Nematodes in relation to plant growth III. Pratylenchus penetrans (COBB) in tree crops, potatoes and red clover

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Summary

Studies in five rotation and fumigation experiments and additional surveys demonstrate, that *Pratylenchus penetrans* is a major cause of sickness symptoms and crop rotation effects in many crops of woody plants, potato and red clover (*Photo's* 1, 2, 3, 4; *Fig.* 3). The nematode is fairly widespread on light and medium soils, especially so in nurseries, fruit orchards and in the Veenkoloniën but it is irregularly distributed even in these areas; 9 % of all fields examined in a representative survey were heavily infested harbouring more than 100 specimens per 100 ml of soil.
Figs. 1, 2, 4 and 5 demonstrate significant linear relations between the logarithm of initial population density or of population density within roots and growth deficit of the susceptible crops. These relations, however significant, appear to vary markedly with test crop, soil, year, standardisation of the extraction technique and absence or presence of other growth factors; results of different experiments must therefore not normally be superimposed. Two other factors have incidentally caused noticeable yield differences, viz. the nitrogen effect of clover (*Fig.* 3, 4) and minor adverse influences on potato (*Fig.* 3b) and on apple (*Fig.* 1). Indications were obtained, that impaired nitrogen fixation, as recorded earlier for nematode-infested peas, may also occur in red clover as a consequence of nematode infestation.
Three control measures of the damage on infested soil are suggested by the trial results: soil sample examination as a basis for advisory work, soil treatment with nematicides when precious crops are grown and selected rotations. It seems advisable to avoid cultivation of potato, oats, rye and red clover in infested nurseries and to grow beet or mangold prior to potato or red clover on heavily infested arable land. Cultivation of red clover had perhaps be omitted at all on infested soil.
Five special host-parasite relationships apart from *P. penetrans* are apparent from *Tables* 1, 3 and 4, and summarized on page 207.

1. Introduction

The endoparasitic root-infesting nematode *Pratylenchus penetrans* is recognised as the cause of sickness symptoms in tree crops, potatoes and red clover in Europe and North America (CHAPMAN, 1959; DECKER, 1960; MAI and PARKER, 1956; MOUNTAIN and BOYCE, 1958; OOSTENBRINK, 1954, 1955a). Several other crops may also be infested (auctores diversi). The nematode is fairly widespread, especially in light soils. Distribution may take place by means of rooted plants; however, potato tubers, bulbs and plants with dried roots are not efficient carriers (JENSEN, 1953 a; OOSTENBRINK,

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1957; SLOOTWEG, 1956). Its significance as a parasite of the forementioned crops was proved by inoculations (CHAPMAN, 1959; DECKER, 1960; MAI, 1960; OOSTENBRINK. 1955a, 1958; PITCHER, PATRICK and MOUNTAIN, 1961). The nematode is very polyphagous (JENSEN, 1953 b; SHER and ALLEN, 1953; GOODEY, 1956/'59; OOSTENBRINK, S'JACOB and KUIPER, 1957; SOUTHEY, 1959), but great differences in susceptibility to damage and in rate of nematode reproduction were found to exist between crops (OOSTENBRINK, 1956a, 1959).

The last mentioned data served as a base for a number of field trials and observations to study the effect on crop production of this nematode under different agricultural conditions. Rotation effects, sometimes combined with soil treatment effects are correlated with population density of *P. penetrans* and eventually other plant parasitic nematode species present in the same soil. The crops were grown under conditions as near to practice as possible; their development was evaluated according to standard procedures. Some surveys were made to assess the distribution of the nematode. Its populations in soil or root samples were estimated by standardised methods described by the author (1960).

