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Nematode Problems in the Woburn Ley–Arable Experiment, and Changes in *Longidorus leptocephalus* Population Density Associated with Time, Depth, Cropping and Soil Type

K. EVANS

Introduction

The Woburn Ley–Arable experiment was begun in 1938 to test the effects on soil fertility of a 3-year grazed ley, 3 years of lucerne (cut) and 3-year arable rotations which include either a 1-year ley or no ley. The effects of these crop sequences were measured by the yields of two successive test crops, a root crop and a cereal until 1976 (except for the period 1968–70 when both test crops were barley). Each rotation therefore has five courses (see Table 1 for the cropping scheme from 1956 to 1967 and the changes in cropping since 1956) and there are five blocks, one for each phase of the cycle; each course of each rotation is present every year. There are eight whole plots in each block and four of these carry the same rotation repeatedly ('continuous' plots). The other four plots carry the four rotations in succession ('alternating' plots) to give 20-year rotations. The overall sequences are shown in Table 2, from which it is clear that the four 'alternating' plots in each block are always one in each rotation every year. For further details of basal and experimental treatments see Rothamsted Experimental Station (1970).

TABLE 1

Cropping scheme over 5 years, Woburn Ley–Arable experiment, 1956–67

Rotation	Year: 1	2 (Treatment)	3	4 (Test crops)	5
Grazed ley		3 year grazed ley		Sugar beet	Barley
Lucerne/sainfoin		3 year lucerne cut for hay		Sugar beet	Barley
Arable (hay)	Potatoes	Rye	Hay	Sugar beet	Barley
Arable (roots)	Potatoes	Rye	Carrots	Sugar beet	Barley

Changes in the cropping:

1956 Sugar beet replaced potatoes as first test crop
1964 Sainfoin replaced lucerne
1966 Maris Piper replaced Majestic as the potato variety
1968 Barley replaced sugar beet as first test crop
1971 Potatoes replaced barley as the first test crop
1972 Clover replaced sainfoin, wheat replaced barley as second test crop and barley replaced carrots and rye
1976 Major changes were introduced in order to allow studies of soil organic matter content

TABLE 2

Cropping sequences in the Woburn Ley–Arable experiment, 1938–75

	Continuous		Alternating
1	Grazed ley (L)	1	L, Ah, Lu, A
2	Lucerne for hay (Lu)	2	Lu, A, L, Ah
3	Arable with hay (Ah)	3	Ah, L, A, Lu
4	Arable with roots (A)	4	A, Lu, Ah, L

The continuous rotations are 5-year sequences and the alternating rotations are 20-year sequences

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TABLE 3

Yields of first treatment crop potatoes (total tubers, t ha⁻¹) from Block 4 only

Rotation		1955	1960	1965	1970	1975*
Grazed ley	Alternating	19·4	38·6	42·9	35·4	13·7
Lucerne/sainfoin	Alternating	14·7	37·3	36·2	29·1	12·0
Arable (hay)	Continuous	4·8	31·2	10·2	24·3	10·3
Arable (roots)	Continuous	3·8	26·6	12·9	26·3	12·9

*Very dry summer

Population density of Globodera rostochiensis *Ro1 in the continuous arable plots*

	eggs g^{-1} soil				
Block:	1	2	3	4	5
Year					
1956	10	1	16	89	9
1970	4	0	8	91†	3

†Large population remaining from the last susceptible potato crop in 1965

Until 1956 the first test crop and first treatment crop in the arable rotations were both potatoes. In 1955 the eighth crop of potatoes in 18 years was grown as first treatment crop potatoes in the continuous arable sequences of Block 4. The yield was very poor on the continuous arable plots and below average on the alternating plots (six potato crops in 18 years). Soil samples taken the following year showed there were serious infestations of potato cyst-nematodes (*Globodera rostochiensis*, pathotype Ro1) on these plots with moderate infestations on many others. For this reason sugar beet was substituted for potatoes as first test crop in 1956. The effects that this and the introduction in 1966 of the *G. rostochiensis* Ro1 resistant variety of potato Maris Piper had on potato yields in Block 4 (and cyst-nematode populations in all five blocks between 1956 and 1970) are in Table 3. Potato yields improved in 1960, perhaps because of a cyst-nematode population crash in 1955 or the much greater than average summer rainfall of 1960, but were poor again in 1965, the last year that the susceptible variety Majestic was grown. Even in 1970, some 5 years after the last susceptible potato crop, an average population density of 91 eggs g^{-1} of soil was found in Block 4. Such a population density would cause significant yield loss even in cyst-nematode resistant varieties, which prevent nematode reproduction but do not necessarily tolerate the damaging effects of invasion by juveniles (Evans & Franco, 1979). By 1975 populations were much smaller, but any effect that they had on yield was masked by the effects of an extremely dry summer, when yields averaged only 12·2 t ha^{-1}.

Stem eelworm (*Ditylenchus dipsaci*) became troublesome in lucerne plots in 1958 and after unsuccessful efforts to control it by sowing fumigated seed and treating plots with thionazin, metham sodium and 'D-D', sainfoin (*Onobrychus viciifolia* Scop.) was grown instead from 1964 followed by red clover (*Trifolium pratense* L.) from 1972. Further information on treatments is in Rothamsted Experimental Station (1978).

Yields of the potato crops

Despite the introduction of the cyst-nematode resistant variety Maris Piper and comparatively few potato cyst-nematodes on Blocks 2 and 1, yields from the first treatment crop potatoes in the continuous arable sequences were still small in 1966 and 1967 (19·3 and 7·8 t ha^{-1} respectively, compared with 36·0 and 22·4 t ha^{-1} respectively in the alternating sequences). It was thought that free-living nematodes might be damaging the potato roots. Also in July 1967 the fungus *Verticillium* was found infecting 38% of stems

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of the continuous arable (with roots) series but only 6% of stems in the alternating series. *Rhizoctonia* was equally widespread in both series.

Fumigating the soil with chloropicrin was expected to control nematodes (both cyst-forming and free-living) and soil-borne fungi but not tuber-borne fungi. Accordingly, in 1968, plots in Block 3 were split to test the effects of seed tubers dusted with 50% thiram and choropicrin injected at 440 kg ha^{-1}. Potato yields are in Table 4. Thiram had no

TABLE 4

Effects of chloropicrin fumigation and thiram seed treatment on first treatment crop potato yields in 1968

total tubers, t ha^{-1}, Block 3

Rotation	No chloropicrin	Chloropicrin at 440 kg ha^{-1}	No thiram	Thiram
Grazed ley	44·6	52·8	48·0	49·5
Sainfoin	45·5	55·3	52·2	48·7
Arable (hay)	21·4	48·2	35·9	33·6
Arable (roots)	22·7	53·6	35·4	40·9
Mean	33·6	52·5	42·9	43·2

effect on yield even though thiram-treated seed was also chitted and emerged earlier than the undusted, unchitted seed. Chloropicrin increased yields on average from 33·6 to 52·5 t ha^{-1} and the increase was much greater in the continuous arable series than in the alternating series. Control of fungal pathogens was probably not responsible for this increase as only traces of *Verticillium* were found even in the untreated plots and *Rhizoctonia solani* was more common on plants from fumigated plots. Samples of washed fine roots from untreated soil were plated on water agar and 22% yielded *Pythium*, 16% *Phoma*, 12% *Cylindrocarpon*, 6% *Cephalosporium*, 4% *Verticillium*, 4% *Polyscytalum* and 3% *Rhizoctonia*. Those from fumigated soil yielded less *Pythium* (11%) and *Cylindrocarpon* (6%) but similar or increased amounts of the other genera. *Pythium* and *Cylindrocarpon* were equally common on the continuous and alternating series, so it is unlikely that they contributed significantly to the poor growth of potatoes in the continuous arable series (Salt, 1969).

