

NEMATODES IN RELATION TO PLANT GROWTH¹⁾

I *The nematode distribution pattern of typical farms and nurseries*¹⁾

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SUMMARY

The nematode population in every field of ten representative farms and nurseries in various parts of the country was analysed and estimated (tables 1–8). Each field contained a mixed population of plant-parasitic nematodes as well as saprozoic forms. Comparison of the results of the analysis revealed marked qualitative and quantitative differences in the nematode distribution according to soil type, cropping and manuring.

The total number of active nematodes per 100 ml. of soil from individual fields ranged from 1,005 to 16,105 with an overall average of 3,004. Known and suspected phytophagous nematodes ranged from 120 to 3,510 per 100 ml. of soil with an overall average of 909. The prevalent phytophagous genera were *Heterodera*, *Paratylenchus*, *Pratylenchus*, *Rotylenchus*, *Tylenchorhynchus* and *Meloidogyne*. In one or more fields of each holding some species reached population densities which are known or suspected to be of critical importance for the growth of one or more main crops (c.f. p. 342). The results of these and similar farm surveys are considered to be a starting point for further research into a number of obscure crop husbandry problems and may be used as a basis for advisory work.

INTRODUCTION

The presence of a phytophagous nematode population in most cultivated soils has been indicated in earlier publications (8, 12) and its significance has been outlined in general terms (13, 14). The tables now presented give a fuller documentation and provide a basis for discussing certain problems concerning crop rotation and soil sickness. Some of these problems will be considered in subsequent issues.

MATERIALS AND METHODS

A number of representative farms and nurseries in various parts of the country were surveyed, soil samples being drawn from every field on the farms chosen, and estimates made of the average nematode populations present.

Comparable data on cropping history and other circumstances were available for the interpretation and evaluation of the results. The lastgrown crop is recorded in the tables and details of the preceding crops for three years or sometimes more are available for the discussion.

The methods employed are routine procedures at the Plantenziektenkundige Dienst and the Landbouwhogeschool and are summarized elsewhere (4, 16). Soil samples were taken from each plot with a one cm. borer to the depth of the tilth during the autumn or winter. Each sample was made up of sixty prods and consisted of approximately one litre of soil. Larval counts were made on the *Heterodera* cysts collected from a dried subsample of 100 ml. All cysts were identified and squeezed individually to determine their contents. Active nematodes were usually extracted from 100 ml. of soil, but in some

1) Received for publication September 9, 1959.

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cases larger subsamples were used. Twenty per cent of each nematode suspension collected was examined under the stereoscopic microscope and generic counts made. When specific identifications were required about 50 specimens from the prevalent genera were identified under a compound microscope. The results are expressed per 100 ml. of soil.

It is considered that the methods used to extract *Heterodera* cysts from the soil and estimate their larval contents gave consistent results. However, in certain species some of the cyst contents may have been lost during the drying of the soil samples.

In tables 1–5 the average loss of active nematodes is estimated at twenty per cent, about twentyfive per cent of the small species and fifteen per cent of the large species being lost in the extraction process. In the results recorded in tables 6–8 losses were further reduced by using four sieves instead of two to collect the nematodes.

Active nematodes and larvae within cysts are the main groups recoverable from soil in winter. Nematodes within plant roots or debris, eggs free in the soil, and inactive non-cystforming species are lost in the extraction process.

The statistical significance of differences between fields cannot be read directly from the tables, except where the results of several fields support each other. The consistency of the routine methods, however, is well known. Analysis of a fixed quantity of soil and of a fixed aliquot of suspension gives rise to increasing variability as numbers decrease. Further variability is introduced when generic counts are split up into species by the identification of a fixed number of specimens. Allowance has to be made for this variability and therefore discussion has been restricted to the most outstanding differences. For example, with cysts, at populations of ± 100 a difference of at least 30 is required for significance and at populations of ± 10 a difference of at least 5. With larvae within cysts or active nematodes at populations of ± 2000 the least significant difference considered is 500 and at populations of ± 200 it is 100. Figures under 50 are not considered to differ significantly except, for example, in table 8 where large aliquots have been analysed, or where one of the figures is zero. On this basis figures within the tables are comparable since personal bias in sampling, storing, extraction and analysis has been excluded.

The genera *Heterodera*, *Paratylenchus*, *Pratylenchus*, *Rotylenchus*, *Tylenchorhynchus* and *Meloidogyne* are recorded separately. The headings "other Tylenchida" and "saprozoic nematodes" are used to record all other nematodes. Specific identifications have been made mainly in the genera *Heterodera* and *Pratylenchus*. *Heterodera* species were identified according to HIJNER, OOSTENBRINK and DEN OUDEN (3) and OOSTENBRINK and DEN OUDEN (9); the name *H. trifolii* is used *sensu lato*.

To avoid misunderstanding we have adhered, as in our earlier *Pratylenchus* studies, to the genus revision by SHER and ALLEN (18). *P. pratensis* however is meant *sensu lato*. The same holds for *P. minyus* to include the species *P. neglectus* (RENSCH), as re-established by LOOF in 1957 (7). The authors realise that the taxonomy and nomenclature of the genus *Pratylenchus* awaits some correction and that some specific names recorded in this study may be altered subsequently.