2. Results and observations

A. *Tree nursery KW at Winschoten*

In a tree nursery on sandy peat soil where *P. penetrans* caused damage to *Prunus*, *Crataegus* and other tree crops in previous years, four crops were compared in 1955, viz. rye (*Secale cereale* L.), plum seedling (*Prunus cerasifera* EHRH. var. *myrobalana*), beet (*Beta vulgaris* L.) and potato (*Solanum tuberosum* L.). Each crop was grown across two pairs of differently fertilized strips; the four strips, however, are considered as equivalent replicates since manuring did not influence the crop yields or the nematode populations significantly. The whole experiment (Trial I) was replicated in the same field (Trial II). Rye and beet developed well in 1955, potato grew fairly well but the plum crop had a poor and hollow stand.

In the autumn of 1955, after the crops were removed, nematode populations in the soil were estimated. In both trials consistent differences between crops appeared with respect to the population level of *Pratylenchus* (mainly *penetrans*). This was also true for *Tylenchorhynchus* (mainly *dubius* (BÜTSCHLI)), but not for the other Tylenchida and for the saprozoic nematodes. These differences were not present before the experiment started, as could be judged from root and soil sample examinations in 1954. The mean numbers of *Pratylenchus* extracted from 100 ml of soil of Trial I were 630, 560, 410 and 200 for the rye, potato, beet and plum seedling plots respectively. Comparative figures of Trial II were, in the same range but at a higher level, 1420, 730, 640 and 480 respectively. This difference in level has no bearing upon the experiment. It is explained by the fact that the samples of Trial II were incubated for a month at room temperature, which caused a better catch of this endoparasitic species; the catch of other nematode species was not influenced. [1]

[1] Root residues of the 1955 plum seedling crop collected from the soil of the corresponding plots about nine months after uprooting the plants, therefore during the growth of the test crop apple, still harboured several thousands of active *Pratylenchus* specimens per 10 g. Delayed hatch of *Pratylenchus* species from root residues of former crops must be considered an important variability factor in the assay of their populations by means of flotation methods. This is especially true when samples of different origin have to be compared. See also observations by *De Maeseneer* and *Van den Brande* (1960).

TABLE 1. Field KW, Trial I. Nematode populations following four different crops and growth of a subsequent crop of apple seedling, *Malus pumila* MILL ; means of four plots.

P. = *Pratylenchus*, mainly *penetrans* T. = *Tylenchorhynchus*, mainly *dubius*
O. = other Tylenchida S. = saprozoic nematodes

Crops in 1955	Nematodes autumn 1955 per 100 ml of soil				Test crop apple seedling in 1956 (c.f. FIG. 1)			
	P.	T.	O.	S.	Growth evaluation (high figure = good crop) 3. August	Number of plants per plot of 17,4 sq.m 26. November	Percentage of the plants with stem diameter $>$ 6 mm (at left) and 4—6 mm 26. November	
(1)	(2)				(3)	(4)	(5)	
Rye (*Secale cereale* L.)	630	300	180	2450	3,8	1047	0,1	2,9
Plum (*Prunus cerasifera* Ehrh. var. *myrobalana*)	200	95	140	1960	8,8	1378	16	32
Beet (*Beta vulgaris* L.)	410	63	160	2120	8,8	1322	18	34
Potato (*Solanum tuberosum* L.)	560	110	170	2510	7,0	1189	5,1	21
L.S.D.[1] 95 %	143	99			1,17	135	5,6	8,8
99 %	215	148			1,76	202	8,4	13,2
F-value[2]	14,5++	9,67++	0,41—	0,58—	32,3++	9,63++	19,1++	21,1++