Fumigation with chloropicrin undoubtedly controlled nematodes, but whether the improved yields were due entirely to nematode control and if so which genera of nematodes, was uncertain. Samples in 1969 showed that even after growing the resistant variety Maris Piper the continuous arable (with hay) plots still contained an average of 23 eggs g^{-1} soil of potato cyst-nematode and the continuous arable (with roots) plots an average of 13 eggs g^{-1} of soil. Since these counts probably reflect pre-planting populations of some 40–70 eggs g^{-1} of soil in 1968, control of potato cyst-nematodes was probably largely responsible for the increases in yield obtained in 1968 following chloropicrin fumigation.

When the oxime carbamate nematicide aldicarb ('Temik') became available it provided an opportunity to test the effects of controlling nematodes without the complications of soil fumigation. Treatments for the potatoes on Block 5 in 1969 (first treatment crop) therefore included both nematicide (aldicarb) at 11 kg ha^{-1} a.i. and chloropicrin at 440 kg ha^{-1}. The yields and pre-planting cyst-nematode population densities are in Table 5. Both aldicarb and chloropicrin increased yields significantly, and both together gave greater yields than either alone. Yields from the untreated plots were poorest on the continuous arable sequences and this was also true of plots treated with aldicarb. When chloropicrin was applied, however, either with or without aldicarb, yields from the continuous arable plots were almost as good as those from the alternating plots. Since the

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TABLE 5

Effects of chloropicrin and aldicarb on first treatment crop potato yields in 1969

total tubers, t ha⁻¹, Block 5

Rotation	No treatment	Aldicarb 11 kg ha^{-1} a.i.	Chloropicrin 440 kg ha^{-1}	Aldicarb plus chloropicrin	*G. rostochiensis* (eggs g^{-1} soil)
Grazed ley	45·0	51·9	47·6	56·3	<1
Sainfoin	46·7	51·1	57·0	59·4	<1
Arable (hay)	34·7	42·6	52·6	55·4	8
Arable (roots)	34·5	41·4	44·1	47·1	3
Mean	40·3	46·8	50·3	54·6	

cyst-nematode population was below a damaging density it seemed likely that the responses to aldicarb were due to control of ectoparasitic nematodes. (Aldicarb is also a systemic insecticide but no aphid infestations were recorded.) Responses to chloropicrin were greater than those to aldicarb but this is to be expected as chloropicrin controls not only nematodes but also soil-borne diseases and releases mineral nutrients, especially nitrogen.

The numbers and kinds of ectoparasitic nematodes present in treated and untreated plots were estimated from soil samples taken to a depth of 20 cm and extracted by Seinhorst's Two-Flask method (Southey, 1970). The commonest species were *Tylenchorhynchus dubius*, *Paratylenchus microdorus*, *Trichodorus primitivus* and *Pratylenchus neglectus*, with small numbers of *Hemicycliophora typica*, *Longidorus caespiticola*, *Longidorus leptocephalus* and others. *Pratylenchus neglectus* is a migratory root endoparasite and numbers in soil samples do not reveal those in roots. However, these were very few. Although some of the other nematodes damage field crops, none was numerous enough to be injurious, except perhaps *Tylenchorhynchus dubius*. Regression analysis of yield on numbers of this nematode did not reveal a significant correlation but Kyrou (1968) suggested that it may have affected potato yield in another field on Woburn Experimental Farm.

Repeating the experimental treatments in 1970 (with the first treatment crop potatoes on Block 4) again resulted in large yield responses to aldicarb and chloropicrin (Table 6).

TABLE 6

Effects of chloropicrin and aldicarb on first treatment crop potato yields in 1970

total tubers, t ha⁻¹, Block 4

Rotation	No treatment	Aldicarb 11 kg ha^{-1} a.i.	Chloropicrin 440 kg ha^{-1}	Aldicarb plus chloropicrin	*G. rostochiensis* (eggs g^{-1} soil)
Grazed ley	35·4	39·1	52·3	48·2	5
Sainfoin	29·1	42·0	38·7	43·2	6
Arable (hay)	24·3	33·9	39·9	42·3	96
Arable (roots)	26·3	33·9	38·8	40·4	86
Mean	28·8	37·4	42·4	43·5	

Large numbers of cyst-nematodes were present in the continuous arable plots of this block but the responses to soil treatment (especially with chloropicrin) were almost as great in the alternating plots (with few cyst-nematodes). Ectoparasitic nematodes found in the top 20 cm of soil again seemed too few to cause damage but because chloropicrin fumigation penetrates the soil to a greater depth than 20 cm, and because it produced a greater yield increase than aldicarb rotavated into the top 20 cm of soil, samples (5 cm diam. cores) were taken to a depth of 60 cm in those plots where responses to chloropicrin were greatest. Nematodes were extracted using a submerged sieving technique (see

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Appendix) and the numbers of *Longidorus leptocephalus* collected from 10 cm fractions are in Table 7. Very few were found at the normal sampling depth of 0–20 cm or even

TABLE 7

Numbers of Longidorus leptocephalus *litre*$^{-1}$ *of soil in first treatment crop potato plots, 1970*

Rotation	Treatment	Depth in cm 0–10	10–20	20–30	30–40	40–50	50–60	Yield (t ha^{-1})
Grazed ley	Chloropicrin	0	0	0	0	0	0	52·3
	No treatment	0	10	15	220	195	250	35·4
Arable (hay)	Chloropicrin	0	0	0	0	0	20	39·9
	No treatment	0	0	5	160	175	145	24·3

0–30 cm, but large numbers were found between 30 and 60 cm beneath the soil surface. Where chloropicrin was applied the nematode had been virtually eradicated, apart from a few below 50 cm in the arable (with hay) sequence. The yield response which accompanied this eradication was 15·6 t ha^{-1} in the arable sequence and 16·9 t ha^{-1} in the ley, but may not have been due entirely to nematode control (see above).

In 1971 potatoes were grown as the first test crop (on Block 3, where large yield increases after chloropicrin fumigation were obtained in 1968) in place of barley, and the opportunity was taken of comparing cyst-nematode resistant (Maris Piper) and susceptible (Pentland Crown) potato varieties. To test the residual effects from chloropicrin applied in 1967, the 1971 tests compared them with aldicarb and chloropicrin applied in combination. Table 8 gives potato yields and counts of nematodes. Both residual chloropicrin and freshly applied chloropicrin and aldicarb significantly increased yields of both varieties, but the greater response was to the fresh application and this response was greater in Maris Piper than in Pentland Crown. Residual chloropicrin plus fresh treatment did not yield more than fresh treatment alone. Potato cyst-nematode numbers were small and none of the yield differences between the varieties could be ascribed to them. Total numbers of ectoparasitic nematodes (excluding *Longidorus* spp.) were more than 8000 litre^{-1} both in untreated plots and plots fumigated with chloropicrin in 1967, but were only about 3000 litre^{-1} in freshly treated plots. *Longidorus leptocephalus* numbers, however, were much reduced in plots treated in 1967 (5 compared with 180 litre^{-1} in untreated plots) but were only reduced to 55 litre^{-1} by fresh application of chloropicrin

TABLE 8

Effects of chloropicrin and aldicarb on first test crop potato yields (total tubers, t ha^{-1}*) and numbers of nematodes* in 1971*

