ROTHAMSTED RESEARCH

Rothamsted Report for 1967

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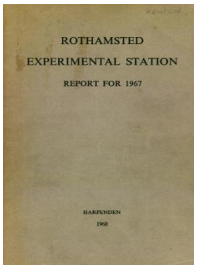

Nematology Department

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NEMATOLOGY DEPARTMENT

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The department studies the biology and control of known or suspected plant parasitic nematodes (eelworms), of which over six hundred species have been described and more are being found every year. A few live and feed on the aerial parts of plants, but most live in soil and feed externally or internally on plant roots or underground stems. Many other species of nematodes feed on bacteria, fungi or other nematodes. Wounds or rotting plant tissues always contain free-living nematodes whether or not they also contain plant-parasitic nematodes. In arable soils harmful species are often abundant down to plough depth, with fewer in the subsoil, but in orchards and plantations some species penetrate deeply along with tree roots. Pasture and arable soils often contain totals of the order of thousands of millions per acre which, before they can be identified or used in experiments, must be extracted from plants or soil—a tedious process!

Effects of soil structure and moisture on nematodes

Available space. Nematodes may squeeze through pore necks somewhat narrower than themselves and push aside loosely held fine particles in very wet soils, but with few exceptions they cannot deform soil structure and so are confined to existing passages and spaces. Their ability to penetrate soils is therefore determined by the diameter of pore necks and the amount of free passage possible before they meet blind ends or impassable necks. Soil nematodes are mostly from 15 to 60 μ in diameter: juveniles of the slenderest species are thinner than 5 μ (e.g. *Ecphyadophora*), and exceptionally stout species may be 150 μ (e.g. *Dorylaimus stagnalis*). Except in helping to visualise the problem, theoretical studies of artificial soils composed of uniform spheres in different states of packing have little relevance to field soils. Nevertheless, they suggest that, in all but the coarsest soils, nematodes cannot penetrate the spaces between primary particles but are confined to secondary spaces between aggregates.

TABLE 1

Geescroft Wilderness: Percent volume of solids and of space Xiphinema diversicaudatum *can and cannot occupy*

Depth in cm	2	6	18	30
Solids	48	59	67	77
Unavailable space	39	33	27	18
Available space	13	8	6	5

In untilled compacted clay soils and subsoils all nematodes are confined to cracks and fissures. Table 1 shows the proportions of the volume at different depths in the clay soil beneath the tree cover of Geescroft Wilderness that is space passable by *Xiphinema diversicaudatum*. In such a soil the space for nematodes to live in is small and, even though the cracks may

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contain many roots, fewer nematodes can feed in them than might in a more open soil. (Larbey)

In tilled soil containing more than 10% clay, seed-bed preparations create a network of pore spaces and channels accessible to nematodes, but how long the channels stay open depends on the stability of the aggregates. A few exceptional soils with weak aggregates have parent particles in such proportions and of such shapes that they pack densely with so few pores that they become almost totally impassable to nematodes. One such soil from the Cantley area of Norfolk, in which sugar beet grows well but the beet cyst-nematode multiplies very little, was sectioned and photographed. After natural compaction fine particles filled the spaces between angular coarse particles almost completely.

Cyst-nematodes multiply well in most soils with good structure (i.e. well aggregated), even though these contain much clay. To some extent they avoid adverse soil conditions because their larvae invade roots early in the season and become immobile, although males become mobile again and return to the soil. Thus any degradation of soil structure later in the year from weathering, particularly from heavy rain, has little effect on them. By contrast, root ectoparasitic nematodes, such as *Trichodorus*, *Longidorus* and *Tylenchorhynchus*, remain wholly in the soil and must move to feed and reproduce. Compaction of the soil limits this feeding and mating. Only in very coarse sandy soils (less than 10% clay and more than 80% coarse fractions) are they active from the seed-bed onwards. Consequently, whereas cyst-nematodes (*Heterodera schachtii* and *H. rostochiensis*) are abundant and injurious both in well-aggregated soils with much clay and in coarse sandy soils with little, ectoparasitic species (*Longidorus*, *Trichodorus*, *Tylenchorhynchus*) are abundant and injurious only in coarse sandy soils. (Jones and Parrott)

No evidence was found that irrigation of potatoes grown in a coarse well-drained soil consistently affects the populations of potato cyst-nematode. The population of *H. rostochiensis* in plants at Woburn was only

TABLE 2

Effect of irrigation on numbers of H. rostochiensis *in Woburn soil.*

No. of potato crops since 1949	Potatoes last grown	Sampled in winter of	Eggs/g soil		Water added in.
			Unirrigated	Irrigated	
2	1953	1955/56	5	5	1·3
3	1954	1955/56	9	16	2·2
3	1955	1955/56	28	28	4·2
3	1956	1956/57	56	50	0·5
6	1966	1966/67	136	115	3·0
1	1966	1966/67	26	30	3·0
7	1967	1967/68	89	69	4·3
2	1967	1967/68	41	45	4·3

slightly changed by irrigating potatoes in the years 1953–56 and 1966–67 (Table 2). As the larvae invade roots early in the season when water is rarely lacking and the females are sedentary and probably obtain their water from the potato roots, irrigation from late May onwards is unlikely to affect them much.

In 1959 some microplots were filled with coarse sandy soil from Woburn

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and others with chalky soil from the Winchester area. The microplots, which were made from slotted concrete posts and paving slabs, each had an area of 2–3 sq yards and held about half a ton of soil and were sited on a well-drained slope at Rothamsted. Both soils were naturally infested with *H. avenae*, but although cereals grew well in them from 1959 to 1962, the number of eggs/g soil decreased until they were negligible. The Woburn soil was also naturally infested with *H. rostochiensis*, but, so far as could be ascertained, both soils were free from other species of *Heterodera*.

In 1963 rows of plots were inoculated with cysts of other species and appropriate host crops grown continuously thereafter (Table 3). By 1967

TABLE 3

Multiplication of Heterodera *spp. in microplots containing soil from Winchester and Woburn. Mean number of eggs/g soil.*

Host	Species	Soil	Years 1963	1964	1965	1966	1967
Oats	*H. avenae*	Winchester	—	—	—	0·2	—
		Woburn	—	—	—	—	—
Potatoes	*H. rostochiensis*	Winchester	—	1·8	83·0	77·6	119·1
		Woburn	14·6	106·0	223·1	180·4	145·4
Brussels sprouts	*H. cruciferae*	Winchester	0·4	4·1	0·3	6·7	5·0
		Woburn	0·3	—	0·4	2·0	2·5
Peas	*H. goettingiana*	Winchester	1·0	13·5	41·7	19·7	29·1
		Woburn	1·0	10·3	50·3	60·4	81·2
Carrots	*H. carotae*	Winchester	—	0·1	0·5	2·9	2·3
		Woburn	—	—	4·4	1·5	1·4

H. rostochiensis and *H. goettingiana* were well established in both soils, *H. cruciferae* and *H. carotae* showed signs of increase, and only *H. avenae* failed to multiply. Lack of moisture in the well-drained microplots did not prevent *H. rostochiensis* and *H. goettingiana* from multiplying, so unless the other species have very different moisture requirements, it was not the factor preventing their multiplication.

Some agent independent of soil moisture and structure limits multiplication of *H. avenae* in the soils from Woburn, Winchester and Rothamsted and possibly elsewhere. At Woburn drenching the soil with formalin solution removes the inhibiting effect and allows *H. avenae* to multiply (see p. 158). Evidently the inhibitor is an enemy or competitor (possibly another root-infesting nematode) and its identity is being sought.