1 Calculation from untransformed figures. 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.

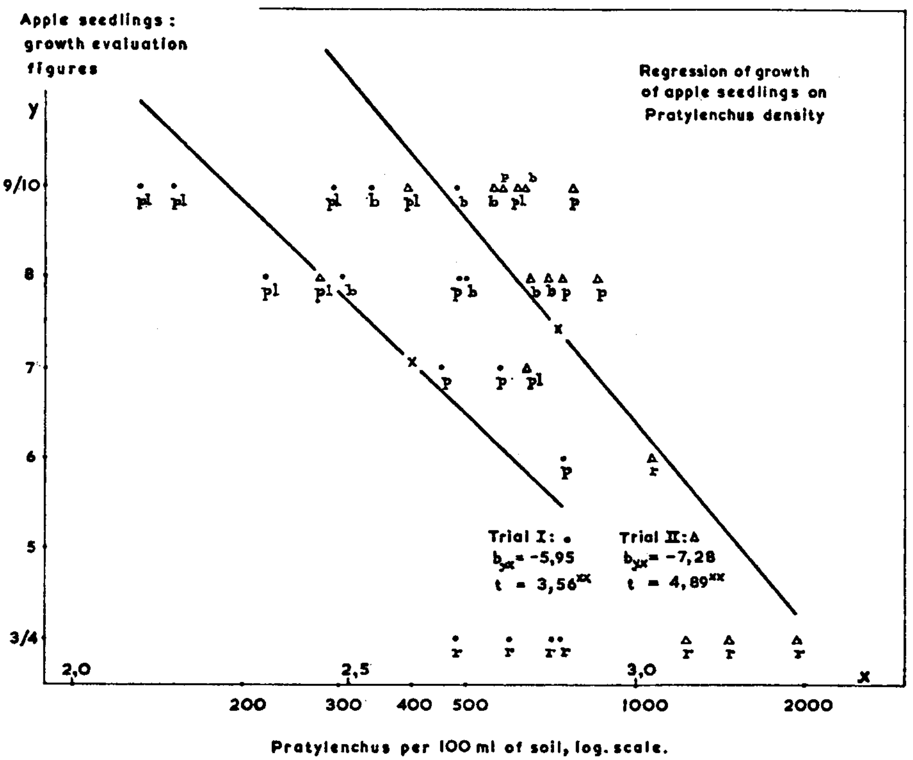
In April 1956 apple seedlings, *Malus pumila* MILL., were sown as a test crop on all plots. Marked growth differences appeared in relation to the preceding crops (PHOTO 1). The numerical data of Trial I are recorded in TABLE 1; Trial II gave essentially the same results. Growth evaluation figures of all individual plots were plotted against the corresponding *Pratylenclus* populations in the soil and regression lines were calculated and drawn, separately for both trials (FIG 1). In 1957 rose, *Rosa canina* L., was sown on all plots. The influence of the 1955 crops was still visible. Mean growth evaluation figures on the former rye, plum seedling, beet and potato plots were 6, 8, 9 and 7½ respectively.

Discussion : This experiment confirms our earlier observations (1956a) that rye and potato cause marked loss of young plants (*Table* 1, Col. 4) and poor growth (*Table* 1, Col. 3 and 5) in subsequent tree crops in nurseries infested by *P. penetrans.* We know that this is not the case in uninfested soil. The unfavourable influence of one crop of rye or potatoes evidently may be visible in at least two subsequent tree crops. The nematode is known as a primary parasite of apple, and this relation is confirmed by the significant negative regressions of growth of the apple seedlings on the *Pratylenchus* density (*Fig.* 1). It is evident, therefore, that the growth differences must at least partly be due to this nematode.
The *Pratylenchus* population was on an average highest following the rye crop, followed by potato, beet and finally plum seedling (*Table* 1). *Table* 1 and *Fig.* 1, however, indicate that plum seedling was not better than beet as a preceding crop. It is probable that the nematode figures recorded

on the plum plots are relatively too low because a greater part of the *Pratylenchus* population will normally escape extraction in root residues of late, woody crops (c.f. footnote on p. 189). This is also supported by the fact that the linear relationship in Trial II is more significant than in Trial I. A second reason is probably that *P. crenatus* was present in low numbers next to *P. penetrans*, whereas the proportion of *crenatus* in the *Pratylenchus* mixture is normally lower after woody crops (*Oostenbrink*, 1956a).