RESULTS

Table 1 *Arable farm on clay soil in a cereal district of Groningen*

Cereals had been grown the previous year in eight or nine of the ten plots in table 1. Populations range from 1,865 to 5,795 viable nematodes per 100 ml. of soil and at least four phytophagous genera are present in each plot. Cereal root eelworm, *Heterodera avenae* Wollenweber, is present in all plots but the highest populations are to be found in the four adjoining plots nos. 1–4. Clover root eelworm, *Heterodera trifolii* s.l., occurs sporadically in light concentrations (nos. 6, 7). All plots harbour *Pratylenchus* species, mainly *P. minyus* s.l., *Paratylenchus* spp. and *Tylenchorhynchus* spp. The lightest cereal root eelworm populations and the highest *Paratylenchus* populations are found in three plots (nos. 8–10) of heavier soil in an old polder.

The prevalence of *H. avenae* and migratory root infesting nematodes of the genera *Pratylenchus*, *Paratylenchus* and *Tylenchorhynchus* is apparently related to cereal cultivation.

H. avenae which is widespread in this district was first recorded here as a cereal parasite in 1891 (17). Between 1949 and 1951 more than 2600 fields were examined and lemon-shaped cysts, mainly cereal root eelworm, were found in 72% of them (unpublished). Its role as a cause of poor growth in certain cereals, mainly oats and barley, is beyond doubt (2, 5). The population in plots 4, and to a lesser extent in 1–3, is well above the level which we consider safe for the cultivation of oats; the farmer's experience with plot 4 in recent years confirmed this. The low populations in plots 8–10 may demonstrate that nematode reproduction and crop damage is restricted in heavy soil.

The *Pratylenchus*-*Paratylenchus*-*Tylenchorhynchus*-complex occurs in all plots. The same or a similar complex was found in several samples from other farms in this district, in other clay-soil areas in the Netherlands, and in widely separated localities abroad. Its relation to the crop is not clear from table 1, but may be better understood when the results of a number of field trials are considered. The species in this complex are probably identical to those in an experimental field in this area which were shown to be cereal root parasites. The *Pratylenchus* population in this and other clay soils normally comprises the species *P. minyus* s.l. and/or *P. thornei* SHER and ALLEN. From preliminary results in experimental rotation fields in the Noordoostpolder, the Wieringermeer, Zaltbommel and Goes (partly published in 1956 (12)) we conclude that *minyus* is promoted by most cereals (barley, oats and probably wheat also), whereas *thornei* is promoted specifically by wheat and to a lesser extent by potatoes. Beet, beans and peas seem to suppress both species.

Results from crop rotation and soil disinfection trials indicate that this nematode complex hinders the growth of such cereals as wheat to a moderate extent. *P. minyus* is recorded by BENEDICT and MOUNTAIN (1) from Canada as being an etiological factor in a root rot of wheat. There are indications also of a similar relationship between this nematode complex and other crops of clay soils.

Table 2 *Arable farm on clay soil in Zeeland*

Twenty adjoining fields of 2–9 ha on this very large farm were sampled.

Table 1 Nematode populations on an arable farm on clay soil in Groningen.
Number of nematodes per 100 ml. of soil, 1957/'58.

P. = *Pratylenchus*; Pa. = *Paratylenchus*; T. = *Tylenchorhynchus*; Het. = *Heterodera*-larvae;
O. = other *Tylenchida*; S = saprozoic nematodes; c. = cysts; vc. = viable cysts, l = larvae.

Preceding crop	Active nematodes					<i>Heterodera</i> -cysts				
	P.	Pa.	T.	Het.	O.	S.	<i>avenae</i>		<i>trifolii</i>	
							c.	= vc.	= l.	= l.
1. Oats	330	55	65	—	75	2240	66	= 12	= 450	—
2. Summer wheat	335	45	250	25	275	1920	86	= 12	= 640	—
3. Oats + potato	380	17	180	20	120	1950	32	= 16	= 830	—*)
4. Summer barley	235	10	170	30	105	2285	78	= 25	= 2960	—
5. Oats	480	10	95	20	100	1905	38	= 8	= 290	—
6. Winter barley	560	5	405	15	385	1880	48	= 11	= 430	—
7. Potato	230	5	50	30	200	1230	24	= 8	= 260	20
8. Oats	110	185	285	—	505	2265	20	= 5	= 90	—
9. Oats	385	245	90	70	300	2120	4	= —	= —	—*)
10. Summer wheat	55	195	30	25	145	1185	20	= 5	= 230	—
Farm average	310	77	162	24	221	1898	42	= 10	= 618	0.7 = 0.1 = 2

*) There were in addition some unidentified cysts.

Eelworm cysts were extracted from separate samples of 100 ml. soil per ha ; active nematodes from an average sample of 100 ml. per field. A wide crop rotation is practised and over the last three years has averaged 32% cereals, 20% beet and cruciferous crops, 13% potatoes, 8% peas, 9% other leguminous crops and 18% flax, mawseed and onions. The nematode populations range from 1,425 to 3,666 per 100 ml. of soil. There are again at least four phytophagous genera in each plot. Four species of cyst-forming *Heterodera*'s are present. Most plots harbour a mixture of three of these species. In general their populations are low. Cereal root eelworm, *H. avenae*, is the prevalent species and plots 1, 6, 13, 18 and 20 harbour moderately high populations. Clover root eelworm, *H. trifolii*, and beet root eelworm, *H. schachtii* Schmidt, are present in light concentrations in several fields. Pea root eelworm, *H. goettingiana* Liebscher, is found in three fields only. *Pratylenchus minyus* is nearly always present, three high populations following barley (nos. 7, 18, 20). *P. thornei* is present erratically on the farm and has its densest population in the wheat plot (no. 10). *Rotylenchus* species of which *R. robustus* (Filipjev) de Man (syn. *Hoplolaimus uniformis* Thorne) is the most common and *Paratylenchus* species are present in low numbers in most fields. The highest *Rotylenchus* populations are in the three beet plots (nos. 12, 14, 16). *Tylenchorhynchus* species are present in varying numbers. The large numbers of free *Heterodera* larvae which were found in plots nos. 1 and 13 correspond with the high larval counts recorded in the *H. avenae* cysts extracted from these plots. The saprozoic nematodes are numerous in two barley plots, nos. 4 and 7, and scarce in the beet plot, no. 19.