Trichodorus or *Longidorus* spp. remaining in the soil from the previous crop can greatly stunt sugar-beet seedlings, but little is known of their behaviour, so they were observed in observation boxes. The ectoparasitic nematodes assemble around root tips and begin to feed as soon as the seed germinates and continue to feed so long as the soil is moist enough. While they are numerous and active, root tips are stunted or killed, plants fail to establish branched root systems, grow poorly and show signs of nitrogen and magnesium deficiency. For them to be fully active, the force binding water to soil particles must be weak (no more than 100–150 cm of water suction), so the best conditions for the nematodes are when the soil is draining after rain. The first prolonged dry spell of the season probably creates moisture tensions great enough to stop nematodes moving and feeding, but not nearly enough to inhibit root growth. During this period roots

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probably proliferate and the plants grow away, as they do in moist chambers after washing free from soil and nematodes. When rain falls again the nematodes resume feeding, but the ratio of root tips to nematodes has probably increased and the plant is now less affected by the nematode's feeding. Table 4 shows the pattern of rainfall in the sandy areas of East

TABLE 4

The weather in dry weeks, in subsequent weeks, the active period for ecto-parasitic nematodes and the incidence of Docking disorder from 1963 to 1967

	Dry weeks			Subsequent weeks				
Year	Weeks, Shaw Nos.	Rainfall, 100ths in.	Days with rain		Average rainfall, 100th in.	Average No. of days with rain	Active period for nematodes weeks	Incidence of Docking disorder, acres
1963	*17	1	1	Next 4 weeks wet	50	4	9	Severe
	†22	0	0	Next 3 weeks dry	17	2		
1964	†19	12	2	Next week dry	14	3	6½	947
1965	†19	0	0	Next week dry	24	3	6	768
1966	†17	3	1	Next 6 weeks dry	23	3	4	32
1967	*17	29	2	Next 4 weeks wet	77	5	9	2317
	†22	15	2	Next 3 weeks dry	15	2		

* Ineffective dry weeks, followed by wet weather.
† Effective dry weeks, followed by a further week or more of relatively dry weather.

Anglia from 1963 to 1967 between the last week in March and the end of June. The number of weeks that rain was enough to allow nematodes to be almost continuously active from germination in the first week of April to the first inhibiting dry spell accords well with the incidence of Docking disorder. (Jones, Parrott and Whitehead)

Stem nematode on Rothamsted farm

Most plots of field beans on Rothamsted farm were infested with *Ditylenchus dipsaci* when examined in July 1967. Infested plants had an even brown discoloration in the stems, which darkened with age and began at the base and sometimes extended to the pod-bearing region. The incidence of the infestations on the bean plots and the previous cropping history suggested that some of them were seed-borne. Some of the seed pods were collected from infested plants in September. *D. dipsaci*, mainly dry fourth-stage larvae, which survive drying, were attached to seeds, especially in the slit in the hilum. Some seeds, which had necrotic patches on the cotyledons at the base of the hypocotyl, contained up to 9000 nematodes. Saving our own seed may have spread *D. dipsaci* around the farm and infested some fields previously free, but a new stock bought in 1966 was probably already infested. The infestation of beans *via* the seed had little effect on the vigour of the crop, but heavier attacks from soil infested by growing previous crops of oats or beans depressed yields. The poorest beans were where oats were heavily infested in 1966, and patches of the worst plants coincided with patches where oats were most heavily infested in 1966.

Two blocks of an experiment on Long Hoos III and the adjoining field

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crop were heavily infested, and most of the plants had brown stems. This area was where beans were grown in 1960, 1961 and 1962; but since 1962 crops that are not hosts for *D. dipsaci* were grown. On two adjoining blocks where beans have not been grown during the last seven years there were only a few infested plants. This suggests that the 1960–62 bean crops built up an infestation of *D. dipsaci* which persisted on weeds until 1967. Although there was no obvious difference between the vigour of the infested and uninfested plants, the two infested blocks yielded about 2 cwt of beans per acre less than the other two.

The oat varieties Peniarth and Manod, which are resistant to *D. dipsaci*, grew well on fields where a susceptible variety yielded very poorly in 1966. (Hooper)

The cereal root-knot nematode

Meloidogyne naasi was again reported on wheat, barley and on sugar beet. Those from sugar beet reproduced on barley (including a variety resistant to *Heterodera avenae*), wheat and ryegrass. The roots of sugar-beet plants that otherwise seemed healthy carried galls similar to those on stunted plants. Soil samples were taken from around healthy and stunted plants 0–3, 3–6 and 6–8 in. deep and the larvae extracted and counted. Significantly more were found in soil around stunted plants than around larger ones at depths below 3 in., but there was no difference in the top 3 in. of soil, which suggests that *M. naasi* larvae stunted the beet. The soil samples were taken in June before the nematodes of the current season had started to lay eggs, so the larvae extracted were produced on the previous seasons' crops, barley in 1966 and wheat in 1965.

The numbers of root-knot larvae necessary to injure crops have not been determined. Infestations are usually estimated by counting galls on test plants, which must be removed before larvae hatch from the newly formed eggs. Tests take several weeks, and the test plant does not necessarily pick up all the potential larvae initially present as eggs, which may not hatch during the period of growth allowed to the plant. *Meloidogyne* eggs, although aggregated in masses, cannot be extracted from soil in the way that *Heterodera* cysts can. Methods of processing soil infested with *M. naasi* were therefore tried to find out how to extract larvae quantitatively. A preliminary test, using infested field soil stored at 4° C and a standard extraction method at room temperature (*c.* 18° C), extracted about 86% in 2 days. A few larvae continued to emerge from the soil for 4 weeks: these probably hatched from egg-masses loose in the soil and in old galls. To encourage hatching before the start of extraction, batches of the soil were stored at 15°, 20° or 30° C for 1, 2 or 3 weeks. Larvae were extracted as before and counted after 24 and 72 hours. After 24 hours' extraction most were obtained from soil stored at 20° C, irrespective of the duration of storage. The soil stored at 30° C yielded the fewest larvae, and the numbers of larvae decreased significantly the longer the soil was stored. When counted after extracting for 72 hours, most were obtained from the soil stored at 15° and 20° C, and prolonging storage had no effect. Significantly fewer larvae were extracted from soil stored at 30° than at any other temperature, and significantly fewer at 25° than at 20° or 15° C.

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These tests indicate that, when comparing populations of *Meloidogyne* larvae in soil, all the samples should be treated in the same way. By storing the soil at a suitable temperature before extraction, extraction is complete within a week. The optimum storage temperature for different species of *Meloidogyne* needs to be found by experiment.

To study the development of the cereal root-knot nematode (*Meloidogyne naasi*) in barley and ryegrass outdoors, seeds were sown every month and roots were examined at intervals until embryonated eggs were found. Roots of plants sown between October and February were not invaded before April, roots of plants sown in March and April were invaded during May, but plants sown later were invaded within a fortnight of germination. This suggests that the eggs that had overwintered in the soil did not hatch until soil temperatures had risen in spring. The first embryonated eggs were found during July in both autumn- and spring-sown barley and ryegrass.

Barley plants sown in September became infested in October, but the nematodes developed no further during the winter. Mature females were found in March, but eggs were not observed in them until July; meanwhile more larvae invaded the roots at the end of May. Larvae invading in April or May have time to mature and produce embryonated eggs before the barley stubble is ploughed, but a second generation is impossible. In ryegrass newly formed, first-generation, larvae may invade in late summer, but their development is unlikely to be completed until June of the following year.