Table 1 and *Fig.* 1 also suggest, that rye was excessively poor as a preceding crop to apple. This was less marked in Trial II than in Trial I, and it may, therefore, be due to the forementioned irregularity in *Pratylenchus* extraction. It may, however, also be real and in this case *Tylenchorhynchus dubius* could be the cause, for yield loss in this field was also correlated with *Tylenchorhynchus* density. In other experiments this nematode appeared to be less noxious to woody crops than *P. penetrans*, but it did attack apple and reproduced on its roots. It can therefore have been of some importance in this field.

FIG. 1. Field KW. Growth evaluation figures of apple seedling of individual plots on 3. August 1956 plotted against pre-cropping *Pratylenchus* populations in the soil, separately for Trial I and II.
In each trial four crops (r = rye, pl = plum seedling, b = beet, p = potato) were grown fourreplicate in the preceding year. Statistical data (c.f. SNEDECOR, 1956): b_{yx} = regression coefficient, t = Student's t-distribution, xx = probabilities more than 99 %



B. *Tree nursery WP at Nieuwe Pekela*

P. penetrans caused damage to tree crops and potatoes in this field for several years; *P. crenatus, T. dubius* and other root-infesting nematodes were also present in this soil. In 1956 and 1957 different rotations were practised. Since then a permanent rotation trial was started, which is discussed hereafter.
Three equivalent strips of this trial were grown with potato (*Solanum tuberosum* L.), rose (*Rosa canina* L.) and oats (*Avena sativa* L.) in 1958. In 1959 the same crops were again grown in strips, but at right angles to the 1958 strips and the cropping was repeated according to the 1958 design in 1960. This is indicated in the plan below which also indicates plot numbers. The strips were as a whole comparable with respect to the preceding crops of earlier years.

Crops in 1959:	Crops in 1958 and 1960: Oats	Rose	Potato
Potato	A 1	B 1	C 1
Rose	A 2	B 2	C 2
Oats	A 3	B 3	C 3

←8 m→

Nematode populations in the soil were estimated and growth and yield figures of the crops were determined each year. No marked differences were present in the year 1958. The crops in this year are considered as controls: potato on plots C 1, C 2 and C 3 yielded 200, 194 and 206 kg of tubers, oats on plots A 1, A 2 and A 3 weighed 105, 103 and 116 kg (seed + straw), rose on plots B 1, B 2 and B 3 was evaluated 7,6; 7,1 and 7,2 respectively (0 = no crop; 10 = very good crop). Conspicuous rotational effects, which exceeded by far the differences in the 1958 crops, became visible in all three crops in 1959 and 1960. They can be explained on the basis of nematode infestations. Growth evaluations of potato and rose and pre-cropping population density of *Pratylenchus,* mainly *penetrans,* are recorded in FIG. 2.