Table 2 though presenting a similar situation as table 1 reflects a more differentiated and less extreme picture due, no doubt, to the wide crop rotation consciously maintained on this farm.

The population level of the cyst-forming *Heterodera*'s on this farm is much lower than on the previous farm. The prevalent species is *H. avenae*. Although cereals are grown in a three year rotation this species was detected in nearly all plots. As the three plots most severely infested (nos. 1, 6 and 13), had not grown cereals the previous summer the population at that time must have been even higher. This infestation may not be serious, since neither oats nor barley will be grown on these three plots next season. *Heterodera* damage on infested soil is avoided here by the adoption of a wide rotation and although populations may rise to a high level under a host crop, they should decrease during the starvation period under non-host crops to a level at which crops escape damage. *H. schachtii* (20% host crops) and *H. trifolii* (perhaps promoted by weeds) do not reach critical levels. The population of *H. goettingiana* is worthy of note. On average over the last three years peas, the only host, covered no more than 8% of the land. In 1955 peas were grown on plots 15 and 17 and in 1956 on plots 11 and 13, but in 1957 no peas were grown. *H. goettingiana* is now present in noticeable numbers in three out of the four plots in which a pea crop was grown in the last three years. All other plots were apparently free. This confirms the high reproduction rate of this species observed in earlier population studies in other fields on this farm.

H. rostochiensis Wollenweber, the potato root eelworm, was not found on the farm (13% potatoes). Nevertheless it is to be noted that although their

Table 2 Nematode populations on a large arable farm on clay soil in Zeeland.
Number of nematodes per 100 ml. of soil, 1957/58.

P. = *Pratylenchus*; min. = *minutus* s.l.; thorn. = *thornei*; Pa. = *Paratylenchus*; R. = *Rotylenchus*; T. = *Tylenchorhynchus*; Het. = *Heterodera*-larvae; O. = other *Tylenchida*; S. = saprozoic nematodes; c. = cysts; vc. = viable cysts; l. = larvae.

Preceding crop	Active nematodes							Heterodera-cysts				
	P. min.	P. thorn.	Pa.	R.	T.	Het.	O.	S.	avenae	trifolii	schachtii	goettingiana
									c. = vc. = l.	c. = vc. = l.	c. = vc. = l.	c. = vc. = l.
1. Potato	140	20	5	20	220	250	135	1730	29.7 = 10.0 = 690	0.3 =	4.0 =	—
2. Onion	150	30	5	30	125	—	50	1625	5.0 = 0.5 = 10	—	20.0 =	—
3. Flax	100	75	20	55	175	15	155	2115	1.0 = —	—	0.3 =	—
4. Barley	195	195	15	15	310	—	100	2350	2.7 = —	—	10.7 =	—
5. Poppy	160	65	5	45	115	5	110	1050	9.4 = 2.0 = 54	1.0 = 0.6 = 8	3.4 =	—
6. Flax	440	50	25	35	90	5	90	925	17.8 = 7.8 = 450	0.3 =	1.3 =	—
7. Barley	420	—	5	20	195	—	95	2415	0.7 = —	2.3 = 0.3 = 7	4.3 =	—
8. Lucerne	305	15	—	60	130	—	145	1040	0.1 = 0.1 = 20	0.4 =	0.7 =	—
9. Lucerne	225	—	—	45	120	—	200	1160	2.3 = 1.3 = 63	2.0 = 0.7 = 10	0.3 =	—
10. Wheat	—	300	15	15	125	25	85	1480	4.8 = 1.8 = 88	0.2 =	9.4 =	—
11. Colza	150	—	10	35	145	—	130	1375	3.7 = 0.5 = 13	—	0.3 =	—
12. Beet	115	—	25	75	360	15	140	1425	2.0 = —	1.0 =	—	0.2 =
13. Colza	215	—	50	55	405	55	145	1425	45.5 = 21.0 = 962	1.7 = 0.8 = 62	4.0 =	8.5 = 6.8 = 270
14. Beet	30	—	5	65	105	10	135	1250	—	—	0.3 =	—
15. Potato	220	—	5	40	90	—	110	1350	—	—	—	1.8 = 1.8 = 58
16. Beet	225	—	—	145	145	10	235	1305	4.2 = 0.5 = 17	0.2 = 0.2 = 7	—	—
17. Potato	355	—	20	40	90	—	195	1100	3.3 = 0.8 = 30	2.5 = 2.5 = 125	0.3 =	—
18. Barley	605	—	15	15	80	5	110	1375	20.4 = 6.3 = 399	0.7 = 0.3 = 7	3.4 = 0.1 = 1	—
19. Beet	340	110	—	10	50	10	105	775	4.0 = 1.0 = 45	—	0.5 =	—
20. Barley	630	—	—	15	145	5	110	1075	6.0 = 2.3 = 115	0.3 =	1.0 =	—
Farm average	251	43	11	42	161	21	129	1416	8.2 = 2.8 = 148	0.6 = 0.3 = 11	3.2 = .02 = 5	0.5 = 0.4 = 16

populations are low, four *Heterodera* species have become established in spite of a good rotation. The large amount of soil examined for *Heterodera* cysts, viz. 100 ml. per ha or 200–900 ml. per field, may partly explain the varied patterns recorded in the table. This illustrates that even on well-managed farms, failure to carry out a wide rotation may, within a few years, result in a *Heterodera* problem.