Although the shortest time between invasion and development of embryonated eggs may be 8 weeks in summer, contrary to earlier observations, it seems unlikely that two complete generations of *M. naasi* can be produced in one year in England, at least on barley. (Franklin and Clark)

Biology of cyst-nematodes

Mating behaviour. A bioassay developed to measure the attractiveness of substances in solution to males of cyst-nematodes has allowed the reactions of the males to the secretions of the females to be studied. Males move continuously forwards only when the concentration of the female's secretions is constant or increasing. A slight decrease in concentration increases the nematode's rate of turning (klinokinesis), and a large decrease causes a shock reaction, characterised by writhing and random turning similar to behaviour when an electric potential gradient is reversed (Jones, F. G. W. *Meded. LandbHogesch., Gent* (1960) **125**, 1009–1024). The secretions added to water on agar plates or to sand stimulate males to move and to continue moving. Males collected from aerated water containing roots bearing females are very active, with 60–70% moving at any time, and remain active for some time, whereas those from ordinary water move slowly after 2–3 hours, and only 10% are active after 24 hours. When secretions from females are added to water containing inactive males about half become active and continue moving for 24 hours. In tubes of moist sand without female secretions males of *Heterodera rostochiensis* and *H. schachtii* move little, even when warmed, and movement ceases within 24

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hours. Adding one female made males at the far end of a 6-cm tube respond, and adding ten females made males at the far end of a 15-cm tube very active. Incorporating female extracts uniformly in the sand (i.e. without concentration gradients) stimulated the males into activity. Secretions from fully developed females evidently contain an activant as well as an attractant or a single substance with both properties. Very young females do not attract males, and males placed close to them do not leave them, because they have not yet begun to produce either attractant or activant.

The tests in sand, agar and water suggested that the attractant acted by diffusion through the water. However, other tests suggested that the attractant was volatile. For example, agar blocks put in an enclosed space with extracts of females but not in contact with them acquired enough attractant within 15 hours to attract males. Similarly, extracts enclosed with males but not connected to them by water stimulated them to move actively for more than a day. The substances were not destroyed by drying at 60° C or *in vacuo*, but steam distillates were apparently not active. If the volatile substances are distinct from those that act by diffusion through water, they seem to have similar properties in attracting and activating males. (Green, Greet and Evans)

Females of *H. rostochiensis* can be seen on the outside of roots 5 weeks after the larvae invade, but most have been fertilised by the fourth week, before they are readily visible to the naked eye. Experiments suggest they are mated many times. Females prevented from mating remain white; they are still receptive to males and can produce as many eggs when mated 10 weeks after invading plants as when mated 6 weeks after. Although attempts to estimate, by mating on agar plates, the number of males a female will accept, and the number of females one male will visit, were inconclusive, they showed that a male can copulate several times and fertilise more than one female, also that a scarcity of males need not limit the number of eggs a female produces.

Males had an active life of about 10 days, whether or not provided with host roots. The presence of females or their secretions stimulated males but did not shorten their active life. In pots containing infected potato plants the number of males emerging daily from the roots rose to a peak 24 days after invasion, but the number that were active fell to much less than a half 10 days after the peak. Most females are fertilised within 5 days of most males emerging, so there seems no reason why males should survive for long.

Throughout the season weekly counts were made of *H. rostochiensis* larvae in the roots of potato plants growing in an infested field, the cyst content of the soil, the egg content of the cysts, the males free in the soil and the males emerging from the roots. There was evidence of either a partial second generation or a second wave of invasion, beginning in July with the males emerging from the roots and into the soil during August. Up to 3000 larvae per g of root were counted on 24 May when about 60% of the plants had emerged. (Evans)

Matings between like and unlike populations of potato cyst-nematodes. The inheritance of pathotype behaviour in *H. rostochiensis* has still to be

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determined unequivocally by single male–female matings followed by tests of the progeny produced. As a preliminary to such matings, virgin females from seven populations were mated with males from their own and from other populations. The matings were made on agar in plastic cells. Successful matings, those giving fertile eggs containing larvae, are expressed as percentages in Table 5. The populations used fall into two groups

TABLE 5

Single female/single male crosses of Heterodera rostochiensis, *combined results from reciprocal crosses*

Populations (females)	% females with eggs			% females produced relative to Arran Banner = 100		
				ex *andigenum*		ex *multi-dissectum*
	Selfed	Mated within group	Mated outside group	NY24/7 (CPC1685)	W46/1 (CPC1690)	Q 53/4
Group 1	(Mainly pathotype A)*					
Sandy	56	62	23	1	9	50
Woburn	77	56	7	1	8	136
Feltwell	57	42	14	1	2	93
Group 2	(Mainly pathotype E)†					
St. Brelades	58	55	23	2	113	94
Gosberton	73	66	26	23	111	65
Frampton	61	76	14	6	125	59
Cadishead	47	75	14	44	108	15

*A = O and A of Cole & Howard (1966), 0 and 2 of Jones & Parrott (1965).
†E = O, B and C of Cole & Howard (1966), 0, 1 and 1,2 of Jones & Parrott (1965).

Jones, F. G. W. & Parrott, D. M. (1965). The genetic relationships of pathotypes of *Heterodera rostochiensis* Woll. which reproduce on hybrid potatoes with genes for resistance. *Ann. appl. Biol.* **56**, 27–36.

Cole, C. S. & Howard, H. W. (1966). The effects on a population of potato-root eelworm (*Heterodera rostochiensis*) of growing potatoes resistant to pathotype B. *Ann. appl. Biol.* **58**, 487–495.

according to their ability to reproduce on hybrid potatoes bearing a gene for resistance derived from *Solanum tuberosum* ssp. *andigena*. The first group reproduced little on hybrids arising from Line 1685 of the Commonwealth Potato Collection and only very slightly better on Line 1690, whereas the second group multiplied to a variable extent on Line 1685 and fully on Line 1690. All populations reproduced well but variably on a hybrid with another gene for resistance derived from *Solanum multidissectum*. Matings within population groups were equally as successful as selfings, but populations from different groups mated much less successfully. Until the progeny of the crosses have been multiplied and tested it is impossible to say whether crosses between groups produce viable larvae. If they do not, the differences between pathotypes are greater than previously supposed and might indicate distinct subspecies. Because of the incompatibility between populations, it may be necessary to look within populations that seem to be mixtures of pathotypes to see whether all types interbreed. (Parrott)

Coloration of females of potato cyst-nematodes. Guile (*Pl. Path.* (1966), **15**, 125–128) showed that females (cysts) of *H. rostochiensis* from different populations differed in colour. All females are white at first, but those from

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populations containing mainly pathotype A soon turn bright golden yellow and remain so until the female dies and her body wall tans and turns brown, whereas females from populations mainly pathotype E remain white, and those of pathotype B become pale yellow (Mabbott, *in litt*).