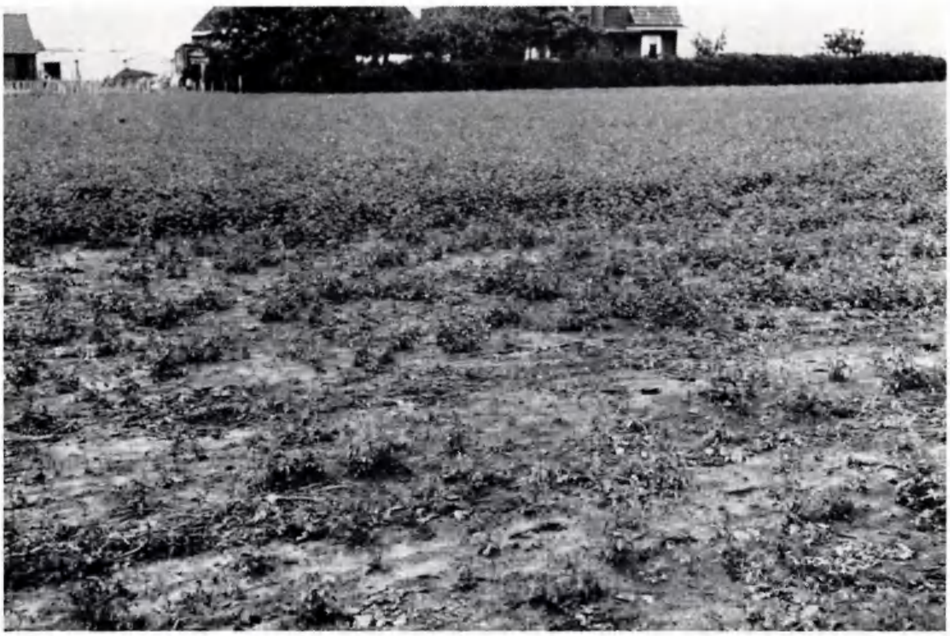
Discussion: Poor growth of rose and potato appears to be associated with dense populations of *Pratylenchus.* These crops developed best following rose. Potato yields 1959 were markedly depressed by drought on all plots but were nevertheless 35 % and 20 % higher on previous rose plots than on previous oats and potato plots. These figures were 16 % and 35 % respectively in 1960. Comparison of potato yields in 1960 with potato yields in 1958 of the same plots indicates, that these differences were not originally present. Oats and potato were therefore both unfavourable as preceding crops. Their sequence is not clear since the 1959 and 1960 results are different in this respect; this stresses the fact that results of different nematode trials cannot normally be superimposed. *Fig.* 2, however, demonstrates a close association between poor growth of the forementioned test crops and the density of the *Pratylenchus,* especially the *P. penetrans* population

PHOTO 1. Field KW. Rotational effects in the test crop apple seedling following rye (r), plum seedling (pl), beet (b), potato (p), and a replicate series of the same crops in the same order. Photograph on 29. July 1956.

PHOTO 2. Field LH. Marked rotational effects in the test crop potato, variety Noordeling, on untreated plots: poor growth following red clover (A, c), good growth following mangold (A, m). No rotational effects on comparable plots fumigated with DD: good growth following mangold (B, m) and red clover (B, c). C.f. FIG. 3a. Fumigation in the spring of 1955, preceding crops grown in 1955, photograph taken on 15. June 1956

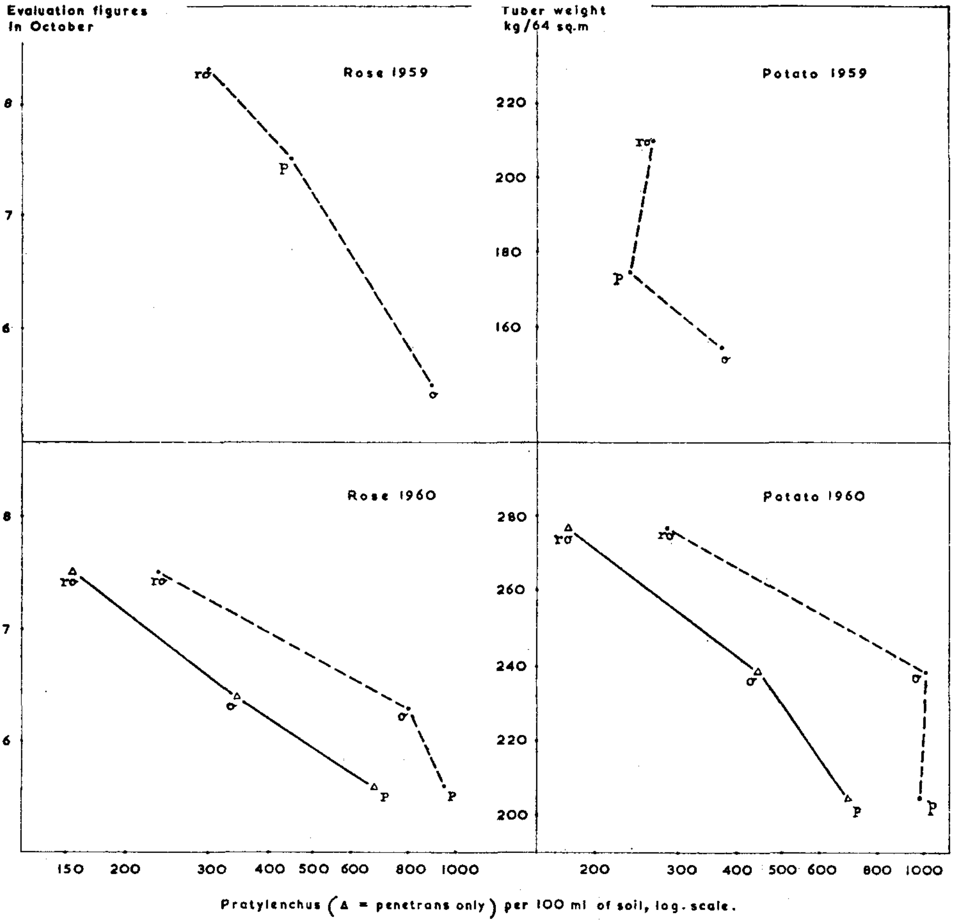
PHOTO 3. Field VMO. Red clover, sown in the spring of 1956. At left (= A) on untreated soil, at right (= B) on soil fumigated with DD in the autumn of 1954. Photograph taken on 22. June 1956.