The complex of migratory root-attacking nematodes in table 2 is also strongly varied. No specific crop relationships are indicated in table 2 for the *Tylenchorhynchus* and *Pratylenchus* species, though some significant differences between fields are noticed. The apparent affinities of *Pratylenchus minyus* to barley and of *P. thornei* to wheat are known to be significant. *Rotylenchus*, mainly *R. robustus* is known to attack beet, peas and several horticultural crops; its population is suppressed by some cereals and potatoes (6). The three highest *R. robustus* populations can be correlated with preceding beet crops, indicating that the appearance of the nematode on this farm is due in the first place to the cultivation of beet. Although the present numbers are too low to play a significant role, increased cropping with beet and legumes could quickly build up noxious *Rotylenchus* infestations.

Table 3 *Experimental farm Bo 31/32, situated in a potato root eelworm focus in the Veenkoloniën*

Potatoes covered more than 50% of the land in this area until the official regulations for the control of potato root eelworm, *Heterodera rostochiensis* restricted their cultivation. From about 1950 the cereal acreage has been markedly increased. To study the disease limited potato culture was practised on this farm in a few lightly infested fields. Recently beet and other root crops were introduced as new crops. Cereals, oats and rye covered only two of the eleven plots in 1957, but in 1955 and 1956 cereals were grown in seven of the eleven plots. The nematode survey took place in the autumn of 1957.

Nematode populations in table 3 range from 1,650 to 4,450 per 100 ml. of soil and comprise three to five or more phytophagous genera, each of which may be represented by several species. A young population of *H. rostochiensis* is present in several plots; potatoes in 1957 evidently increased the population (nos. 1, 3, 4). *H. avenae* is present in light concentrations in most fields and in high concentrations in plot no. 5. The high number of free *Heterodera* larvae found in the soil from plot 5 coincides with the high larval count in the *H. avenae* cysts. *H. trifolii* is present in notable numbers in some plots (nos. 6, 10). *Pratylenchus pratensis* s.l. is present in limited numbers in all plots. *Tylenchorhynchus*, in this case mainly *T. dubius* (Bütschli) Filipjev is also found in limited numbers, its highest population level being found after oats (no. 5). *Pratylenchus penetrans* (Cobb) Chitwood and Oteifa is present in most plots, often in fairly large numbers (nos. 3–5). Its population is suppressed by beet (nos. 2, 9–11) and other root crops (nos. 6, 7). A *Pratylenchus* sp. and a third *Pratylenchus* species are present sporadically. *Rotylenchus*, mainly *R. robustus* is present in most fields in low numbers. The lowest densities of saprozoic nematodes follow beet (nos. 2, 10 and 11).

The nematode picture of table 3 is thus quite different from the foregoing tables, because soil types and crop rotations differ.

H. rostochiensis occurs locally in this district and has reached this farm

recently. The regulations of 1949 have reduced the cultivation of potatoes to less than $\frac{1}{2}$ of the arable land. Consequently cereal growing has been intensified, and *H. avenae* has become a new pest: plot no. 5, which is seriously infested, appears to be the only plot on the farm with three successive cereal crops, viz. rye or oats. It is evident from this table, and to a lesser extent from tables 1 and 2, that active larvae of *H. avenae* may normally be present free in the soil in winter. Fairly high numbers of *H. trifolii* s.l. have built up probably on *Stellaria media* and *Galeopsis* sp., which are common crop weeds in this area.

Pratylenchus pratensis is primarily a cereal parasite in the lighter soils. As a rule it is accompanied by *Tylenchorhynchus dubius*, a species which is increased also by Gramineae and white clover. The significance of these two species in the growth of cereals, grass and clover is probably high (8, 11) but is not fully explained. *P. penetrans* which causes sickness symptoms in potatoes, nursery stock and other crops (11, 15) is undoubtedly a problem on this farm. To some extent beet was introduced to control this nematode. The concentration of *P. penetrans* present in this arable soil would appear to be a hidden danger for nursery stock and several horticultural crops.

Some of the other species found may be potential plant parasites but probably cause no damage in their present concentrations.

Table 4 Arable farm on diluvial sandy soil in Utrecht

Rye, potatoes and oats are the major crops, and green manuring is practised occasionally. Nematode populations in each plot range from 1,175 to 10,685 per 100 ml. of soil and comprise four or more phytophagous genera. *H. avenae* is present in moderate densities in four plots (nos. 2, 3, 8, 9); *H. trifolii* is present in most fields in low to moderate numbers. *P. pratensis* and *T. dubius* are again present in all plots, but at a somewhat higher level than in table 3. The highest populations of both follow oats (no. 11). *P. penetrans* and *R. robustus* are present in most fields, sometimes in notable concentrations. A third *Pratylenchus* species and *Paratylenchus* spp. are found in low numbers. One sample had a high number of other Tylenchida (no. 8). The saprozoic nematodes are lowest following potatoes (nos. 3, 4, 5) and evidently have been encouraged by the green manure crop (nos. 8, 10).