The colour developed by females from five populations was followed by placing them in rows on agar and checking the tint developed against a colour chart divided into eight grades: 1–3 white to grey-white, 4–7 increasing depth of yellow and 8 golden yellow. Grades 4, 5 and possibly 6 corresponded to Guile's pale creamy yellow. The results confirmed Guile's except that the division into white and yellow was not absolute, for some populations developed intermediate colours. Females from Gosberton, Cadishead and Jersey had the same proportions of white and pale yellow individuals on potato var. Arran Banner as on hybrids with a gene for resistance derived from *Solanum tuberosum* ssp. *andigena* (91 to 9% and 92 to 8% respectively), but on resistant plants with a different gene for resistance derived from *S. multidissectum* the proportion of pale yellow cysts was 19%. Colour intensity also increased in females from the Woburn and Feltwell populations on ex *multidissectum* hybrids. A few cysts collected from ex *andigena* hybrids infested by the Woburn population were bright yellow, suggesting they were pathotype A, which does not usually reproduce on ex *andigena* plants. Such females may arise because root tips occasionally mutate and lose the ability to resist. (Parrott)

Influence of resistant potatoes on development and sex. The root systems of hybrid potato plants with genes for resistance are invaded by almost as many larvae of *H. rostochiensis* as are those of susceptible varieties. Larvae can become male or female according to circumstances; in the roots of resistant hybrids few of some populations become female and most become males. This led to the hypothesis that larvae able to become female have the genotype that evokes a favourable response in the tissues of the potato root (i.e. induces giant cells), whereas those of the incorrect genotype do not and therefore become males. On this hypothesis larvae able to become female are selected, but there is no selection of males. Evidence,

TABLE 6

The numbers of adults produced on susceptible potato and three resistant hybrids. Means of three tests

Population of potato cyst-nematode	Number of adults susceptible Arran Banner	Adults as a % of adults on Arran Banner Resistant hybrids		
		ex *andigena*	ex *multi-dissectum*	ex both
	ab	*Ab*	*aB*	*AB*
Sandy	1614	37	94	20
Woburn	2359	48	105	28
Feltwell	2070	54	104	37
Duddingston	1617	66	70	24
St. Brelades	1911	105	141	88
Gosberton	2054	108	90	90
Jersey	1952	76	117	95
Frampton	2268	79	93	44
Cadishead	2255	98	48	54
Means	2011	75	96	53

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however, has accumulated suggesting that males also are selected, and recent experiments confirm this. Table 6 compares the numbers of adults produced in standardised tests by nine populations on the susceptible variety Arran Banner and on the three resistant potato hybrids grown in pots. Arran Banner lacks the genes for resistance the hybrids have and is designated *ab*; one hybrid has a dominant gene for resistance derived from *Solanum tuberosum* ssp. *andigena*, another one from *S. multidissectum* and a third has both: they are designated *Ab*, *aB* and *AB* respectively. With two exceptions (Duddingston and Cadishead populations) as many or more larvae reached maturity on the *aB* as on the *ab* plants, but many fewer larvae matured on *Ab* and *AB*, and populations behaved very differently towards these hybrids. Evidently the larvae of some populations failed to mature even as males.

Table 7 compares the proportions of males and females produced by the

TABLE 7

The numbers of males and females produced on Arran Banner and on three resistant hybrid potatoes. Means of three tests

Population of potato cyst-nematode	Numbers on susceptible Arran Banner *ab*		Numbers as a percentage of those on Arran Banner — Resistant hybrids					
			ex *andigena* *Ab*		ex *multi-dissectum* *aB*		ex both *AB*	
	♂	♀	♂	♀	♂	♀	♂	♀
Sandy	963	651	62	1	124	50	33	2
Woburn	1737	622	65	2	93	136	38	1
Feltwell	1384	686	81	1	109	93	55	1
Duddingston	1000	617	94	21	78	57	48	1
St. Brelades	1490	421	134	2	189	94	102	35
Gosberton	1213	841	168	22	106	65	121	46
Jersey	1108	844	117	22	186	25	153	19
Frampton	1580	688	110	6	108	59	55	20
Cadishead	1258	997	141	44	76	16	88	12
Means	1304	707	108	13	119	66	76	15

same populations on the same plants. All populations produced significantly fewer females on *Ab* and *AB* hybrids than on Arran Banner (*ab*), but some populations (St. Brelades, Gosberton, Cadishead on *Ab* hybrids; Gosberton, Jersey on *AB* hybrids) produced many more males. The main effect of selection on larvae of these populations was to change the sex ratio, whereas with others in addition to the change many larvae were eliminated. The *AB* hybrid eliminated most larvae and *aB* hybrids fewest. (Trudgill and Parrott)

Behaviour through the life cycle. Examination of film sequences led to the conclusion that the behaviour patterns in successive stages in the life cycles of *Heterodera* species depend on a few activities mostly initiated by external stimuli, although one activity may initiate another and lead to the next stage. The basic activities include pharyngeal gland secretion, locomotion (including pushing against resistant surfaces), thrusting the mouth stylet and movements of the pharyngeal musculature. Second-stage larvae in eggs show these activities in sequence after stimulation with root-

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diffusates. Forward bodily thrust, pressing the lips against the egg shell and, later, against cell walls in the host root seem to stimulate or even to initiate stylet thrusting. When opposing surfaces were not rigid, as in an artificially softened egg shell and in plant cell walls distant from their junctions with others, there was less stylet thrusting. In the plant, this response leads to selection of parts of cell walls mechanically best suited for penetration; those held rigidly are chosen rather than those that bend under pressure from head or stylet.

Co-ordination of activities to produce an appropriate behaviour pattern takes time to develop, but considerable precision is ultimately achieved. This may involve corrective behaviour, as was shown by a larva making a slit in its egg shell; perforations were made by the stylet close enough for each to join the preceding one, but sometimes the stylet was thrust too far and with too little force to perforate. Instead of increasing the power of the next thrust and making an isolated perforation, the larva redirected the thrust close to the preceding perforation and continued the cut successfully. That the stylet protractor muscles may have proprioceptor sense organs associated with them is suggested both by the use of the stylet as a sensory probe and by apparent control of the power behind stylet thrusts. Plant cell walls and the egg shell are both cut similarly, and forward bodily thrust forces open the slit produced. Adult males emerging from the third-stage ensheathing cuticle behave similarly.

Stylet thrusting and locomotion alone seem adequate to explain emergence from the egg and penetration of host cells, and there is no evidence for or against secretions being emitted from glands before the larva reaches its feeding site. Contractions of individual muscles in the pharyngeal median bulb squeeze the duct that passes between them and assist forward flow of secretions: this action occurs both in the egg and at the feeding site. However, its significance in the egg may only be that the secretions stimulate bulbar muscles to contract; such contractions were not seen in larvae with empty ducts.

The subventral pharyngeal glands of all stages inside the host seem much less active than the dorsal gland, but in infective second-stage larvae and adult males the sub-ventral gland ducts are full. Adult males seemed not to feed, although physically equipped to do so, perhaps because they were not stimulated enough or lacked the instinct. (Doncaster)

A new cyst-nematode on cereals. A cyst-nematode from the roots of cereals in the Mediterranean region differs from the cereal cyst-nematode, *Heterodera avenae*, endemic in Europe in having a distinctive cyst cone with a wider vulval bridge, a shorter vulval slit and a more conspicuous underbridge with splayed-out ends. The larvae average 0·45 mm long (0·55–0·60 mm in *H. avenae*) and have a different form of lateral line. Males have three or four annules on the head. *H. turcomanica* from the U.S.S.R. has cysts similar to those of the new species, but was described from cysts only, and the host plant is unknown. The new species is unknown in Britain and cannot be tested outdoors, but it can multiply under the same conditions as *H. avenae* because it occurs together with *H. avenae* in soil from Tripoli. (Franklin)

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Nematodes and Verticillium wilt of potatoes

Heterodera rostochiensis and *Pratylenchus neglectus* are two nematodes found where Verticillium wilt of potatoes is severe: their part in the disease was studied in pots. Chitted tubers, var. King Edward, were planted in compost and inoculated with *Verticillium dahliae* at potting time and re-inoculated with it a week later, when either 7300 *P. neglectus* were added per pot or enough cysts of *H. rostochiensis* to give 10 and 50 larvae/g soil. Table 8 shows that *H. rostochiensis* increased the severity of wilt: leaf