Block 3 only

	No treatment	Chloropicrin residues (applied autumn '67)	Chloropicrin plus aldicarb	Chloropicrin plus aldicarb plus chloropicrin residues
Yield, Maris Piper	54·1	63·1	72·2	73·9
Yield Pentland Crown	48·0	59·2	63·1	61·8
Longidorus leptocephalus (Number litre^{-1} at 40–60 cm deep)	180	5	55	2
Ectoparasitic nematodes (Number litre^{-1} excluding *Longidorus*)	8410	8110	2905	3305
Globodera rostochiensis Ro1 (Eggs g^{-1} soil)	2	1	1	4

*Nematode counts are means of 30 plots

and aldicarb. Where the fresh applications were combined with chloropicrin residues, numbers of *L. leptocephalus* fell below those found in residual chloropicrin only plots. The failure of the freshly applied chloropicrin to control the nematodes deep down compared with the success of 1967 treatments was probably because the fresh applications were made when the soil was too wet. From Table 8 it is obvious that the large yield increases in plots with chloropicrin residues were not due to cyst-nematodes or ectoparasitic nematodes other than *Longidorus* spp., but may have been due to control of *L. leptocephalus*. Comparing yields from plots with chloropicrin residues and plots freshly treated suggested that control of both *L. leptocephalus* and other ectoparasitic species may have been beneficial. Regression analyses of yield on nematode numbers did not, however, show significant correlations, although both linear and logarithmic regressions suggested that yield might be reduced by over 13·5 t ha^{-1} with 100 *L. leptocephalus* litre^{-1}.

In 1971 in an adjacent barley crop the vertical distribution of *L. leptocephalus* differed from that under potatoes (Fig. 1). Many more were found in the top 20 cm of soil under

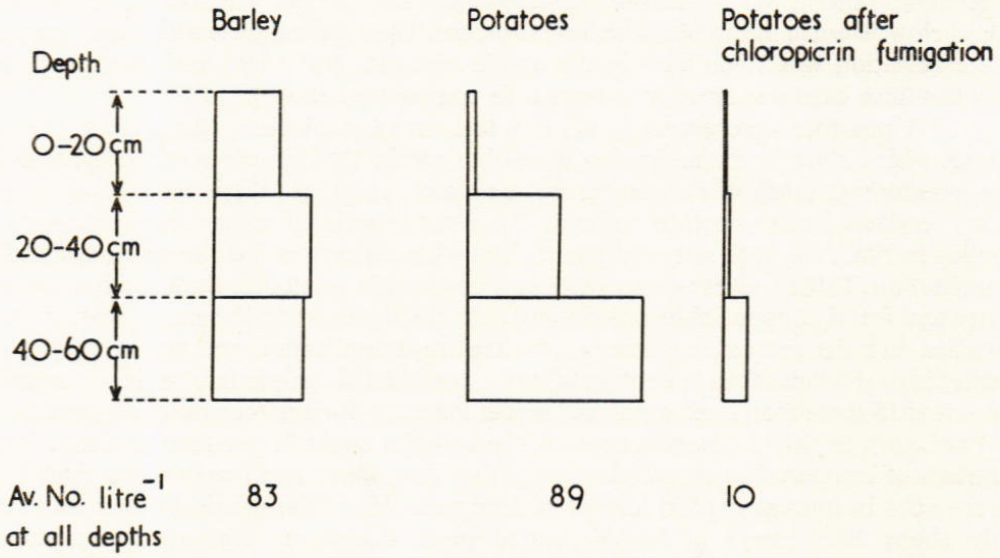

FIG. 1. Vertical distribution of *Longidorus leptocephalus* under barley, potatoes and potatoes after treatment with chloropicrin (figures are means of four plots for barley, 16 plots for potatoes).

barley than under potatoes. As the seedbed preparation for the potatoes included rotavation some of the nematodes may have suffered physical damage and been killed. A test in 1972 of seedbed preparation by spring-tine harrow versus rotavation resulted in the same vertical distribution in both treatments, with slightly more nematodes in the top 20 cm after rotavation than after harrowing. It was concluded that the vertical distribution found under potatoes on this site was from the disturbance of the top 20 cm of soil to form ridges and its rapid drying.

Further tests of nematicides plus fumigants, applied before the potato crops, were made using chloropicrin and aldicarb at 440 and 6·6 kg a.i. ha^{-1} in 1973, and dichloropropene ('Telone') and aldicarb at 220 and 6·6 kg a.i. ha^{-1} in 1974. Treatment with nematicides increased yields and decreased numbers of nematodes. Table 9 shows that the numbers of different nematode genera are all strongly correlated. However, the genera are ranked in Table 10 in order of significance of the covariate variance ratio when numbers of each genera were fitted in turn in covariate analyses of yield. Without covariates, factors other than fumigation accounted for 30% of the variance but when

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TABLE 9

Correlations ($n - 2 = 30$) between log numbers of ectoparasitic nematodes: first test crop potatoes, Block 2, 1974

	Heterodera	*Para-tylenchus*	*Pra-tylenchus*	*Tylencho-rhynchus*	*Tylenchus*	*Longidorus*
All species	**0·55**	**0·67**	**0·69**	**0·85**	**0·72**	**0·74**
Longidorus	**0·55**	0·52	0·51	**0·61**	**0·61**	
Tylenchus	0·43	0·35	**0·55**	**0·64**		
Tylenchorhynchus	0·39	**0·69**	0·50			
Pratylenchus	0·33	0·35				
Paratylenchus	0·02					

$r = 0{\cdot}35, 0{\cdot}45$ and $0{\cdot}55$ for $P < 0{\cdot}05, 0{\cdot}01$ and $0{\cdot}001$ respectively

TABLE 10

Nematode genera ranked in order of significance as covariates in covariate analyses of yield: first test crop potatoes, Block 2, 1974

Nematodes	Numbers in nematicide treated plots as % of untreated	Variance ratio for covariate	Probability point (%)
1 *Longidorus*	8	15·6	0·13
2 *Tylenchorhynchus*	13	11·7	0·38
3 *Paratylenchus*	39	11·1	0·46
4 *Heterodera*	7	8·3	1·10
5 *Pratylenchus*	11	7·4	1·60
6 *Tylenchus*	28	4·5	5·10
All species	16	13·2	0·25

numbers of *Longidorus* were fitted as covariate the percentage of the variance accounted for rose to 66%. All nematode species were fewer in nematicide treated plots than in untreated plots but numbers of *Paratylenchus* and *Tylenchus* decreased less than other genera. *Longidorus* apparently had the greatest effect on yield with *Tylenchorhynchus* second. Perhaps several species of ectoparasitic nematodes contribute to the potato yield losses, their relative effects varying with the season.