Table 5 Mixed farm on diluvial sandy soil in Gelderland

Eight of the ten plots have been under cereals and grass. Nematode populations range from 2,120 to 5,985 per 100 ml. of soil, and again four to five genera are present in each plot.

H. avenae and *H. trifolii* although low to moderate in numbers are almost always present in arable land and in meadows. Grass root eelworm, *H. punctata* s.l., is evidently encouraged under meadow conditions (nos. 6, 7, 10).

Pratylenchus, mainly *P. pratensis*, and *Tylenchorhynchus*, mainly *T. dubius*, are present in each plot. The density varies, but their populations are higher than in tables 3 and 4. Very high populations of *P. pratensis* follow oats/barley (nos. 8, 9). The highest populations of *T. dubius* follow rye and oats/barley (nos. 3, 9). *Paratylenchus* and *Rotylenchus* species (not in this case *R. robustus*) have been promoted also in the meadows (nos. 6, 7, 10). Meadows are there-

Table 4 Nematode populations on an arable farm on diluvial sandy soil in Utrecht.
Number of nematodes per 100 ml. of soil, 1957/58.

P. = *Pratylenchus*; prat. = *pratensis*; pen. = *penetrans*; spec. = *species*; Pa. = *Paratylenchus*; R. = *Rotylenchus*; T. = *Tylenchorhynchus*; O. = other *Tylenchida*; S. = saprozoic nematodes; c. = cysts; vc. = viable cysts; l. = larvae; + = serradella ploughed in as green manure.

Preceding crop	Active nematodes					Heterodera-cysts								
	P. prat.	P. pen.	P. spec.	Pa.	R.	T.	O.	S.	avenae		trifolii			
									c. =	vc. =	l.	c. =	vc. =	l.
1. Rye	170	10	10	10	125	250	40	1155	—	—	—	—	—	—
2. Rye	255	—	15	5	195	300	70	1045	5	4	380	1	1	10
3. Potato	180	140	70	15	45	170	75	1030	3	3	370	—	—	—
4. Potato	150	25	25	25	125	100	45	680	1	—	—	—	—	—
5. Potato	85	110	85	10	125	115	45	705	—	—	—	3	1	20*
6. Oats	180	320	80	5	45	380	95	1290	—	—	—	—	—	—
7. Oats	190	45	60	—	90	460	55	1145	—	—	—	—	—	—
8. Rye +	95	35	15	—	105	440	315	9190	4	3	370	8	2	120
9. Rye	300	15	—	5	65	335	70	2325	10	2	240	34	1	10*
10. Rye +	270	40	25	10	80	270	40	4650	—	—	—	1	1	40
1. Oats	470	110	—	—	90	590	85	1355	—	—	—	3	—	—
2. Lupins	210	—	60	—	15	175	70	3150	—	—	—	1	1	120*
Farm average	213	71	37	7	92	299	84	2310	1.9	1.0	113	4.3	0.6	27

*) There were in addition some unidentified cysts.

Table 5 Nematode populations of a mixed farm on diluvial sandy soil in Gelderland.
 Number of nematodes per 100 ml. of soil, 1957/'58.
 P. = *Pratylenchus pratensis*; Pa. = *Paratylenchus*; R. = *Rotylenchus*; T. = *Tylenchorhynchus*; Het. = *Heterodera*-larvae;
 O. = other *Tylenchida*; S. = saprozoic nematodes; c. = cysts; vc. = viable cysts; l. = larvae.

Preceding crop	Active nematodes						Heterodera-cysts									
	P.	Pa.	R.	T.	Het.	O.	S.	avenae			trifolii			punctata		
								c.	vc.	l.	c.	vc.	l.	c.	vc.	l.
1. Rye	80	—	10	910	5	10	1560	17	3	90	5	2	100	—	—	—
2. Rye	280	—	25	575	—	20	1220	2	—	—	—	—	—	—	—	—
3. Rye	285	—	50	1325	—	155	3000	8	1	30	4	1	160	—	—	—
4. Beet	125	35	25	215	15	80	1280	42	3	300	5	1	20	—	—	—
5. Potato	180	—	90	345	10	105	1960	38	2	50	20	2	40	—	—	—
6. Meadow	260	755	55	605	10	275	2255	22	1	10	32	4	90	—	—	30
7. Meadow	45	305	240	495	25	175	2415	3	2	40	10	4	150	4	1	1260
8. Oats/barley ..	980	50	60	295	—	265	2000	3	1	20	13	1	10	—	—	—
9. Oats/barley ..	590	40	55	1195	5	190	2250	—	—	—	13	—	—	—	—	—
10. Meadow	35	320	335	360	10	230	3145	10	—	—	14	3	60	115	34	1490
Farm average ..	286	151	95	632	8	151	2109	14.5	1.3	54	11.6	1.8	63	16	5.9	278

Table 6 Nematode populations in a vegetable nursery on sandy soil in Friesland.

Number of nematodes per 100 ml. of soil, 1957/'58.

P. = *Pratylenchus pratensis*; R. = *Rotylenchus robustus*; T. = *Tylenchorhynchus dubius*; O. = other Tylenchida; S. = saprozoic nematodes.