TABLE 8

The enhancement of Verticillium wilt in potatoes by Heterodera rostochiensis *and* Pratylenchus neglectus

	Tuber weight g/pot	Score for haulm symptoms at 11 weeks (0–6)	Stems with micro-sclerotia at 14 weeks	Score for micro-sclerotial intensity at 18 weeks (0–3)
Control, uninfected				
1	233	0	—	—
2	242	1	1	0·2
H. rostochiensis only				
10 eggs/g	222	0	0	0·0
50 eggs/g	221	1	1	0·0
Verticillium dahliae only	193	2	6	1·7
Verticillium plus *H. rostochiensis*				
10 eggs/g	171*	3	6	3·0
50 eggs/g	156*	6	6	2·7
Verticillium plus *P. neglectus*	222	3	5	2·3

* Significantly less than the controls at P = 0·05

symptoms appeared earlier and tuber weights were significantly depressed when *H. rostochiensis* and *V. dahliae* were inoculated together (Table 8). Whether *P. neglectus* also interacts with *V. dahliae* is uncertain, but when both were inoculated together symptoms were more intense at first than in plants inoculated with *V. dahliae* alone. (Corbett with Hide, Plant Pathology Department)

Control with chemicals

Amino-acid antimetabolites. Females of *H. rostochiensis* produce many eggs, which requires the synthesis of much protein. Of amino-acids that are antimetabolites for naturally occurring amino acids and were screened for their ability to affect egg production, DL-methionine was most active. However, applying it at weekly intervals showed that it acted by poisoning the nematode rather than by interfering with egg production. When applied early enough almost 100% of the nematodes were killed, but the host plants were only slightly harmed. For this reason an attempt was made to control the nematode on tomatoes grown in beds by adding DL-methionine in water solution as a soil drench. Some plants grown in soil so treated were better than those grown in soil fumigated with methyl bromide. (Evans)

Of 16 amino-acid antimetabolites tested as drenches applied to soil containing potato plants, L-3-nitro tyrosine, DL-5-methyl tryptophane,

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7-aza-indole, 7-aza-tryptophane and DL-ethionine were very toxic both to plants and *H. rostochiensis*. DL-methionine was nematicidal but relatively harmless to the plants. In 7·5-cm-diameter pots containing 200 g of soil, 0·25 mg/g of soil decreased the number of adult nematodes by 95% and increased the height of the potato plants by 20%. DL-methionine also decreased the number of nematodes when sprayed on to the leaves of the potato plants.

DL-tyrosine applied to infected tomato seedlings growing in a controlled environment changed the proportion of adult males and females that developed on the roots. In three tests 0·25 mg of DL-tyrosine/g of sand decreased the number of females by 95% and more than doubled the number of males. The effect depended on the concentration, and 0·01 mg/g did not change the sex ratio. Concentrations of more than 0·25 mg/g of sand decreased the number of adults. L-tyrosine had no apparent effect on the sex of the larvae. D-tryptophane behaved like DL-methionine, and in two experiments 0·075 mg/g halved the number of females and greatly increased the number of males. In contrast, L-tryptophane at less than 0·01 mg/g of soil increased the number of females; greater concentrations killed many larvae. (Trudgill)

DL-methionine, L-hydroxy-proline, D-β-phenyl-α-alanine significantly decreased the galling of tomato roots in pots by *Meloidogyne incognita*, *M. javanica* and *M. hapla*. DL-valine decreased galling by *M. incognita*, DL-methionine sulphoxide galling by *M. javanica* and L-tyrosine galling by *M. hapla*. The effects of the last three amino acids seemed specific, L-hydroxy-proline and DL-ethionine damaged the plants. Soil drenching had more effect on nematodes than spraying leaves with the antimetabolites. L and DL forms of methionine, applied to soil or to leaves at different stages of development of host plant and parasite, adversely affected the development and reproduction of the nematode in the earlier stages. Except that the root system was smaller, the vigour of the tomato plants was unaffected. Both forms of methionine persisted in the plants for about 2 weeks: weekly dressings with 100 mg/plant applied as a soil drench killed the nematodes in the roots. (Setty)

Hatching agents. In the laboratory many compounds hatch the eggs of the beet cyst-nematode, *Heterodera schachtii* Schm. Some of the most active and easily obtainable of these were applied to small field plots infested with *H. schachtii*. The compounds chosen were sodium metavanadate, acetone and nabam (sodium ethylenebisdithiocarbamate). The last breaks down to give ethylenethiuram monosulphide, which causes hatching. The sodium metavanadate and nabam were applied dissolved in water (10% and 0·3% respectively) as a drench at 2½ gal to 4 sq yards. None of these treatments influenced the number of larvae that hatched from the cysts in soil not carrying a host crop. Whether measured as larvae lost per cyst or per g of soil, losses in the treated soil did not exceed those in plots drenched with water only. (Shepherd)

It was uncertain whether the hatching factor in root diffusates acts on the egg shells of *Heterodera* or the larvae inside, or on both. Ciné films showed that larvae inside eggs are quiescent and move very little until a hatching

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stimulant is applied, but then, after several hours or days, they begin to move around inside the shell. This activity culminates in the larva thrusting its stylet at the egg shell and eventually making a cut through which it emerges.

To see whether quiescent second-stage *H. rostochiensis* larvae released from the egg shell were influenced by root diffusate, they were carefully removed from unstimulated eggs by gentle pressure and separated from eggs and empty shells by washing on a 37-μ sieve. The released larvae were placed in batches of about 500 on filter pads in Baermann funnels filled with water or root diffusate, and those that passed through the filter pad, i.e. had been activated, were estimated. In eight out of nine experiments, each lasting about 3 weeks, significantly more larvae passed through a filter in potato-root diffusate (about 30%) than in water (about 10%), suggesting that some constituent of the root diffusate activated the larvae. Thus, the hatching factors for *Heterodera* spp. need not differ intrinsically from the activants females emit that stimulate males (see p. 146) or plants emit that activate nematodes in soil. If this is so, substances similar in effect to hatching factors may be widespread and play an important part in the persistence and survival of nematodes in soil. (Shepherd with Clarke, Biochemistry Department)

Beet cyst-nematode. At Burnt Fen (Cambridgeshire) on a field heavily infested with *Heterodera schachtii* up to 20 gal/acre of "D-D" (dichloropropene-dichloropropane) injected under predetermined beet rows during ploughing in December failed to control the nematode. Nevertheless,

TABLE 9

Yields of sugar in cwt/acre after treatments with nematicides against beet cyst-nematode

Treatments		Injected beneath predetermined beet rows in winter	Applied to beet rows in spring
Untreated		39·1	39·0
"D–D"	5 gal/acre	40·3	
	10 ,,	44·3*	
	20 ,,	44·8*	
"Telone"	4		40·2
	13		45·5
	33½		54·0***
"Temik 10G"	8 lb/acre		36·9
	16 ,,		36·5
	32 ,,		44·5
"Lannate"	3/4 lb/acre		35·7
	1½ ,,		37·5
	3 ,,		34·8
L.S.D. (5%)		5·2	6·9

10 or 20 gal/acre significantly increased yield by about 5 cwt sugar/acre (Table 9). In the spring 33½ gal/acre of "Telone" (dichloropropenes) injected beneath the predetermined beet rows immediately before drilling decreased the number of females of *H. schachtii* on the roots at the end of May by 70% and increased sugar yield by 15 cwt. Thirty-two lb/acre of

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"Temik" (2-methyl 2-methylthioproprionaldehyde-*O*-carbamoyl oxime) incorporated into the topsoil in the beet rows immediately before drilling decreased the number of females on the roots at the end of May by 58%, but did not increase sugar yield significantly. "Lannate" (*S*-methyl *N*-methylcarbamoyl-oxy-thioacetimidate) band-sprayed over the beet rows immediately after drilling neither affected *H. schachtii* nor increased yield.