A *Longidorus* population between 30 and 60 cm beneath the soil surface would damage only deep roots, so that its effect on yield would be more noticeable in years with dry summers, when deep roots become important for water uptake. Observations in the field certainly suggested that potatoes in plots without fumigant or nematicide wilted and senesced suddenly in hot, dry spells. Jones (1975) discussed the effects of accumulated temperature and rainfall on ectoparasitic nematodes active near the soil surface (e.g. *Tylenchorhynchus*), and in a free-draining soil such as that of the Woburn Ley–Arable experiment they would be expected to decrease crop yield most in years when May rainfall is heavy, so allowing maximum nematode activity while young roots are developing. Fig. 2 records spring and summer rainfalls and their deviations from the long-term mean, responses of potato yield to fumigation treatments and pre-planting potato cyst-nematode populations (means of all plots) for the years 1968 to 1974. Greatest responses were obtained in 1968 and 1970 when potato cyst-nematode populations were greatest (up to 70 and 96 eggs g^{-1} soil respectively), but significant responses were obtained in all other years. Responses tended to be greater when spring rainfall was copious (encouraging *Tylenchorhynchus* activity) or summer rainfall was slight (increasing the effects of *Longidorus* damage), with the smallest response in 1974 when potato cyst-nematodes were virtually absent and spring rainfall was least. However, July rainfall in 1974 was below average and regression of yield on *L. leptocephalus* numbers (transformed to log $(x + 1)$) was significant at $P < 0{\cdot}05$. Thus it seems that potato yields in this experiment can only

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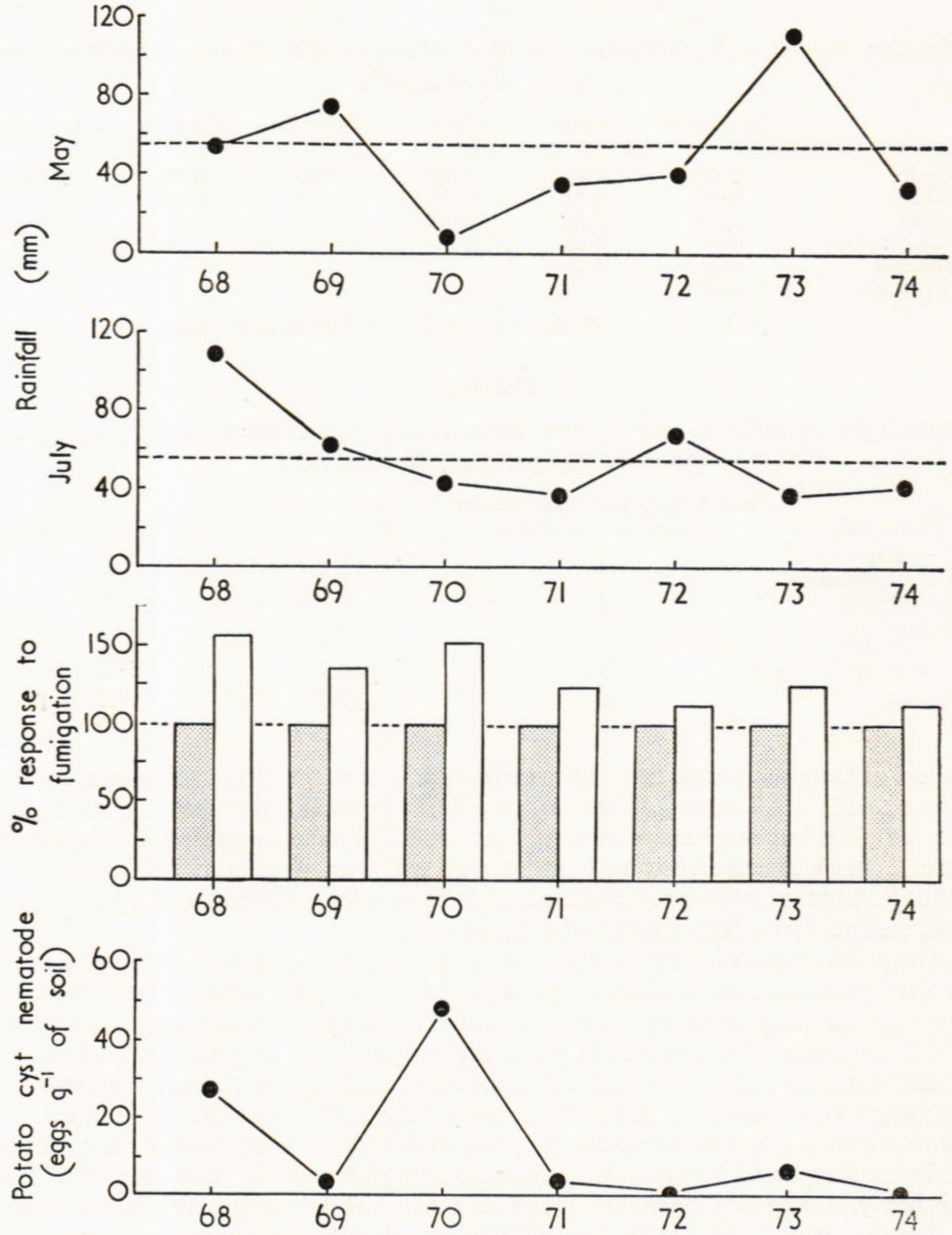

FIG. 2. May and July rainfalls, potato yield responses to fumigants, and potato cyst-nematode populations in the Woburn Ley–Arable for the years 1968–74.

be related to ectoparasitic nematode population densities when the effects of season are also taken into account: unlike cyst-nematodes, which pass most of their life in a protected environment inside the root, the influence and activity of ectoparasitic nematodes is greatly affected by season, especially by rainfall.

The population dynamics of *Longidorus leptocephalus*

Measurements of *L. leptocephalus* from the experiment (Table 11), although slightly different from those in Anon. (1973), show that the population is the 'large form'. Since

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TABLE 11

Measurements (μm) of juveniles and adult females of Longidorus leptocephalus *found in the Woburn Ley–Arable experiment*

Stage:	J1	J2	J3	J4	†Female
Number measured	48	59	30	27	28
Mean body length	1176 (±13) 826–1400*	1811 (±20) 1470–2130	2674 (±36) 2310–3040	3668 (±45) 3170–4290	5083 (±85) 4050–5800
Distance of vulva from tip of head % body length	—	—	—	—	53 (±0·4) (47–56)
Mean length of odontostyle	45 (±1) 36–60	50 (±1) 32–65	58 (±1) 48–68	64 (±1) 55–81	74 (±1) 67–80
Mean length of odontophore	38 (±1) 27–60	44 (±1) 28–60	52 (±1) 44–84	54 (±1) 41–65	56 (±1) 43–75
Mean length of replacement odontostyle	49 (±1) 28–61	58 (±1) 37–64	66 (±1) 55–72	72 (±1) 59–80	—

*Range
†Males of this species are rare: none was found during this study

little was known of the biology and population dynamics of this species, changes in its numbers and vertical distribution over a 12 month period were followed. Samples were taken with a 5 cm Jarrett auger to a depth of 60 cm in 20 cm fractions at monthly intervals in the winter wheat test crop of 1972 (Block 3) from a plot never treated with nematicide. After harvest the plot was grassed down for its 3-year ley. Eggs were extracted by a modification of the sugar-centrifugation method described by Flegg and McNamara (1968)—see Appendix.

Results are in Fig. 3 where the abbreviations J1, J2, J3 and J4 denote first, second, third and fourth stage juveniles respectively. Total numbers extracted varied from 232 litre^{-1} of soil in May to 650 litre^{-1} of soil in February, so the number of nematodes at each stage is shown as a percentage of the total number for that date. The most striking result was that eggs were recovered in large numbers during June and July only, suggesting that egg laying occurs only once yearly as Flegg (1966) found for *Xiphinema vuittenezi*. A few eggs were recovered between August and December, but these may have been ones which took a long time to hatch and not freshly laid. Most eggs hatched soon after laying as the proportion of J1 increased from 4% in July to 44% in November. However, this increase in J1 was not followed by corresponding increases in subsequent juvenile stages. This suggests that the length of these stages may be long: since most eggs had hatched by August some of the many J1 found in April of the following year before egg laying began must have been 7 or 8 months old. The proportions of J2 varied between 9 and 32%, J3 between 12 and 25% and J4 between 8 and 20%. The absence of seasonal fluctuations in stages J2–4 and in numbers of adult females (which varied between 14 and 31%) suggests that individual nematodes live for more than 1 year and perhaps for several years, a conclusion also reached by Flegg (1968a). Further evidence for the lengthy survival of adults is that each juvenile stage forms a smaller proportion of the population than the previous one whereas adults usually form a greater proportion of the population than all other stages except J1. The long survival of individual nematodes and the life cycle of 2 or even 3 years suggested by Flegg (1968b) would explain the persistent effect on *Longidorus* numbers of chloropicrin applied in good soil conditions in 1967 (Table 8). The numbers of ectoparasitic nematodes other than *Longidorus* had recovered in 1971 to those found in untreated plots, but *Longidorus* numbers remained extremely small.