PHOTO 4. Rotation effect in rose, *Rosa canina* L., on arable field at Sappemeer infested with *P. penetrans*. Rose following potato in front, rose following beet in the background; infestations 19.500 and 7.350 *Pratylenchus* per 10 g of roots respectively. Root samples and photograph taken 19. July 1956.



and there is little doubt that this nematode is the main cause of the rotational effects on this field. Only the droughty potato crop of 1959 was not conclusive.
Poor growth of oats was associated with dense populations of *P. crenatus* and *T. dubius*; this relation is not further illustrated or discussed here. Other nematode species did not show noticeable response to the crops.

FIG. 2. Field WP. Growth evaluation of rose, *Rosa canina* L., and tuber weight of potato, *Solanum tuberosum* L., plotted against pre-cropping *Pratylenchus* populations



C. *Arable land LH at Hijken*

The sandy soil of this field was reclaimed from bush and heather about 50 years ago. Potatoes were not grown here in the period 1946—'53 inclusive. The potato crop of 1954, following rye undersown with red clover, showed extremely poor growth which was considered to be due to heavy infestation by *P. penetrans*. *Tylenchorhynchus*, *Paratylenchus* and *Rotylenchus* species were present in the soil in barely measurable densities, in addition to saprozoic nematodes.

A combined fumigation and rotation experiment was started in 1955. Mangold (*Beta vulgaris* L.), oats (*Avena sativa* L.), potato (*Solanum tuberosum* L.) and red clover (*Trifolium pratense* L.) were grown in 1955 in tworeplicate strips of 12,50 × 3,30 m; half of each strip had been fumigated with DD (dichloropropane-dichloropropene mixture) beforehand, which increased the number of treatments to eight and the number of plots to sixteen. These sixteen plots were again split up in halves. On one half of each plot potato (*Noordeling*) was grown as a test crop in 1956, followed by red clover in 1957 (Trial I). On the other half of the plots the crops of 1955 were again grown in 1956; in 1957 potato (*Bintje*) and a row of red clover were grown as test crops (Trial II). TABLE 2 summarizes the effects of the soil fumigation on the nematode population and on the yield of the different crops in

TABLE 2. Trial field LH. Kill of *Pratylenchus* population (between brackets of the other Tylenchida) and increase of yield on plots fumigated with DD expressed as % of untreated plots. (Soil fumigation 4. April 1955)