Potato cyst-nematode. On Butt Furlong, Woburn, on a patch of light land heavily infested with potato cyst-nematode (*H. rostochiensis*, 100–250 live eggs/g soil), 16 gal/acre of "D-D" injected through tines on a tractor-drawn toolbar 9 in. below the top of the ridges on 7 March 1967 before planting in the ridges on 19 April 1967, increased yield of ware potatoes (var. Majestic) sevenfold (Table 10). In alternately treated and un-

TABLE 10

Effect of "D-D" applied in potato ridges during spring to light land infested with potato cyst-nematode

Amount of "D–D" applied gal/acre	Interval between applying "D–D" and planting	Ware potatoes ton/acre
None		1·4
4	6 weeks	4·6***
8	,,	6·6***
16	,,	10·0***
L.S.D. (5%)		1·2
8	2 weeks	10·3

treated ridges at the side of the main experiment 8 gal/acre of "D-D" applied in the same way to the ridges on 6 April also increased sevenfold the yield of potatoes planted in the ridges on 20 April. Cooked tubers from treated plots were not tainted. The growth of tops early in the season on plots treated with "D-D" at 4 gal/acre was somewhat better than with 8 or 16 gal/acre, suggesting that the greater amounts of "D-D" in the ridge had retarded growth slightly. Later in the year the other plots improved, the haulm grew strongly and remained healthy longer. All treatments increased yield so much that the costs were more than covered (see also p. 261). (Whitehead and Tite)

Stunt nematodes, *Tylenchorhynchus* spp. In an experiment at Woburn in which potato varieties resistant and susceptible to cyst-eelworm were grown continuously or alternately on plots that were fumigated or not and irrigated or not, the combination of resistant potatoes in 1966 and irrigation and fumigation in 1967 gave the greatest yields of ware tubers (see p. 260). Two years' cropping with the susceptible variety on unfumigated and unirrigated plots sited on the half of the experiment most heavily infested with the potato cyst-nematode produced a tuber yield of less than 1 ton/acre, whereas the best combination of treatments yielded more than 14 tons. One of the aims of this experiment is to define conditions in which potatoes can be grown and yield well continuously. (Jones and Parrott)

Controlling the cyst-nematode suggested that the root ectoparasite *Tylenchorhynchus* (mainly *T. dubius*) was important. To find its effect on the

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growth of potatoes, experiments were done in pots using a logarithmic series of inocula. After 10 weeks there was evidence that the nematodes had begun to multiply. Root and haulm weights and haulm lengths all decreased as the numbers of *Tylenchorhynchus* added to the pots increased, suggesting the nematodes were harmful. No specific symptoms from feeding around root tips were observed other than a smaller root system. Fumigation in the previous winter decreased the numbers of *Tylenchorhynchus* in June, and they were more numerous in the half of the experiment after ley and lucerne than on the half after arable crops. Irrigation for a short period had no effect on numbers, and the plots of the variety Maris Piper, which is resistant to potato cyst-nematode, contained as many as the susceptible variety Pentland Dell. (Kyrou)

Cereal cyst-nematode. At Woburn the residual effects of a range of soil sterilants applied in 1965 and 1966 before cropping with spring wheat were tested by growing barley (var. Maris Badger) in 1967. Fumigation with chloropicrin, methyl bromide and "D-D" in 1965 only, greatly decreased the larval invasion of the barley roots, and the second fumigation with the same fumigant in 1966 decreased it by a further 50–60%. The anomalous effects of formalin were again evident (*Rothamsted Report* for 1965, p. 149, and for 1966, p. 143). Applied in 1965 and 1966 it increased the number of larvae in the roots by 50%. Treatment with chloropicrin, methyl bromide, dazomet and "D-D" in 1965 only, increased yields from 23·4 to 27·7, 34·1, 28·4 and 31·7 cwt grain/acre, whereas treatments in both 1965 and 1966 increased yields to 31·0, 30·1, 30·4 and 32·4 cwt/acre respectively. Plots given 0·4 cwt N/acre and treated with formalin in 1965 only yielded half the grain harvested from controls: giving 1·2 cwt N/acre brought the yield to the same as that from controls. Plots treated with formalin in 1965 and 1966 yielded two-thirds as much as the untreated plots with 0·4 cwt N/acre and slightly less than the controls with 1·2 cwt N/acre. Effects on straw yields were similar to grain yields, except that the beneficial effects of "D-D" and methyl bromide were greater. Cereal cyst-nematode eggs in the soil after harvest were most abundant in plots that received formalin in 1965 and 1966 (18 eggs/g soil) and fewest after chloropicrin in 1965 and 1966 (2 eggs/g): untreated plots had 5 eggs/g.

In an experiment sown with wheat (variety Kloka) at Woburn to test the residual effects of "D-D" and dazomet (*Rothamsted Report* for 1966, p. 144), plots were split so that comparisons could be made between treatments applied in 1966 and 1967 and in 1966 only. All treatments controlled larval invasion of roots. After 2 years' treatment with dazomet at 100, 200 and 400 lb/acre the nematode was barely detectable and invasion slight after 400 lb/acre dazomet in 1966 only. Grain yields were best after dazomet at 200 and 400 lb/acre for two years (55 and 57 cwt/acre at 1·0 cwt N/acre compared with 52·1 cwt/acre with controls). The yields from plots treated with dazomet in 1966 were only equal to or less than those from controls, especially at 0·5 cwt N/acre (26 cwt/acre compared with 38 cwt/acre). "Take-all" fungus was prevalent on plots fumigated with dazomet in 1966 (see p. 137). Many plants on "D-D"-treated plots were conspicuous because of the white-tipped ears; a similar harmful effect was

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noted in an experiment at Rothamsted (see p. 138), but not in another experiment in an adjoining field at Woburn fumigated at almost the same time and planted with the same variety. The damage increased with increasing amounts of "D-D" and nitrogen. ("D-D" at 200 lb/acre, N 0·5 cwt/acre, 10% ears affected; "D-D" at 400 lb/acre, N 1·5 cwt, 27%, and "D-D" at 800 lb/acre, N 1·5 cwt/acre, 46%). (Assessed by D. Ebbels, Plant Pathology Department.) Increasing N had the greater effect. The largest grain yield attained with "D-D" was from treatment in 1966 with 800 lb/acre and 1·0 cwt N/acre in 1967. (Control 52·0 cwt/acre, treated 55·7 cwt.) The smallest yield, 35 cwt/acre, followed "D-D" at 800 lb/acre in 1967 at 1·5 cwt N/acre; at the same N rate 400 lb/acre "D-D" gave 45 cwt.