Fig. 4 shows the age structure of the population at three depths. Flegg (1968c) found the population structures of the species he studied were similar at all depths, but this

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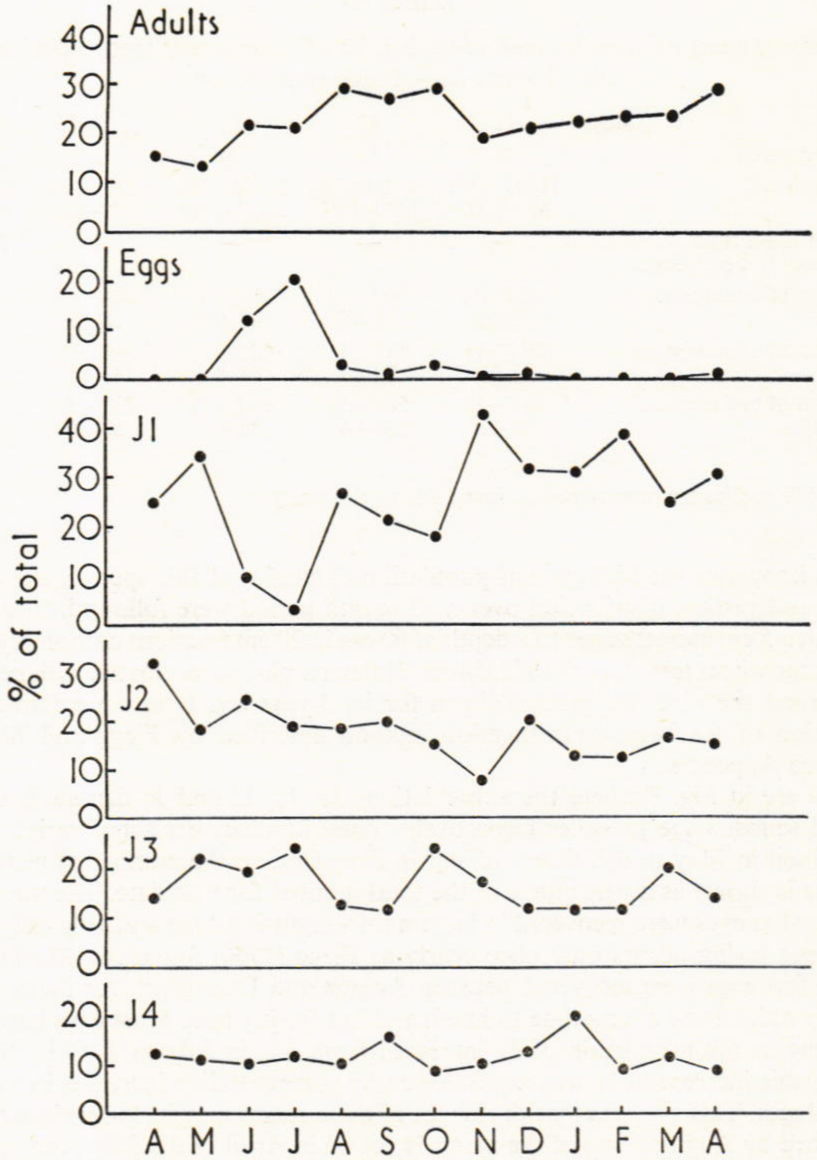

FIG. 3. Percentages of egg, juvenile and adult stages of *Longidorus leptocephalus* in soil to a depth of 60 cm beneath a winter wheat crop (1971–72, followed by a ley from October 1972) in Block 3 of the Woburn Ley–Arable experiment.

was not entirely true for *L. leptocephalus* at Woburn, the greatest variation being found in the top 20 cm. Most adults were 40–60 cm deep (the sudden decrease in numbers after October at this depth may reflect the temporary loss of the food supply when the winter wheat was harvested and the ley sown) and fewest adults were found at 0–20 cm. However, the proportion of females in the top 20 cm tripled between February and April (just before egg laying), with the result that many more eggs were laid in the top 20 cm of soil than elsewhere. Whether this represents migration to the upper soil at a time of year when it is moist and warming up is uncertain but it seems to ensure that eggs are laid where roots will be plentiful. No striking effects of depth on proportions of the juvenile stages were noted but J1 numbers increased in late summer at all depths after the brief period of egg laying in June and July.

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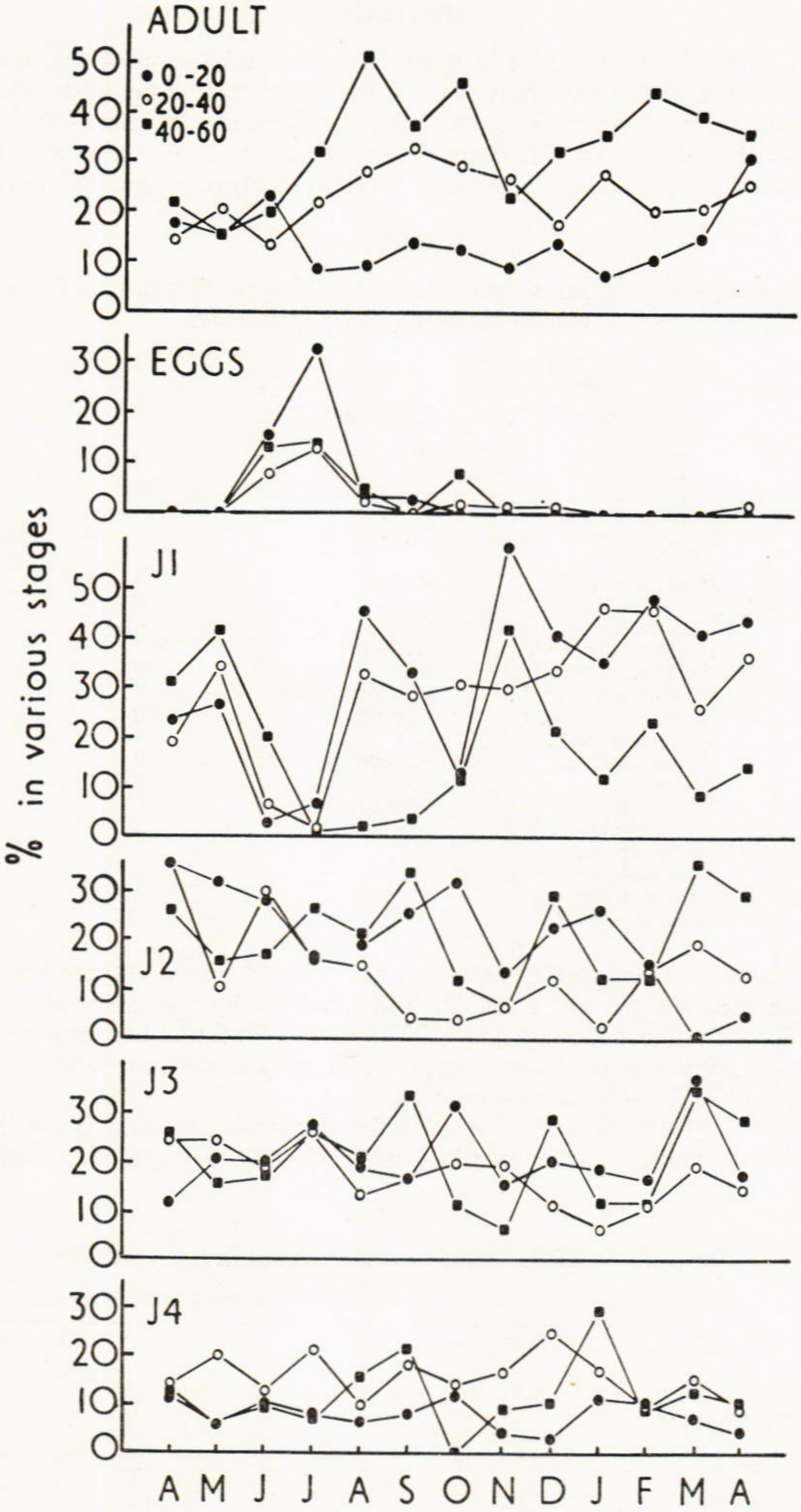

