Nematodes in relation to plant growth. II. The influence of the crop on the nematode population

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Summary

Population studies in three rotation trials demonstrated the marked influence of cropping on nematode populations in cultivated soil. One year's cultivation of different crops caused shifts in the population densities of at least four different plant parasitic nematodes in both a silt soil and a sandy soil (*tables* 1 and 3). The influence of one or two years' cultivation of a crop may be noticeable in the nematode infestation of subsequent crops for at least two seasons. This appears to hold for *Heterodera, Meloidogyne* as well as for migratory root-infesting species. *Table* 2 stresses the decisive influence of one-sided cultures on the appearance of different *Heterodera* species in a field and gives an insight into the epidemiology of *Heterodera* infestations and the preventative value of crop rotation.
Nine special host-parasite relationships are apparent from the tables and are summarized on p. 4 and 5.

1. Introduction

The overall occurrence of a dense, mixed population of plant parasitic and saprozoic nematodes in cultivated soil was substantiated in publication I of this series (KLEYBURG and OOSTENBRINK, 1959). The density of known and suspected plant parasitic nematodes from a hundred different fields in the Netherlands ranged from 120 to 3510, with an average of more than 900 per 100 ml of soil; 77 % of the fields contained *Heterodera* cysts of different kinds. The occurrence of 4—6 genera of plant parasites, and also the occurrence of two or more species of a genus at the same place appeared to be common. The results of field trials indicated, that the density and the composition of a nematode population fluctuate markedly with the crops grown. This holds true for the plant parasites, each with its own plant-parasite relationship, and the saprozoic nematodes, which are influenced by the availability of decaying organic matter. Examples have been published earlier (OOSTENBRINK, S' JACOB and KUIPER, 1956; OOSTENBRINK, 1957, 1960 a in Druck). In the following tables results of three trial fields are recorded to demonstrate the general characteristics of this population dynamics. The methods for extracting, counting and analysing of the nematodes are described elsewhere (OOSTENBRINK, 1960 b). Some relationships between population density of plant parasitic nematodes and the appearance of disease symptoms, or rotation effects in subsequent crops, will be reated later.

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2. Results

A. *Non-cystforming nematodes in sandy silt soil at Ellecom*

The original field was fairly uniformly infested in the spring of 1953. The prevailing phytophagous genera were *Pratylenchus, Tylenchorhynchus* and *Rotylenchus. Meloidogyne, Paratylenchus* and some other stylet-bearing genera were present in lower numbers, *Heterodera* was not found here.

Corn, witloof, potato and beet were each grown on two plots of 100 sq. metres in 1953. The same crops were grown on the same plots in 1954, except potato which was replaced by carrot. In 1955 nine crops were grown on each of the original eight plots, increasing the number of plots to 72. The nematode populations were estimated

TABLE 1. Influence of the last grown and of two preceding crops on a mixed population of root-infesting, non-cystforming nematodes in sandy silt soil at Ellecom. Four different rotations in 1953—'54. Nine different crops following each rotation in 1955.
Nematode figures determined per 100 ml of soil in the spring of 1956.
P. = *Pratylenchus;* T. = *Tylenchorhynchus;* R. = *Rotylenchus;* M. = *Meloidogyne;* Pa. = *Paratylenchus;* O. = other Tylenchida; S. = saprozoic nematodes.

A. Crop 1955	Nematodes 1956, per 100 ml of soil (mean of eight plots)						
	P.	T.	R.	M.	Pa.	O.	S.
Ley = grass + white clover ..	610	230	410	100	69	200	1100
Rye (*Secale cereale* L.)	440	180	290	6	2	240	1030
Oats (*Avena sativa* L.)	440	130	290	8	4	260	1180
Barley (*Hordeum vulgare* L.) .	420	180	300	4	0	240	990
Beet (*Beta vulgaris* L.)	340	43	550	110	6	130	1020
Potato (*Solanum tuberosum* L.)	330	32	230	87	0	190	890
Witloof (*Cichorium intybus* L.)	260	23	290	14	0	140	1050
Pea (*Pisum sativum* L.)	250	71	310	200	0	130	1010
Carrot (*Daucus carota* L.)	240	31	490	28	0	140	1120
L.S.D.[1] 95 %	128	70	125	67		83	223
99 %	192	105	188	100		124	335
F-value[2]	7,17++	10,3++	5,76++	8,25++		3,26+	1,14—