Soil samples taken in February 1967 from plots treated with sterilants in November/December 1966 demonstrated pronounced effects on ammonium nitrogen. Untreated plots averaged 3·1 ppm N, dazomet at 400 lb/acre 20·2 ppm N and "D-D" plots ranged from 8 to 11 ppm N. Amounts of ammonium nitrogen did not increase so markedly with increased rates of "D-D" as with increased rates of dazomet. This is possibly because of the large amount of N in the dazomet molecule. As in other experiments at Woburn and Rothamsted, *H. avenae* failed to multiply in untreated plots. (Williams with Salt and Ebbels, Plant Pathology Department)

Spring barley segregates resistant and susceptible to *H. avenae*, kindly provided by Dr. J. D. Hayes of the Welsh Plant Breeding Station, were sown on a site where formalin applied in previous years had increased the population and on an adjacent site, which had not recently grown cereals, and contained few *H. avenae*. Although similar numbers of larvae invaded the roots of resistant and susceptible plants on the heavily infested site (180/g root), the numbers of female *H. avenae* in May differed greatly (3/g root in resistant plants, 42/g in susceptible). On the heavily infested site resistant and susceptible barleys yielded similarly, whereas on the slightly infested site the susceptible segregate outyielded the resistant one

TABLE 11

Yields of resistant and susceptible barley at sites heavily and lightly infested with cereal cyst-nematode (grain, cwt/acre)

	0·4 cwt N/acre	0·8 cwt N/acre	1·2 cwt N/acre	Mean
Heavily infested site				
Resistant	14·7	21·1	26·2	20·7
Susceptible	14·6	22·1	28·6	21·8
Lightly infested site				
Resistant	16·8	27·7	27·3	23·9
Susceptible	23·6	27·4	38·3	29·8

by 21% (Table 11). This difference was not, however, significant, due to the high standard error per plot—31%.

The numbers of *H. avenae* after harvest were 15 eggs/g after susceptible and 6 eggs/g after resistant barley. Before sowing, the numbers were 24 and 20 eggs/g. The susceptible barley segregate did not maintain the numbers built up on spring wheat in 1966. An unexpected result of this

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experiment was that the formalin applied in 1966 (which had no detectable effect on yield in 1966 or on root invasion in 1967) produced 20 eggs/g at the end of 1967, double that in the untreated plots; yet another instance of the curious effect of formalin on the multiplication of *H. avenae*. Formalin seems to remove some as yet unknown factor that restricts *H. avenae* but not the potato cyst-nematode, *H. rostochiensis*, which multiplies abundantly in Woburn soils.

To assess the effects of trap-cropping and fumigation on *H. avenae* in crops free from "take-all", a site was prepared by sowing a uniform oat crop in March 1966. In May 1966 strips were rotavated to kill *H. avenae* larvae developing in the oat roots, and a further set of rotavated strips was fumigated with "D-D" at 400 lb/acre. *H. avenae* did not increase much on the oats allowed to grow to maturity and numbers after harvest were small, but the treatments greatly affected the invasion by larvae of the barley and wheat sown in 1967 and had some effects on yields (Table 12). Barley was less invaded than wheat, and its yield was increased less.

TABLE 12

H. avenae *invasion and yields of spring wheat and barley following oats in 1966*

	Harvested	Rotavated May	Rotavated and fumigated
	OATS 1966		
H. avenae/g soil (before fumigation)	1·4	0·3	(0·3)
	WHEAT 1967		
H. avenae/g root	58·2	21·8 N.S.	9·0***
Grain, cwt/acre	34·7	36·9 N.S.	41·1*
	BARLEY 1967		
H. avenae/g root	33·4	18·5**	5·3***
Grain, cwt/acre	34·1	36·5 N.S.	37·3 N.S.

(Williams)

Effect of herbicides in minimum tillage. Nematode population changes over two years were observed in an experiment at Woburn comparing the effects on a wheat crop of minimum tillage using paraquat with conventional ploughing. Part of the experiment also assessed the effects of a soil-applied insecticide mixture consisting of DDT, chlordane, diazinon and zinophos. Nematodes were identified into nine generic, family and super-family groups. Spring wheat was grown in 1966, the first year after permanent grass, and winter wheat in 1967. The principal parasitic nematodes present were *Pratylenchus neglectus*, *P. crenatus*, *Tylenchorhynchus dubius*, *T. brevidens*, *Paratylenchus curvitatus*, *Hemicycliophora*, sp. nr *similis*, *Trichodorus primitivus* and *Longidorus elongatus*.

In the first year, *Pratylenchus* spp. were significantly fewer in roots and soil of the paraquat-treated plots than in the ploughed plots. In the second year the numbers were similar except in March, when roots of plants from paraquat-treated plots had fewer than those from ploughed plots. The total number of plant-feeding nematodes decreased from March to July 1966, mainly because *Tylenchorhynchus*, a residue from the grassland, became fewer. Total plant feeders were fewer in paraquat-treated plots in

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July 1966, but there was no significant difference at other times. Counts of all nematodes (plant feeding and other) in the soil did not differ significantly between treatments at any time, but there were fewer nematodes within roots in July 1966 and March 1967 in paraquat-treated than in ploughed plots. The insecticide mixture significantly depressed *Pratylenchus* spp. and the totals of plant feeding nematodes in July 1966, but at no other time.

The only result of interest so far in this experiment is the depression of *Pratylenchus* spp. in direct-seeded plots, which was greatest in March 1966 on the day the paraquat was applied. The direct-seeded (paraquat) plots were pre-treated with a herbicide containing amino-triazole and *Pratylenchus* spp. are thought to have been affected by this herbicide, because in the second year, when it was not used, populations on paraquat-treated and ploughed plots were similar. (Corbett and Webb)

Root ectoparasitic nematodes of sugar beet

The bionomics and control of stubby root nematode, *Trichodorus* spp. and of the needle nematode, *L. attenuatus*, causal agents of Docking disorder, were further studied in experiments at Docking and Gayton (West Norfolk), and Thornton (East Yorkshire). Experiments at Gayton to study the bionomics and control of *L. attenuatus*, *Trichodorus* spp. and other plant-parasitic nematodes, begun in 1965 after a poor crop of sugar beet in 1964, were completed. Plots of unfumigated soil, some of which grew crops of sugar beet, barley, red clover or ryegrass, while others were kept bare or left to grow weeds in 1965 and 1966, were sown with sugar beet in 1967; so, too, were plots fumigated with 33½ gal/acre "D-D" or chloropicrin in February 1965 and which had also grown sugar beet in 1965 and 1966. *Trichodorus* (mainly *T. cylindricus*) was abundant (about 4000/l soil) in the topsoil of the unfumigated plots where beet was grown each year, and these plots were most severely stunted in June. *L. attenuatus* was very numerous before sowing in 1967 only in those plots that grew red clover in 1965 and 1966 (140/l soil). Plots least affected by Docking disorder were those previously bare fallowed or those which grew ryegrass and were treated with "D-D" or chloropicrin in 1965, in which *Trichodorus* and *Longidorus* were still few in 1967 (Table 13). Herbicide was not used on these plots between 1965 and 1967, so Docking disorder can occur without the debilitation of seedlings sometimes caused by herbicides. Sugar yields in 1967 were less in the unfumigated plots where beet was grown continuously and in the plots where weeds grew in 1965 and 1966 than in plots fumigated in 1965 or those that had grown other crops in 1965 and 1966. The tops and roots were removed from all the beet plots in 1965 and 1966, so the responses to "D-D" or chloropicrin in 1967 were not from ploughing in the extra tops obtained from the first and second crops after fumigation.