FIG. 4. Depth distribution of egg, juvenile and adult stages of *Longidorus leptocephalus* as in Fig. 3. (● = 0–20, ○ = 20–40 and ■ = 40–60 cm beneath soil surface.)

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Host range

Pot tests. Flegg (1968b) was able to maintain cultures of *Xiphinema* spp. which were started with hand-picked specimens, so it was decided to test the host suitability of various crop and weed species in a pot experiment. One hundred hand-picked, freshly extracted J4 or adult females of *L. leptocephalus* were added to pots containing the plant species listed in Table 12. Six months later the total numbers of nematodes in each pot

TABLE 12

Host range test with Longidorus leptocephalus: *total numbers recovered 6 months after inoculating pots with 100 nematodes*

Host	Variety or line	Number of nematodes
Solanum tuberosum L.	J26 × Maris Piper	0
,, ,,	,, × ,, ,,	1
,, ,,	,, × ,, ,,	0
,, ,,	,, × ,, ,,	11
,, ,,	SP2 × ,, ,,	14
Lycopersicon esculentum Mill.	Moneymaker	1
Hordeum vulgare L.	Zephyr	0
,, ,,	,,	0
Avena sativa L.	Condor	0
Triticum vulgare Vill.	Kolibri	3
Trifolium pratense L.	S123	13
Trifolium hybridum L.	Canadian alsike	0
Medicago sativa (L.)	Dupuits	0
Lolium perenne L.	S23	1
Daucus carota L.	Amsterdam Forcing	0
Allium cepa L.	Ailsa Craig	3
Brassica oleracea var. *capitata* L.	Blood Red	0
Sinapis alba L.	—	2
Chenopodium amaranticolor Coste & Reyn	—	2
Stellaria media (L.)	—	0

were counted. Either the handling procedure and growing conditions were unsuitable or none of the species tested was a suitable host as populations in most pots declined to zero, the largest number found being 14. Thomas (1969) found that crop plants were poor hosts of *Longidorus elongatus*, whereas weeds, grasses and clovers were good ones. *Longidorus leptocephalus* failed to survive on any.

Pitcher and Flegg (1968) studied the extraction of nematodes from soil and found that water containing traces of metal (especially copper) is toxic to dorylaimid nematodes like

TABLE 13

Survival of adult Longidorus leptocephalus *in test solutions*

Test solution	Total numbers of nematodes surviving after									
	16 h	24 h	48 h	72 h	6 days	9 days	13 days	16 days	20 days	24 days
Distilled water	30	25	15	12	11	10	9	8	7	7
Double distilled water	12	12	10	10	10	10	10	10	8	8
Tap water	24	24	4	4	2	1	1	1	0	0
Mains tap water	30	30	30	30	29	28	25	25	22	22
Ringer's solution	30	30	30	30	29	23	11	11	6	6
$CuS0_4.5H_20$ at 2 mg l^{-1}	0	0	0	0	0	0	0	0	0	0
$CuS0_4.5H_20$ at 0·2 mg l^{-1}	30	30	22	21	14	7	7	7	2	2
Cu	0	0	0	0	0	0	0	0	0	0

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Longidorus. To see whether *L. leptocephalus* was affected three batches of ten adult females were placed in various solutions in watch glasses and their activity recorded. The test solutions were: distilled water, double distilled water, laboratory tap water, tap water collected after prolonged flushing of the laboratory tap ('mains tap water'), Ringer's solution, copper sulphate solutions of 2 and 0·2 mg litre^{-1} of distilled water, and distilled water allowed to stand overnight in contact with copper filings. Results are in Table 13. Nematodes survived best in mains tap water, only 24 h in tap water but slightly longer in distilled water; survival seemed slightly poorer if the distilled water was double distilled. Nematodes in Ringer's solution survived almost as long as those in mains tap water but copper sulphate was very toxic, especially at 2 mg litre^{-1} when nematodes died almost immediately, as they did in water that had been in contact with copper filings. It seems, therefore, that mains tap water is not toxic but may pick up toxic substances from pipework (often copper) inside buildings. Distilled water may pick up toxic substances from materials used in the construction of the still.

Field studies. Samples were taken in September 1971 from a number of experimental sites at Woburn Farm where the same crop had been grown for at least 3 years and the population density might be expected to reflect host suitability. Samples were also taken from hedgerows. The numbers of nematodes found at three depths are in Table 14. Many

TABLE 14

Longidorus leptocephalus *in fields of Woburn Experimental Farm, 1971*

Field	Experiment	Treatment	Crop	Number of years continuous cropping	Nematode numbers litre^{-1} at depths (cm) 0–20	20–40	40–60
White Horse Field	Direct seeding	Mechanical cultivation	Winter wheat	6	122	176	107
		Directly seeded	,,	6	177	234	170
Stackyard I	Intensive cereals	Continuous wheat	,,	6	3	18	0
Butt Furlong	Take-all sampling site	—	Barley	5	5	13	8
Butt Close, Series III	Fumigants and irrigation	Unfumigated	,,	4	0	0	0
Stackyard I	Intensive cereals	Continuous barley	,,	6	0	10	10
Road Piece	Tillage on soil properties	(headland)	,,	3	0	5	0
Stackyard D	Woburn Ley–Arable	Continuous ley	Ley	3	5	285	65
Butt Furlong	Fumigation and N	Fumigated	Spring beans	3	0	8	7
		Unfumigated	,,	3	0	10	15
Butt Close, Series IV	Irrigation and eelworms	Unfumigated	Potatoes	6	0	0	0
Stackyard A	Preparatory potatoes	(headland)	,,	3	0	10	0
Stackyard hedgerow		—	—	—	0	0	0
Butt Close hedgerow		—	—	—	0	0	0
Long Mead hedgerow		—	—	—	0	0	0

fields contained no *L. leptocephalus* and large numbers were found only in White Horse Field and part of Stackyard Field and only under winter wheat or grass ley. Even after 6 years of continuous winter wheat in the Intensive Cereals experiment on Stackyard I numbers of *L. leptocephalus* remained small. In the Direct Seeding experiment on White Horse Field numbers of *L. leptocephalus* were consistently greater in the directly seeded plots than in the plots mechanically cultivated, the reverse of results obtained by Corbett

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TABLE 15

Numbers of Longidorus leptocephalus *litre*$^{-1}$ *under monoculture of various crops, White Horse Field, 1975–77*