Preceding crop	Active nematodes					<i>Heterodera</i> -cysts			
	P.	R.	T.	O.	S.	c.	=	vc.	= l.
1. Kidney bean	5	485	160	125	2170	1	=	-	= -
2. Kidney bean + caulif.	20	370	105	175	2230	2	=	-	= -
3. Cauliflower	5	185	100	265	5340	-	=	-	= -
4. Lettuce + carrot . . .	-	295	-	140	4905	1	=	-	= -
5. Lettuce	185	405	25	160	2460	-	=	-	= -
6. Carrot	55	660	10	150	3260	3	=	-	= -
7. Carrot	35	715	30	260	7925	-	=	-	= -
8. Kidney bean	80	225	15	145	4380	-	=	-	= -
Average	48	418	56	178	4084	0.9	=	-	= -

fore marked by dense populations of at least three phytophagous nematode species.

Table 6 Vegetable nursery on sandy soil in Friesland

Vegetables were grown in all plots and no agricultural crops are grown. Nematode populations range from 2,900 to 8,965 per 100 ml. of soil and are relatively uncomplicated. *Rotylenchus robustus* is the prevalent phytophagous species in all plots, the densest populations following carrots (nos. 6, 7).

Heterodera species and *Tylenchorhynchus dubius* are present in low numbers.

Table 7 Nematode populations in a garden complex on sandy soil in Gelderland.

Number of nematodes per 100 ml. of soil, 1957/'58.

P. = *Pratylenchus*; R. = *Rotylenchus robustus*; T. = *Tylenchorhynchus dubius*;Het. = *Heterodera*-larvae; Mel. = *Meloidogyne*-larvae; Pa. = *Paratylenchus*;Cric. = *Criconemoides*; O. = other Tylenchida; S. = saprozoic nematodes; c. = cysts;

vc. = viable cysts; l. = larvae.

Preceding crop	Active nematodes									<i>Heterodera</i> -cysts		
	P.	R.	T.	Het.	Mel.	Pa.	Cric.	O.	S.	c.	=	vc. = l.
1. Kidney bean	410	20	590	5	245	-	-	415	2985	3	=	- = -
2. Potato	190	75	170	-	630	-	-	230	2365	-	=	- = -
3. Carrot	355	-	1185	-	70	75	-	165	4445	-	=	- = -
4. Potato	470	60	395	5	720	-	-	210	2705	8	=	4 = 250
5. Strawberry	240	335	190	-	35	20	-	80	2775	2	=	- = -
6. Pea	75	680	290	-	30	-	-	235	3020	-	=	- = -
7. Kidney bean	60	815	320	-	160	-	-	225	1960	-	=	- = -
8. Ligustrum hedge .	5	330	25	-	115	10	-	505	1640	1	=	- = -
9. Lawn	30	220	595	-	20	180	10	175	1885	1	=	1 = 10
10. Cerastium-bed . .	25	190	760	-	50	190	110	230	1740	1	=	- = -
Average	186	273	452	1	208	48	12	247	2552	1.6	=	0.5 = 26

Table 7 Garden complex on light sandy soil in Gelderland

Several years ago a commercial vegetable nursery was divided here into three portions. Since then the first portion (nos. 1-3) has often grown potatoes and maize and the second section vegetables (nos. 4-7); the third portion has been made a permanent ornamental garden.

Nematode populations range from 2,630-6,295 per 100 ml. of soil and four to six phytophagous genera are encountered in each plot. The *Heterodera* population is low and consists mainly of *H. schachtii* probably because cabbage has often been the second crop.

Pratylenchus (mainly *P. pratensis*, though *penetrans* and *minyus* are also present) occurs in most plots. *Rotylenchus robustus*, *Tylenchorhynchus dubius* and *Meloidogyne hapla* are present in nearly all plots. In plots 1-4 high popu-

Table 8 Nematode populations in nurseries on silt (A) and on dune sand (B and C) in the western part of the country. Number of nematodes per 400 ml. of soil, 1957/'58. Number of nematodes per 100 ml. of soil, 1957/'58.

P. = *Pratylenchus*; pen. = *penetrans*; min. = *minyus*; spec. = *species*; R. = *Rotylenchus*; T. = *Tylenchorhynchus*; Het. = *Heterodera*-larvae; O. = other Tylenchida; S. = saprozoic Het. = *Heterodera*-larvae; O. = other Tylenchida; S. = saprozoic nematodes; c. = cysts; vc. = viable cysts; l. = larvae.