	Year	Crops	Yield increase	Nematode kill
Trial I	1955	Red clover	24	
		Potato	11	69 *
		Oats	3	
		Mangold	—2	
	1956	Potato	83	37 (58)
		(on all plots)		52 *
	1957	Red clover	13	
		(on all plots)		
Trial II	1955	Same as in Trial I		
	1956	Red clover	61	37 (52)
		Potato	71	39 (49)
		Oats	0	—4 (67)
		Mangold	3	75 (58)
	1957	Potato	14	23 (41)
		(on all plots)		

* Figures determined by root sample extraction, contrary to the others which are determined by soil sample extraction.

both trials. It was noted that the red clover roots had fewer nitrogen nodules on the untreated soil. In FIG. 3a-d the yields of the test crops potato and clover are compared after the different preceding crops, when the latter are grown once and twice in succession, on unfumigated as well as on fumigated soil. PHOTO 2 demonstrates the character of the growth differences in the potato crop of 1956. It may be added that starch content of the potato crop was not influenced by the preceding crops or by the soil treatment; it is evidently not connected with the problems under consideration. Two sets of data are available to judge the influence of the preceding crops on the infestation of the test crops by *Pratylenchus* and eventually by other nematodes. In the scatter diagram of FIG. 4, yield of the 1956 test crop potato is plotted against *Pratylenchus* density *in* the potato roots for each of the eight different

FIG. 3. Field LH. Two different treatments in the spring of 1955: A = untreated soil, B = soil fumigated with DD; four different crops in 1955: c = red clover, p = potato, o = oats, m = mangold.

3a: Yield of potato 1956: preceding crops grown once (in 1955), on untreated and fumigated soil. 3b: Yield of potato 1957: preceding crops grown twice (in 1955 and 1956), on untreated and fumigated soil. 3c: Red clover 1957: following potato 1956 recorded under 3a. 3d: Red clover 1957: grown on the same plots as potato 1957 recorded under 3b.