B. Crops 1953 & 1954	Nematodes 1956, per 100 ml of soil (mean of eighteen plots)						
	P.	T.	R.	M.	Pa.	O.	S.
Corn — corn	540	220	120	6	4	190	1100
Witloof — witloof	420	42	410	13	1	170	1040
Potato — carrot	260	78	420	110	0	220	980
Beet — beet	240	65	470	120	30	170	1070
L.S.D.[1] 95 %	85	47	84	44		55	149
99 %	128	70	126	67		83	223
F-value[2]	22,1++	24,9++	28,8++	15,2++		1,82—	1—

1 As least significant difference at 95 or 99 % level $2\sqrt{2}$ or $3\sqrt{2}$ times the standard error is taken respectively.

2 Variance ratio. ++ = differences significant at 99 % level, + = at 95 % level, — = non-significant.

in soil samples from all 72 plots in the spring of 1956. They are recorded in TABLE 1, together with general indications about statistical signifiance of the differences observed.

TABLE 1 A shows, that the population in this field comprises at least five genera to which pathogenic species are known to belong. The 1955 crops evidently have caused very significant differences in all these genera, as indicated by the F-values of the common analysis of variance. The differences in the "other Tylenchida" as a whole are barely significant, whereas the "saprozoic nematodes" as a whole do not differ in density.

Further analysis of the differences by means of the "studentized range test" in connection with the analysis of variance (KEULS, 1952) separates the crops listed in TABLE 1 into groups according to their efficiency as host plants as follows:

for *Pratylenchus,* mainly *P. crenatus* Loof (indicated earlier as *P. pratensis* s.l.), the crop groups are: ley — rye, oats, barley — the five remaining crops; for *Tylenchorhynchus,* mainly *T. dubius* (BUETSCHLI): ley — barley, rye, oats — pea — the four remaining crops; for *Rotylenchus,* mainly *R. robustus* (DE MAN): beet, carrot, ley — five other crops — potato; for *Meloidogyne,* here *M. hapla* CHITWOOD: pea — beet, ley, potato — the five remaining crops. No analysis is made of the *Paratylenchus* figures since too many zero's occurred, however, the range ley — beet — remaining crops is suggested. No significant differences were shown to exist by the "studentized range test" in the "other Tylenchida" and in the "saprozoic nematodes".

TABLE 1 B, also based on the nematode figures of spring 1956, shows that the crops in 1953 and 1954 are still causing very significant differences (c.f. F.-values) *after* the 1955 crop in all recorded categories of root-infesting nematodes. The "studentized range test" indicates corn as an efficient host plant of *Pratylenchus* and *Tylenchorhynchus* and as a poor host of *Rotylenchus, Meloidogyne* and *Paratylenchus.* TABLE 1 B confirms the forementioned data of TABLE 1 A and stresses the indication that beet is a good host for *Paratylenchus.* Only witloof appears as a samewhat more efficient host of *Pratylenchus* than would be expected from TABLE 1 A.

B. *Cyst nematodes in a sandy peat soil at Emmercompascuum*

The field was reclaimed by removing a thick peat layer in 1928 and was therefore virgin soil. Three crops of potato, two crops of wheat and one crop of rye were grown in the period 1929 through 1934. From 1935 up till the present seven different fixed cropping systems were practised on parallel plots of about 800 sq. metres in this field, viz. potatoes every year, potatoes every other year, potatoes every three years and monocultures of cereals. From the spring of 1954 on, each plot was examined annually for cystforming nematodes. TABLE 2 gives the results obtained in 1958; these results did not show real differences from those of other years.