Preceding crop	Active nematodes								<i>Heterodera</i> -cysts									
	P. pen.	P. min.	P. spec	R.	T.	Het.	O.	S.	<i>carotae</i> c. = vc. = l.			<i>schachtii</i> c. = vc. = l.						
A. <i>Silt, Rijnsburg</i>																		
1. <i>Physostegia</i>	480	425	45	65	180	5	405	13215	-	=	-	=	-	212	=	8	=	240
2. <i>Tulip</i> *)	85	50	45	20	120	-	160	4060	-	=	-	=	-	20	=	-	=	-
3. <i>Tulip</i> *)	95	35	20	40	380	-	240	5300	24	=	20	=	760	104	=	4	=	240
4. <i>Chrysanthemum</i> *) .	65	295	55	320	840	20	200	5740	-	=	-	=	-	24	=	-	=	-
*) Trench dug to a depth of 60 cm in spring 1957																		
B. <i>Dune sand, Beverwijk</i>																		
1. <i>Vegetables</i>	13	2	2	370	40	-	230	7550	18	=	3	=	60	-	=	-	=	-
2. <i>Iris</i>	5	-	-	450	-	-	250	5390	-	=	-	=	-	-	=	-	=	-
3. <i>Snowdrop</i>	5	7	2	680	-	-	620	6660	-	=	-	=	-	-	=	-	=	-
4. <i>Iris</i> *)	3	-	3	60	20	-	155	4680	-	=	-	=	-	-	=	-	=	-
5. <i>Iris</i> **)	-	-	-	-	-	-	120	3900	-	=	-	=	-	-	=	-	=	-
6. <i>Gladiolus</i> **)	-	-	-	10	-	-	240	5130	-	=	-	=	-	-	=	-	=	-
*) and **) Desinfected with DD in 1955 and 1956 respectively.																		
C. <i>Dune sand, Heemskerk</i>																		
1. <i>Strawberry</i>	20	-	-	150	-	-	370	9150	-	=	-	=	-	-	=	-	=	-
2. <i>Iris/tulip</i>	29	7	7	100	10	-	350	9760	-	=	-	=	-	3	=	-	=	-
3. <i>Tulip</i>	-	-	-	350	-	-	430	19760	-	=	-	=	-	-	=	-	=	-
4. <i>Muscari</i>	4	-	-	215	-	-	300	63900	-	=	-	=	-	6	=	-	=	-
5. <i>Strawberry</i>	29	-	-	470	-	-	120	8620	-	=	-	=	-	3	=	-	=	-
6. <i>Spinach</i>	11	2	-	480	110	-	170	22010	-	=	-	=	-	-	=	-	=	-
7. <i>Carrot</i>	8	-	-	160	-	-	335	6610	-	=	-	=	-	-	=	-	=	-
8. <i>Strawberry/carrot</i> *)	-	-	-	20	-	-	500	4800	-	=	-	=	-	-	=	-	=	-
9. <i>Gladiolus</i>	4	-	-	45	5	-	330	5390	-	=	-	=	-	-	=	-	=	-
*) Trench dug in 1956																		

lations of *Pratylenchus* seem to be correlated with low numbers of *Rotylenchus* and vice-versa. *Tylenchorhynchus*, *Paratylenchus* and *Criconemoides* are numerous in the Cerastium bed and in the lawn (nos. 9, 10), and *Tylenchorhynchus* also in plots nos. 1 and 3. The densest *Meloidogyne* populations follow potatoes (nos. 2, 4). Plots 7–9, the only plots where organic manure has not been used regularly, harbour fewest saprozoic nematodes.

Table 8 A, B, C *Ornamental nurseries on silt (A) and on dune sand (B, C) in the western part of the country*

Nursery A, on silt soil, was under cut flowers last year, but vegetables such as cabbage and carrots are grown regularly as a second crop. *Heterodera schachtii* and *H. carotae* Jones are present in fair numbers in some plots. All plots harbour a complex mixture of *Pratylenchus*, *Rotylenchus robustus* and *Tylenchorhynchus* sp. Nematode populations range from 4,540 to 15,060 per 400 ml. of soil, i.e. from 1,135 to 3,765 per 100 ml. Plots nos. 2–4 which have the lowest nematode numbers, had been trench dug to a depth of 60 cm before the last growing season.

Nursery B and C, on dune sand, have populations ranging per 400 ml. of soil from 4,020 to 8,287 and from 5,320 to 64,419 respectively, i.e. from 1,005 to 2,072 and from 1,330 to 16,105 per 100 ml. The effect of soil disinfection with DD and of trench digging in recent years is well expressed in the tables (B nos. 4–6, C no. 8). Both nurseries show the same uncomplicated pattern, with *Rotylenchus robustus* as the prevalent phytophagous species in all plots. *Pratylenchus penetrans* is present in most plots in low numbers; this population is nevertheless noxious in the culture of flower bulbs (19). In some fields *Heterodera* and other genera are found in low numbers.

GENERAL DISCUSSION

It is clear from the tables that each plot under consideration harbours a mixed population of phytophagous and saprozoic nematodes. This may safely be considered a normal feature of cultivated soil and is in accordance with our earlier observations. There is further confirmation in the experience of the Plantenziektenkundige Dienst and the Bedrijfslaboratorium voor Grond- en Gewasonderzoek as a result of the examination of several thousand soil samples for survey and advisory purposes. No soil is completely free from phytophagous nematodes except where virgin soil without any plant growth or soil recently sterilized is concerned.

The total numbers of *active* nematodes extracted per 100 ml. of soil from the different fields ranged from 1,005 to 16,105, with an overall average of 3,004 i.e. from about 1.0 to 32.2 millions per square metre taken to a depth of 20 cm (the depth of the tilth). The two lowest populations were recorded from the ornamental nurseries (table 8 B no. 5 and 8 A no. 2). In one field the top soil had been recently disinfested by treatment with a nematicide and in the other the top soil had been buried by trench digging. The two highest figures (table 8 C no. 4 and 4 no. 8) relate to fields which recently received stable dung or green manure. Farm averages expressed as millions per sq. metre were 5.4, 4.1, 4.8, 6.2, 6.9, 9.6, 8.0, 4.1, 3.2 and 8.6 respectively. These results are high compared with previously published data on the extraction of active nematodes from soil by other techniques. CAVENESS and

JENSEN (in 1955) record about 2.5–4.7, FRANZ (in 1941 and in 1950) 0.8–4.6, SEINHORST (in 1956) 2–12 and STÖCKLI (in 1943 and 1952) 1.0–18.1 million per sq. metre of farm-, meadow- and woodland.