Crop	Variety	Depth	Spring 1975 Juveniles	Spring 1975 Adult ♀♀	Spring 1975 Total	Autumn 1977 Juveniles	Autumn 1977 Adult ♀♀	Autumn 1977 Total	Multiplication*	Overall Multiplication
Ley	(grass/clover)	0–20	180	20	200	300	40	340	1·7	0·90
		20–40	640	130	770	340	120	460	0·60	
		40–60	250	130	380	370	50	420	1·1	
Barley	Julia	0–20	160	50	210	110	50	160	0·76	0·84
		20–40	190	40	230	170	60	230	1·0	
		40–60	160	30	190	120	20	140	0·74	
Potatoes	Maris Piper	0–20	180	20	200	90	20	110	0·55	0·63
		20–40	210	50	260	100	30	130	0·50	
		40–60	80	30	110	90	30	120	1·1	
Wheat	Maris Huntsman	0–20	70	10	80	50	40	90	1·1	0·52
		20–40	130	20	150	0	0	0	0	
		40–60	30	10	40	40	10	50	1·3	
Sainfoin	Cotswold	0–20	160	70	230	110	10	120	0·52	0·47
		20–40	140	50	190	50	40	90	0·47	
		40–60	90	20	110	30	10	40	0·36	
Sugar beet	Klein E	0–20	310	40	350	130	40	170	0·49	0·45
		20–40	250	90	340	140	50	190	0·56	
		40–60	180	60	240	60	0	60	0·25	
Fallow	—	0–20	280	100	380	30	20	50	0·13	0·26
		20–40	340	110	450	140	20	160	0·36	
		40–60	240	90	330	60	30	90	0·27	
Spring beans	Minden	0–20	380	90	470	50	70	20	0·15	0·16
		20–40	450	140	590	50	20	70	0·12	
		40–60	260	80	340	60	30	90	0·26	
Lucerne	Vertus	0–20	150	30	180	0	0	0	0	0·04
		20–40	250	50	300	20	0	20	0·07	
		40–60	170	30	200	10	0	10	0·05	

* Multiplication = total number autumn 1977 ÷ total number spring 1975

and Webb (1970) who only sampled to a depth of 15 cm. Corbett and Webb's findings may have been because the top layers of soil became compacted, decreasing the pore space available for nematodes. The deeper samples I took in 1971 yielded more nematodes than superficial samples.

In White Horse Field plots 4·28 × 13·72 m were planted with eight different crops grown continuously for 3 years, 1975–77. A ninth plot was fallowed. Table 15 lists the crops and the numbers of *L. leptocephalus* found at different depths at the beginning and end of the experiment. Increase rates over the 3 years were calculated from initial and final numbers of nematodes and the crops ranked in order of these rates. Since most longidorids are thought to be polyphagous (Weischer, 1975) it is not surprising that grasses and cereals are the best hosts as they provide more roots than other crops. It was notable, however, that potatoes were a better host than wheat and that beans and lucerne supported fewer *L. leptocephalus* than the fallow plot. The roots of spring beans were available to the nematodes for only a short period each year, whereas the winter wheat provided roots for a longer period and the grass ley provided roots all year. *L. leptocephalus* numbers declined almost to zero under lucerne which may be a non-host. In fallow, the nematodes may have remained quiescent or found alternative food.

Distribution studies

The problems caused by *L. leptocephalus* in the potato crops of the Woburn Ley–Arable experiment seemed to depend on its non-uniform vertical distribution and the free-draining nature of the soil. In dry summers the potatoes wilted and senesced early, presumably because the deeper roots were damaged. In an attempt to predict where similar types of damage might occur the maps in Fig. 5 were drawn. These show the distribution of potato growing in England and Wales and the distribution of areas with sandy subsoils. These distributions overlap in the West Midlands, Lancashire and the area around the

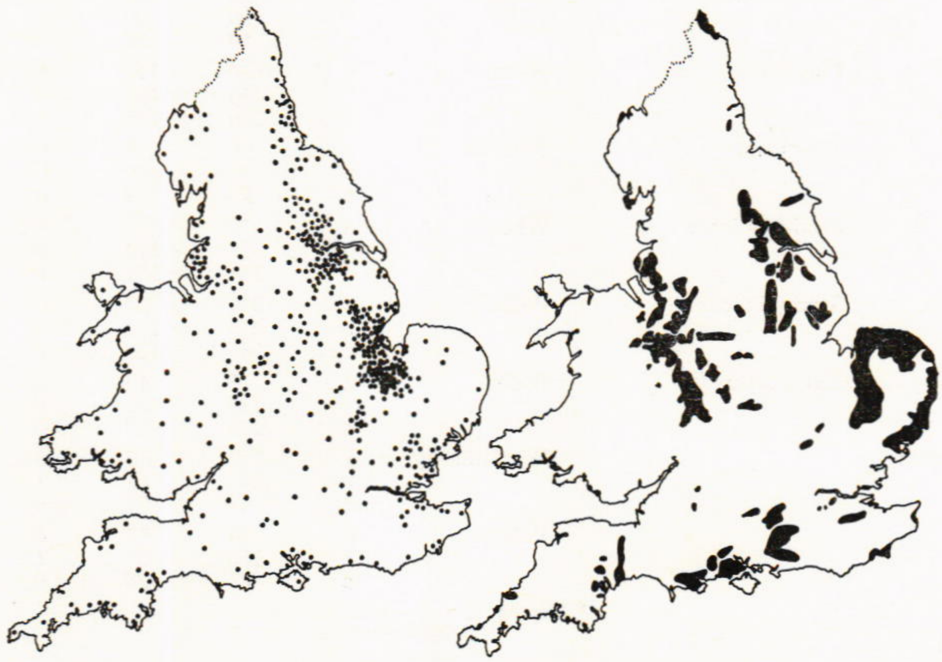

FIG. 5. Maps of England and Wales to show (a) the distribution of potato growing and (b) the distribution of areas with sandy subsoils.

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TABLE 16

Numbers of Longidorus leptocephalus *found in cereal and potato fields in Nottinghamshire, Lincolnshire and South Yorkshire, 1977*

Site		Soil texture†	Crop	Depth*	Nematodes litre^{-1} of soil: Juveniles	Females	Males	Total
Gleadthorpe	m–c	Loamy sand to sandy loam	Barley	a	370	10	0	380
				b	820	180	10	1010
				c	330	170	0	500
,,	m–c	Sandy loam	Potatoes	a	40	0	0	40
				b	140	20	0	160
				c	120	40	0	160
Blidworth Dale		Loamy sand	Barley	a	10	0	0	10
				b	0	0	0	0
				c	0	0	0	0
,, ,,		Loamy sand	Potatoes	a	0	0	0	0
				b	10	20	0	30
				c	20	20	0	40
Ranskill	m	Loamy sand to sandy loam	Barley	a	10	0	0	10
				b	70	20	0	90
				c	70	0	0	70
,,	m	Loamy sand to sandy loam	Potatoes	a	40	0	0	40
				b	10	10	0	20
				c	150	40	0	190
Claxby	m	Sandy loam	Barley	a	40	20	0	60
				b	50	20	0	70
				c	0	10	0	10
,,	m	Sandy loam	Potatoes	a	0	0	0	0
				b	20	20	0	40
				c	0	0	0	0
Roughton	m	Loamy sand to sandy loam	Barley	a	80	10	0	90
				b	70	20	0	90
				c	20	30	0	50
,,	m	Loamy sand	Potatoes	a	50	40	0	90
				b	80	70	0	150
				c	50	30	0	80
Burythorpe		Clay loam	Wheat	a	680	190	0	870
				b	480	160	0	640
				c	340	190	0	530
,,		Clay loam	Potatoes	a	0	0	0	0
				b	10	0	0	10
				c	20	0	0	20
Wickersley		Sandy silt loam	Wheat	a	70	0	0	70
				b	320	110	0	430
				c	185	150	0	335
,,		Sandy silt loam	Potatoes	a	320	50	0	370
				b	470	110	10	590
				c	240	120	0	360
Bilborough	m	Sandy loam	Barley	a	15	10	0	25
				b	130	30	0	160
				c	210	20	0	230
Overall means:			Wheat/Barley	a	159	30	0	189
				b	243	68	1	312
				c	144	71	0	215
			Potatoes	a	64	13	0	77
				b	106	36	1	143
				c	86	36	0	122

