorus compounds have prevented serious damage to potato roots by potato cyst-nematodes and have often lessened or prevented nematode increase but none has worked well in all soils tested. Phoxim, another organophosphate, in pots and two benzimidazoles, benomyl and thiabendazole, at 5.6–22.4 kg a.i./ha, have also shown promising activity against potato cyst-nematodes and, as their toxicity to vertebrates is slight, they can be spread on the soil by spraying, prior to incorporation in the topsoil.

The best nematicides, at present, are oximecarbamates, especially aldicarb and oxamyl which when well incorporated into the topsoil at 11 kg a.i. or less/ha prevent serious injury to host crops by cyst-nematodes and greatly restrict or prevent any increase in nematode numbers. Oximecarbamates work well in sand, peat, silt and clay soils. Another carbamate, carbofuran, is also promising.

Experiments have shown that to control cyst-nematodes granular nematicides must be well incorporated into the topsoil before planting crops like sugar beet or potatoes grown in widely spaced rows. With the possible exception of carbofuran, none of the current nematicides is much translocated within root systems, so narrow-band row treatments with nematicides will not control cyst-nematodes. Attempts are being made to find a more convenient yet equally efficient alternative to rotavation as a means of incorporating granular nematicides in soil.

Potato cyst-nematodes have been found as abundant 25–40 cm deep as 0–25 cm deep in some peat and silt soils in eastern England. Pot and field experiments suggest that large deep infestations may be damaging to potato crops. How common such infestations are is now being determined. Where the deeper soil is sandy it can be fumigated with dichloropropene or methyl isothiocyanate mixtures. Combining deep fumigation with incorporation of dazomet or oxamyl in the topsoil has given excellent control of cyst-nematodes in glasshouse tomatoes and in potatoes. Where the deeper soil has a larger organic matter

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or clay content deep fumigation is less suitable and control measures for these situations are being sought.

Stem nematodes. Chemical control of stem nematodes (*Ditylenchus dipsaci*) presents a stiff challenge: as they can multiply 1000-fold or more on host plants 99.9% or more of the nematodes must be killed or immobilised if population control is to be achieved. Aldicarb or oxamyl applied in the rows when onions, a sensitive crop, are sown, can very greatly increase the yield of dry bulb onions from heavily infested peat, sand or clay soils but do not prevent rapid multiplication of the nematodes on the crop later in the season. A second application of a systemic nematicide, if a satisfactory one can be found, seems necessary to prevent multiplication in stored bulbs. (Whitehead, Tite, Moss, Finch, Fraser, French, Crump and Wright)

Chemical control of human whipworm

At Cell Barnes Hospital, St. Albans, fumigating the soil with large amounts of methyl bromide, chloropicrin, dazomet or chloropicrin and dazomet applied under polythene sheeting controlled weeds very well but did not appear to kill the very tough-shelled eggs of *Trichuris trichiura*. The eggs of this nematode are abundant in the soil of playground areas used by young mental patients who are debilitated by it. Rotation of playground areas seems the only workable solution to the problem. (Whitehead, with Dr. Burdon, Animal Diseases Research Institute, Compton)

Other work

Work not reported includes that on the soil as an environment for nematodes (see page 189) (Jones, with Thomasson and Bullock, Soil Survey, and Williams, Chemistry Department) and two long-term field experiments at Woburn Experimental Farm. One experiment tests the effects of irrigation, fumigation and a resistant and a susceptible potato variety grown every year and in alternate years. Yields are recorded and population changes of potato cyst-nematodes estimated. The experiment is now in its eighth year. The other experiment concerns the effects of soil fumigants in a rotation of barley, sugar beet and potatoes. The fumigants are applied before each crop once in the rotation and before all three crops. Populations of potato cyst-nematodes and cereal cyst-nematodes are estimated annually. The numbers of other species are estimated from time to time.

Dr. R. Bromilow worked in the Chemical Liaison Unit (see page 160).