Heterodera cysts were found in 77% of the fields. The numbers of cysts varied from 0–139 (average 13); viable larvae within cysts were between 0 to 2,960 (average 194) per 100 ml. of soil. Farm averages for viable larvae within cysts were 620, 180, 304, 140, 395, 0, 26, 78, 3 and 0. These figures demonstrate that in our conditions the genus *Heterodera* is widespread especially in farm land (tables 1–5).

Known and suspected phytophagous genera, those with a tylenchid stylet, among the active nematodes reached population densities of between 120 (table 8 B no. 5) and 1,860 per 100 ml. (table 7 no. 4); farm averages per 100 ml. of soil were 794, 658, 548, 803, 1,163, 699, 1,426, 293, 137 and 143, with an overall average of 715. Total viable nematodes of phytophagous or suspected genera, *Heterodera* included, varied from 120 (table 8 B no. 5, a plot treated with a nematicide) to 3,510 (table 1, no. 4) per 100 ml. of soil; farm averages were 1,414, 838, 852, 943, 1,558, 699, 1,452, 371, 140 and 143 with an overall average of 909.

All plots with the possible exception of the disinfested plots recorded in table 8, comprise notable numbers of several phytophagous genera, each with one or more species. The genera *Heterodera*, *Paratylenchus*, *Pratylenchus*, *Rotylenchus*, *Tylenchorhynchus* and *Meloidogyne* are frequently encountered. Each of these genera comprises species which are known to act as true, noxious parasites of certain crops (auctores diversi). Some of the species recorded in our tables are recognized primary parasites; others are suspect, requiring further investigation to determine their significance. The "other Tylenchida" and the so-called "saprozoic nematodes" are unlikely to cause primary damage to our crops, although some of the species may be plant parasitic. In the following discussion foremost attention is given to the plant parasitic species which are present in large numbers.

Comparison of the figures in tables 1–8 reveals marked qualitative and quantitative differences in the nematode pattern of the various farms and nurseries. Sandy soils (tables 3–7, 8 B-C) are characterised by the occurrence of *Pratylenchus pratensis* and/or *penetrans* and *Tylenchorhynchus dubius*. Clay soils (tables 1, 2) on the other hand harbour *Pratylenchus minyus*, *P. thornei* and certain *Tylenchorhynchus* species. The silt soil (table 8 A) is intermediate in this respect. Horticultural nurseries as a rule harbour dense populations of *Rotylenchus robustus*.

Farm land is characterised by the presence of *Heterodera avenae* and *H. trifolii* (tables 1–5), which are absent in the nurseries (tables 6–8). Overcropping with cereals is correlated with dense populations of *H. avenae* (table 1). With a good rotation system several *Heterodera* species may be present but they tend to remain at a low level (table 2).

As has been indicated in the tables differences in nematode populations in relation to the lastgrown crop or crops are noticed in most farms. The relationship may be partly obscured owing to variabilities in the methods used to estimate the populations and to differences in the cropping history, soil type,

and original infestation. In one or more fields of each holding some species reach population densities which are known or suspected to be of critical importance to the growth of one or more main crops. These species are listed below.

- Farm 1*: *Heterodera avenae* and the complex *Pratylenchus/Paratylenchus/Tylenchorhynchus*, on cereals.
- Farm 2*: All four *Heterodera* species on their special host plants; *Pratylenchus minyus* and *P. thornei* on cereals.
- Farm 3*: *Heterodera rostochiensis* and *Pratylenchus penetrans* on potatoes; *Heterodera avenae* and the complex *Pratylenchus pratensis/Tylenchorhynchus dubius* on cereals.
- Farm 4*: *Heterodera avenae* and the complex *Pratylenchus pratensis/Tylenchorhynchus dubius* on cereals, *Pratylenchus penetrans* on potatoes.
- Farm 5*: *Heterodera avenae* and the complex *Pratylenchus pratensis/Tylenchorhynchus dubius* on cereals; several species on grasses and clovers.
- Nursery 6*: *Rotylenchus robustus* on carrots and other crops.
- Nursery 7*: *Rotylenchus robustus*, *Meloidogyne hapla* and probably also the complex *Pratylenchus pratensis/Tylenchorhynchus dubius* on horticultural crops.
- Nursery 8*: A. B. C. *Pratylenchus penetrans*, *Rotylenchus robustus* and in 8 A probably also *Pratylenchus minyus*, on ornamental crops, vegetables and strawberries.

The tables and other data therefore illustrate the overall aspect of nematode infestations and suggest their possible significance as a factor in soil "fertility". This significance has been partly proved by previous inoculation experiments, population studies, soil disinfection results and by practical experience, but in several cases further evidence is required.

Nematode damage normally concerns the principal crops which are regularly grown. The polyphagous nature of some nematode species, however, can also result in damage to crops grown on a farm for the first time. An example of this is damage caused by *P. penetrans* and in other cases by *Rotylenchus robustus* to nursery stock and horticultural crops grown in former farm land.

The data above provide a basis for research into such crop husbandry problems as crop rotation, ley farming and other methods of grassland management, replanting and "soil sickness" problems, soil rehabilitation and soil sterilisation. An approach to these problems from a purely nematological aspect may have practical possibilities. The nematode distribution patterns as presented in the tables, may also prove to be a useful basis for advisory work with respect to these problems. A start has been made with this biological soil analysis.

ACKNOWLEDGEMENTS

The authors are indebted to Mr. T. W. MABBOTT of the Nematology Section, Seed Testing and Plant Pathology Station, Edinburgh for his help in preparing the English text.

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