TABLE 2 demonstrates that three cystforming *Heterodera* species have reached the field, viz. the cereal cyst eelworm *H. avenae* WOLLENWEBER, the potato cyst eelworm *H. rostochiensis* WOLLENWEBER and the *Galeopsis* cyst eelworm, *H. galeopsidis* GOFFART. The first-mentioned two species have built up high, in fact noxious, populations in the plots in which their respective host crops were grown intensively. Plots on which potatoes were grown every year and every other year had high nematode infestation, whereas no infestation was apparent on fields planted to potatoes every third year. Dense populations of *H. avenae* were apparent on soils planted yearly to winter wheat, oats or summer and winter cereals. A dense population of this nematode also occurred in the soil planted to cereals (mainly rye) two times in three

TABLE 2. Influence of one-sided culture on the appearance of noticeable populations of different *Heterodera* species in a sandy peat soil at Emmercompascuum. Seven fixed rotations since 1935. Nematode figures per 40 ml of soil, determined in the spring of 1956.
c. = cysts; vc. = viable cysts; l. = larvae within cysts.

Permanent rotational system	*Heterodera* cysts		
	rostochiensis	*avenae*	*galeopsidis*
	c. = vc. = l.	c. = vc. = l.	c. = vc. = l.
1. Potatoes every year	349 = 296 = 25640	0 = 0 = 0	0 = 0 = 0
2. Potatoes every other year (= cereals every other year)	216 = 205 = 30540	3 = 3 = 70	3 = 0 = 0
3. Potatoes every third year (= cereals two times in three years)	0 = 0 = 0	68 = 5 = 840	2 = 0 = 0
4. Winter rye every year	0 = 0 = 0	150 = 9 = 1480	5 = 5 = 64
5. Winter wheat every year	0 = 0 = 0	71 = 17 = 1460	8 = 3 = 90
6. Summer oats every year	0 = 0 = 0	140 = 14 = 2140	29 = 5 = 90
7. Summer and winter cereals alternatively	0 = 0 = 0	33 = 7 = 1000	40 = 1 = 30

years (= potatoes every third year), but a barely susceptible population was apparent in the soil planted to cereals (mainly rye) every other year (= potatoes every other year). *H. galeopsidis* is present in noticeable concentrations in all plots except the monoculture potato plot. Host plants of this nematode, *Galeopsis* and *Stellaria* spp., are associates of the cereal culture here and occur first apparently in the plots on which cereals are regularly grown.

C. *Root-infesting nematodes in sandy soil at Alteveer*

The prevailing phytophagous nematodes in this field were *Heterodera* (mainly *avenae*), *Pratylenchus* (a mixture of *penetrans* (COBB) and *crenatus*), *Tylenchorhynchus* (mainly *dubius*) and *Paratylenchus* (an unindentified species). In 1957 four crops, viz. beet, oats, potato and rye were grown in long strips. In 1958 the same crops were again grown in strips, but at right angles to the 1957 strips. A nematode census was taken from all plots in the spring of 1959. The results are recorded in TABLE 3.
The data from TABLE 3 suggest that the density of all genera has been influenced by the crops. *Pratylenchus* and *Tylenchorhynchus* seem to be suppressed by beet. *Paratylenchus,* on the contrary, is stimulated markedly by beet. The densest population is found on the plot with two years beet in succession (plot nr. 3), however, the influence of the beet crop of 1957 is also noticeable on the strips with other crops in 1958 (plots nr. 1, 2, 4). *Heterodera* is strikingly stimulated by rye but not by oats. This is visible in the number of free larvae in the soil as well as in the number of cysts and larvae within cysts. The densest population is found on the monoculture rye plot (nr. 14). The influence of the rye crop of 1957 is, as in the case with *Paratylenchus,* also noticeable on the strips with other crops in 1958 (plots nr. 13, 15, 16).

3. Discussion and conclusion

TABLE 3 reflects the complexicity of nematode population dynamics on a sandy farm soil. The crops are common and the nematodes studied are widespread. It may there-

TABLE 3. Influence of different rotations on a mixed population of root-infesting nematodes in sandy soil at Alteveer. Four crops in 1957, the same crops in 1958 following all crops of 1957. Nematode figures determined per 100 ml of soil in the spring of 1959.
Hl. = free *Heterodera* larvae; Pa. = *Paratylenchus;* P. = *Pratylenchus;* T. = *Tylenchorhynchus;* O. = other Tylenchida; S. = saprozoic nematodes. c. = cysts; vc. = viable cysts; l. = larvae within cysts.