Visiting workers

The following worked in the department during the year: Professor L. I. Miller, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA, on a NATO grant; Dr. R. H. Brown, Victorian Plant Research Institute, Burnley, Victoria, Australia. T. Acland, K. Chubb, S. Gash, K. Jones, G. J. King, D. Lewis were sandwich course students and Catherine Hart and Martin Bridgeman worked during the vacation. Mr. D. C. M. Corbett was seconded to the Agricultural Research Council Headquarters for two years.

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GENERAL PAPERS

- 1 CORBETT, D. C. M. (1974) *Pratylenchus vulnus*. Commonwealth Institute of Helminthology. Descriptions of Plant Nematodes. Set 3, No. 37.

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- 4 HOOPER, D. J. (1974) *Aphelenchus avenae*. Commonwealth Institute of Helminthology. Descriptions of plant parasitic nematodes. Set 4, No. 50.
- 5 HOOPER, D. J. (1975) Morphology of trichodorid nematodes. In: *Nematode vectors of plant viruses*. Eds. F. Lamberti, C. E. Taylor and J. W. Seinhorst. London: Plenum Publication Co. Ltd. pp 91–100.
- 6 HOOPER, D. J. (1975) Virus vector nematodes—taxonomy and general introduction. In: *Nematode vectors of plant viruses*. Eds. F. Lamberti, C. E. Taylor and J. W. Seinhorst. London: Plenum Publication Co. Ltd. pp 1–12.
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- 9 STONE, A. R. & COURSE, J. A. (1974) *Heterodera goettingiana*. (A redescription). Commonwealth Institute of Helminthology. Descriptions of Plant Parasitic Nematodes. Set 4, No. 47.

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- 11 DONCASTER, C. C. (1975) Some methods of mounting and maintaining live organisms for cinemicrography. *Nematologica* **21**, 5–11.
- 12 DONCASTER, C. C. & SEYMOUR, M. K. (1974) Passive ingestion in a plant nematode *Hexatylus viviparus* (Neotylenchidae: Tylenchida). *Nematologica* **20**, 297–307.
- 13 GREEN, C. D., STONE, A. R., TURNER, R. H. & CLARK, S. A. (1975) Preparation of nematodes for scanning electron microscopy. *Journal of Microscopy* **103**, 89–100.
- 14 GREET, D. N. (1974) The response of five round-cyst nematodes (Heteroderidae) to five artificial hatching agents. *Nematologica* **20**, 322–323.
- 15 HIDE, G. A. & CORBETT, D. C. M. (1974) Field experiments in the control of *Verticillium dahliae* and *Heterodera rostochiensis* on potatoes. *Annals of Applied Biology* **78**, 295–307.
- 16 JONES, F. G. W. (1975) Accumulated temperature as a measure of nematode development and activity. *Nematologica* **21**, 62–70.
- 17 JONES, F. G. W. (1975) Host parasite relationships of potato cyst-nematodes: a speculation arising from the gene for gene hypothesis. *Nematologica* **20**, 437–444.
- 18 KERRY, B. R. (1974) A fungus associated with young females of the cereal cyst-nematode, *Heterodera avenae* Woll. *Nematologica* **20**, 259–260.
- 19 KERRY, B. R. & HAGUE, N. G. M. (1974) The invasion and development of the cereal cyst-nematode, *Heterodera avenae* Woll. in the roots of autumn and spring-sown cereals. *Annals of Applied Biology* **78**, 319–330.

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- 20 SEYMOUR, M. K. (1974) Defaecation in a passively-feeding plant nematode, *Hexatylus viviparus* (Neotylenchidae: Tylenchida). *Nematologica* **20**, 355–360.
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- 25 WHITEHEAD, A. G., FRASER, J. E., FRENCH, E. M. & WRIGHT, S. M. (1975) Chemical control of potato cyst-nematode, *Heterodera pallida*, on tomatoes grown under glass. *Annals of Applied Biology* **80**, 75–84.
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