* Depths a = 0–20 cm
b = 20–40 cm
c = 40–60 cm

† m = medium
c = coarse

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Humber, including parts of South Yorkshire, Humberside, Nottinghamshire and Lincolnshire. The greatest overlap is around the Humber, so samples were taken throughout this area from cereals and potatoes at each site, to 60 cm deep. The numbers found at three depths are in Table 16, together with the soil texture classification. Greatest populations were found under barley and wheat although at Wickersley as many were found under potatoes as under wheat. However, very large populations under wheat and barley at Burythorpe and Gleadthorpe respectively were associated with very small populations under potatoes in adjacent fields. Sometimes there were fewer nematodes in the top 20 cm of soil than deeper but this was not always true, and in contrast with Woburn large numbers were found in the top 20 cm under potatoes at Wickersley.

TABLE 17

Soil texture related to presence of Longidorus leptocephalus

Soils which contained more than 100 nematodes litre^{-1}			Soils which contained less than 100 nematodes litre^{-1}			Soils which contained no nematodes		
*m	Loamy sand	(1)		Loamy sand	(2)	m	Loamy sand	(2)
m–c	Loamy sand to sandy loam	(1)	m	Loamy sand to sandy loam	(2)	f	Loamy sand	(1)
m	Loamy sand to sandy loam	(1)	m	Sandy loam	(2)	m–c	Sandy loam to loamy sand	(1)
m–c	Sandy loam	(1)		Clay loam	(1)	m–c	Sandy loam	(1)
m	Sandy loam	(1)				f	Sandy loam	(1)
	Sandy silt loam	(2)					Sandy silt loam	(2)
	Clay loam	(1)					Sandy clay loam	(1)
							Silty clay loam	(4)
	Total:	8		Total:	7		Total:	13

* f = fine, m = medium, c = coarse.

Table 17 lists the soil textures for the 28 sites in the survey, and groups them according to whether they contained no nematodes, less than 100 litre^{-1} or more than 100 litre^{-1}. Although Taylor and Brown (1976) usually found *L. leptocephalus* in sandy loam soils, the soils in Table 17 which contained most tended to be coarser sands than those which contained few or none. Wherever *L. leptocephalus* was found there were usually small numbers of *Longidorus caespiticola*, *Longidorus goodeyi*, *Longidorus elongatus* and *Xiphinema diversicaudatum*.

Discussion

Samples from a permanent pasture in 1971 contained more than 2000 *L. leptocephalus* litre^{-1} soil at all depths, which is considerably more than were found under arable crops or short-term leys. Large populations probably build up slowly under permanent pasture where plenty of roots are available and the soil remains undisturbed long enough for the nematodes to complete a number of their relatively long life cycles. When the pasture referred to above was ploughed up to grow cereals nematode numbers declined immediately. Potato yield responses to soil fumigation in the Ley–Arable experiment were large when the potatoes followed 2 years test cropping with barley and it was thought that nematode numbers may have increased sufficiently on the barley (one of the best hosts in Table 15) to damage the following potato crop. Altering the cropping schemes allowed two barley crops to be grown before potatoes in 1974 and 1975, but *L. leptocephalus* numbers and damage were not great in these years. Since it seems likely that the nematode has a 2 or even 3 year life cycle, more than 2 years' cropping with a good host is probably necessary to build up large numbers.

Following years when soil fumigation markedly improved potato yields there was often a marked residual effect on the growth of succeeding cereal crops. This again suggests

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control of a nematode with a long life cycle, especially as the winter wheat yields of the second test crop on Block 3 in 1972 were strongly correlated ($r = 0{\cdot}599$, $P = 0{\cdot}05$) with the numbers of *L. leptocephalus* found under potatoes during the previous year, with a yield reduction of 0·53 t ha^{-1} per 100 nematodes $litre^{-1}$ soil.

The yield increase obtained from fumigation treatments that penetrate deeply into the soil over and above the response to large doses of oxime carbamate nematicide incorporated in the surface layers, also suggests that control of *L. leptocephalus* populations deep down were responsible. All other species of nematodes were fewer below 30 cm than above in this experiment. The effect of deep nematode populations probably depends on soil type and rainfall during the growing season. Such damage is insidious especially when they are absent from the upper layers from which samples are normally taken.

Sykes (1978) assessed the influence of *L. leptocephalus* on yields of wheat, barley and potatoes and obtained significant negative correlations between yield and nematode numbers. The estimated yield reduction for potatoes was 0·55 t ha^{-1} per 200 *L. leptocephalus* $litre^{-1}$, a smaller reduction than found in the Ley–Arable experiment. Sykes found populations greater than 2000 $litre^{-1}$ so the maximum yield reduction was over 5 t ha^{-1}. This approximates to the yield loss predicted at the maximum nematode density found in the Ley–Arable; apparent differences in the yield: nematode numbers relationship between sites may be due to different methods of estimating nematode numbers. Brown and Sykes (1975) suggested that *Longidorus elongatus* also affects potato yields and could find no third factor with which both yield and nematode numbers might be associated. The correlation between yield and untransformed nematode numbers was significant at $P < 0{\cdot}05$, with yield losses of 3 t ha^{-1} for each 100 *L. elongatus* per 200 g soil. All these observations serve to emphasise the losses which dorylaimid nematodes probably cause in many crops.

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APPENDIX

Method used for extraction of *Longidorus* spp. from soil. *Longidorus* spp. seem to be more susceptible than most other soil nematodes to mechanical damage, and recovery rates from soil samples using techniques which employ banks of sieves are poor. Therefore the following procedure, using a single submerged sieve, was used:

1. Measure 100 ml of soil into 200 ml of water in a 400 ml plastic beaker. Allow to stand for 10 min (heavier soils should be left longer).
2. Transfer the soil/water mixture to a 1 litre 'tallform' plastic beaker and make up to 1 litre. Stir carefully and thoroughly to bring all soil into suspension and allow to stand for 10 s.
3. Decant slowly over a submerged 150-mesh (106 μm aperture) sieve, leaving behind heavy soil particles and stones.
4. Make residue up to 1 litre and resuspend. Again allow to stand for 10 s and then pour supernatant over submerged sieve.
5. Wash the contents of the sieve into a beaker.
6. Pour the contents of the beaker slowly through a submerged terylene mesh (90 μm aperture) sieve of 9 cm diam. and place this sieve on supports in a 10 cm diam. glass petri dish containing 'mains tap water'. Leave overnight for the nematodes to pass through the sieve. (If the petri dish is marked for counting the necessity of transferring the suspension to a counting dish is obviated.)

Method used for extraction of *Longidorus* eggs from soil. The method used was essentially that of Flegg and McNamara (1968) differing only in that the stock sugar solution also contained 10 g litre^{-1} of NaCl to act as a flocculant for clay mineral particles (Baver, 1948) and 0·5 g litre^{-1} of phenol crystals rather than 'Aretan' to inhibit bacterial and fungal growth.

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