In another experiment significant increases in yield were also obtained with sugar beet in 1967 after barley in 1966, where all the topsoil or only the soil under the predetermined beet rows was fumigated in February 1965 with "D-D" (Table 13). On light land at Herringswell (West Suffolk), barley in 1967, following sugar beet in 1966, yielded much more in soil

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TABLE 13

Residual effects of "D-D" and previous crops on yield of sugar

February 1965	Previous crops or treatments 1965	1966	Yields sugar cwt/acre 1967
			Gayton, Norfolk
	Sugar beet		37·0
33½ gal "D–D"/acre	,,		52·4***
33½ gal chloropicrin/acre	,,		50·0***
	Barley		48·15***
	Red clover		52·3***
	Ryegrass		55·0***
	Bare fallow		59·0***
	Weeds		42·2
L.S.D. (5%)			5·5
14 gal "D–D"/acre in the rows	Sugar beet	Barley	50·9***
19 ,, ,, ,,	,,	,,	54·2***
38 ,, ,, ,,	,,	,,	54·1***
24 ,, ,, overall	,,	,,	51·4***
34 ,, ,, ,,	,,	,,	51·4***
None, Control	,,	,,	39·7
L.S.D. (5%)			4·6

December 1965	1966	*Docking Norfolk*	*Thornton E. Yorks*
33½ gal "D–D"/acre	Sugar beet	30·2***	20·5*
None, control	,,	14·1	16·0
33½ gal "D–D"/acre	Barley	36·7**	33·5**
None, control	,,	23·3	26·7
L.S.D. (5%)		7·5	3·7

injected with "D-D" at 12 or 24 gal/acre in January 1966 than in untreated soil. In a similar experiment at Gayton Thorpe, however, there was no response by barley to "D-D" applied in January 1966 for sugar beet (Table 14).

Field experiments to study the bionomics and control of *Trichodorus* spp., begun in 1966 after poor crops of sugar beet at Thornton (East Yorkshire) and Docking (West Norfolk), were completed. At both sites in

TABLE 14

Residual effect of "D-D" on yield of barley grain at 15% moisture (cwt/acre)

Treatments Winter 1965/66	1966	Gayton Thorpe N_1 (1966)	Gayton Thorpe N_2 (1966)	Herringswell
"D–D"				
6 gal/acre	Sugar beet	26·5	25·8	31·4
12 ,,	,,	23·5	20·6	38·2*
24 ,,	,,	25·2	27·1	36·6*
Untreated	,,	19·8	24·5	28·5
L.S.D. (5%)		7·3		7·1

* Sugar beet plots split for N in 1966, N_1 (150 units) and N_2 (300 units).

1967 Docking disorder was severe. *Trichodorus* was more abundant on both sites in plots after sugar beet in 1966 than after barley, and sugar yields were larger in 1967 after barley than after beet. At Docking sugar yields in 1967 were greater from plots treated with 33½ gal/acre "D-D" in December 1965 than from untreated plots, but at Thornton, where the fertiliser was applied 7 weeks before sowing beet responded to "D-D" applied in

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December 1965 only after barley (Table 13). At harvest 1967, *T. anemones* was abundant in all plots at Thornton, but at Docking *Trichodorus* (*T. cylindricus*, *T. teres*) was rare in the topsoil. In another experiment at Thornton, land heavily infested with *T. anemones* (3000–7000/l soil in February 1967) grew a very poor beet crop in 1967. 750 *T. anemones* were washed off 1 g of roots in very stunted seedlings in May, whereas only 40 were washed off 1 g of roots of less stunted seedlings. On this site stubby root injury was severe, tap roots became moribund and the harvested roots were small and very fangy.

On a field at Docking where sugar beet was badly injured by *T. cylindricus* in 1967, 9 gal/acre ethylene dibromide applied under the plough sole

TABLE 15

Effect of different doses of ethylene dibromide injected at ploughing on 1 September 1966 on 1967 yield of sugar (cwt/acre) at Docking, Norfolk to control Trichodorus

Treatment Ethylene dibromide	Rotavated after 3 weeks	Not rotavated
3 gal/acre	30·2	27·3
5 ,,	27·8	29·8
9 ,,	41·7*	42·4**
Untreated	30·3	28·3
L.S.D. (5%)	9·4	

during ploughing 9 in. deep on 1 September 1966 and followed by rolling controlled the nematodes well and greatly increased sugar yields. Although 5 or 3 gal/acre controlled *Tylenchorhynchus dubius*, it did not control *Trichodorus* and did not increase sugar yields (Table 15). Rotavating half plots to assist aeration 3 weeks after ethylene dibromide was applied neither controlled nematodes nor increased yields. Applying 11 gal/acre "D-D" under the plough sole during ploughing 9 in. deep controlled *T. cylindricus* in the soil 0–8 in. deep better when done in September than in

TABLE 16

Effect of time of ploughing in "D-D" (11 gal/acre) on yield of sugar, control of Trichodorus *at Docking, Norfolk*

Treatment	Sugar cwt/acre
September	
"D–D"	41·0
Untreated	24·3
November	
"D–D"	35·5
Untreated	23·0
December	
"D–D"	24·7
Untreated	20·9

November, and was ineffective in December. Similarly, sugar yield was increased significantly by doing it in September. Treatment in November was less effective and in December ineffective (Table 16). During ploughing in early November 1966 "D-D" injected in rows 10 in. deep and 18 in. apart, and marked at intervals of 12 ft by winter wheat drills, controlled *T. cylindricus* poorly in the top 8 in. of soil but well in the layer 12–20 in.

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deep, and greatly increased the yield of sugar beet sown in the treated rows (Table 17). Four gal/acre "Telone" (1,3-dichloropropenes and related C_3 hydrocarbons) injected 8 in. deep through tines into the soil close to beet rows at sowing, or 3 lb/acre "Lannate" (*S*-methyl-*N*-methylcarbomoyl-oxythioacetimidate) sprayed in a 6-in.-wide band over the beet rows at

TABLE 17

Effects of applying nematicides to beet rows at Docking, Norfolk, sugar yields in cwt/acre

Treatments		Applied in winter beneath predetermined rows	Applied to rows in spring
Untreated		23·1	22·1
"D–D"	2 gal/acre	21·8	
	4½ ,,	29·4	
	9 ,,	42·7**	
"Telone"	4 ,,		45·9***
	8 ,,		40·4**
	16 ,,		35·1*
"Temik 10G"	8 lb/acre		37·2*
	16 ,,		35·9*
	32 ,,		31·6
"Lannate"	3/4 ,,		28·3
	1½ ,,		34·8*
	3 ,,		43·1***
L.S.D. (5%)		9·5	11·3

drilling, controlled *T. cylindricus* well and greatly increased sugar yields. 8 lb/acre "Temik 10G" (10% granular formulation of 2-methyl-2-methylthio propionaldehyde *O*-methyl carbamoyl oxime), applied in a band over the beet rows 7 days after drilling and lightly raked in, gave moderate control of *T. cylindricus* and significantly increased sugar yield. (Whitehead and Tite)

Conjoint work

Work on growth-regulatory substances and galling by root-knot nematodes was done jointly with the Botany Department (Wheeler and Setty, see p. 104). Work was also done on *Pratylenchus* spp. attacking wheat (Corbett and Webb), on root ectoparasitic nematodes harmful to crops at Woburn (Mojica) and the fine structure of cyst-nematodes (Shepherd and Dart, Microbiology Department).

Staff and visiting workers

Dr. C. J. Nusbaum, Dr. R. A. Rohde and Dr. J. D. Radewald (U.S.A.), Mr. N. Kyrou (Greece), Mr. A. Alfaro (Spain) and Mr. G. Reversat (France) visited the department. Mary T. Franklin, C. D. Green, K. G. H. Setty, Audrey M. Shepherd and T. D. Williams attended the IXth International Symposium of the Society of European Nematologists in Warsaw, and F. G. W. Jones visited the National Agricultural Station, Oeiras, Portugal. Members of the Department assisted with courses at Imperial College Field Station and at the School of Agriculture, Cambridge.

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