Plot Nr	Crops 1957	Crops 1958	Active nematodes Hl.	Pa.	P.	T.	O. + S.	*Heterodera avenae* cysts c.	=	vc.	=	l.
1	Beet	Oats	25	230	210	490	4260	38	=	0	=	0
5	Oats		55	10	200	545	3960	18	=	1	=	20
9	Potato		35	15	410	1045	3850	23	=	1	=	5
13	Rye		580	10	165	675	3040	60	=	12	=	290
			695	265	985	2755	15110	139	=	14	=	315
2	Beet	Rye	210	430	20	495	4115	79	=	26	=	1150
6	Oats		315	0	60	1030	3960	36	=	10	=	360
10	Potato		265	5	235	620	3140	48	=	16	=	795
14	Rye		1190	15	230	1000	4895	145	=	83	=	3340
			1980	450	545	3145	16110	308	=	135	=	5645
3	Beet	Beet	25	3480	45	115	3905	21	=	0	=	0
7	Oats		35	10	95	390	2910	26	=	0	=	0
11	Potato		10	0	15	280	3570	23	=	0	=	0
15	Rye		325	20	55	175	2905	74	=	30	=	1070
			395	3510	210	960	13290	144	=	30	=	1070
4	Beet	Potato	160	135	240	585	4075	21	=	4	=	60
8	Oats		45	25	195	520	4570	17	=	1	=	5
12	Potato		30	5	115	425	3960	32	=	2	=	55
16	Rye		445	15	180	610	3775	58	=	16	=	310
			680	180	730	2140	16380	128	=	23	=	430

fore be expected that these population shifts are normally occurring in practice on this soil. All four crops differ from each other with respect to one or more phytophagous species. The influence of the lastgrown crop is marked. The *Paratylenchus* and *Heterodera* figures show, that negligible populations may rise to a high level in one or two years. The same figures indicate that the influence on the nematode population of one efficient host crop may persist for more years. This was known to be true for *Heterodera* species, but it appears to hold true also for *Paratylenchus.* TABLE 1 illustrates this fact with respect to *Pratylenchus crenatus, Tylenchorhynchus dubius, Rotylenchus robustus* and *Meloidogyne hapla.* In this experiment the preceding crops were grown for two years in succession and their influence is therefore very distinct. A different cropping history may even decide about the occurrence in noticeable numbers of related species as illustrated by TABLE 2. Initial infestations by the three *Heterodera* species recorded can hardly be absent in any of the plots. due to extensive distribution by wind and otherwise, but the crops had to bring them to

the fore. This trial gives an insight into the epidemiology of *Heterodera* infestations and their close association with crop rotation.

Several special plant-parasite relationships become visible from the tables. Some of them are noted earlier, some others will be treated with the help of more data elsewhere. Nine cases are listed here as follows without further discussion:

a. Potatoes every year and every other year caused high populations of *Heterodera rostochiensis,* but potatoes every third year evidently suppressed the nematode up till now (TABLE 2).
b. Monoculture of cereals, including rye, caused high populations of *H. avenae.* Rye every other year evidently kept the nematode at a low level (TABLE 2).
c. Rye (Petkus) was an efficient host of the *H. avenae* population at Alteveer, whereas oats (Marne) was not (TABLE 3).
d. Weeds in the cereal crops, probably *Galeopsis* and *Stellaria* species, built up noticeable populations of *H. galeopsidis* (TABLE 2).
e. Ley, rye, oats, barley and corn were efficient hosts of *Tylenchorhynchus dubius* and of *Pratylenchus crenatus* (TABLES 1 and 3).
f. Beet, carrot and ley (probably the white clover component) were efficient hosts of *Rotylenchus robustus* in comparison to potato (TABLE 1).
g. Pea, beet, ley (white clover) and potato were efficient hosts of *Meloidogyne hapla* (TABLE 1).
h. Ley and beet were efficient hosts of *Paratylenchus* sp. (TABLES 1 and 3).
i. Beet suppressed *Pratylenchus,* mainly *penetrans,* in comparison to oats, rye and potato (TABLE 3).

The examples above indicate the behaviour of some of the major species of the nematode populations present. More relationships may be present or become evident in the same soil.

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