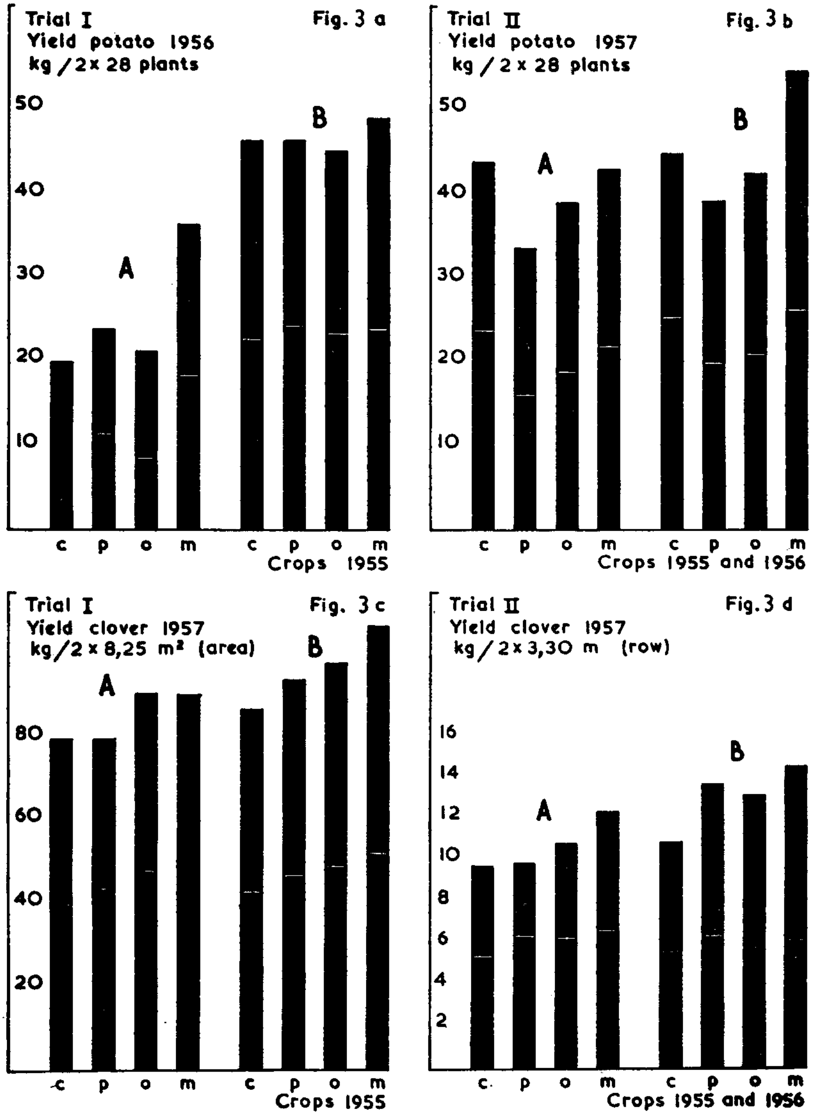
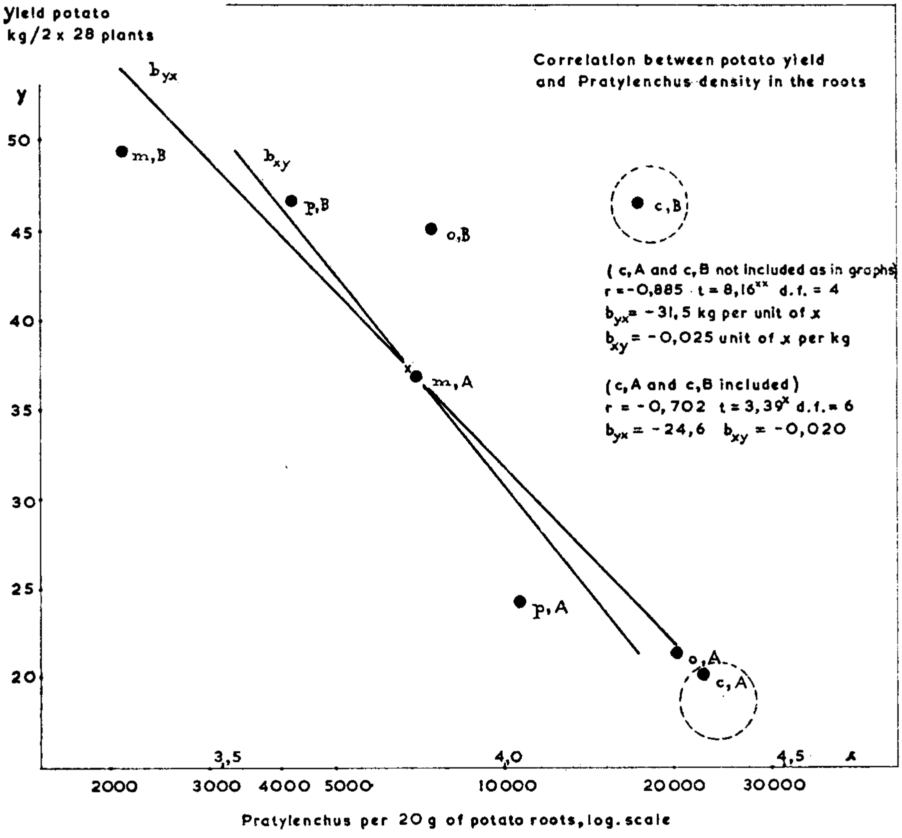


FIG. 4. Trial I of field LH. Correlation between potato yield 1956 and *Pratylenchus* density in the roots on differently treated plots. Two different treatments in the spring of 1955: A = untreated soil, B = soil fumigated with DD; four different crops in 1955: c = red clover, p = potato, o = oats, m = mongold.
Statistical data (c.f. SNEDECOR, 1956): r = correlation coefficient, t = Student's t-distribution, x and xx = probabilities more than 95 % and 99 % respectively, b_{yx} and b_{xy} = regression coefficients.



rotations and treatments; correlation and regression coefficients are recorded. The data are sums of the two replicate plots, as in FIG. 3; essentially the same results were obtained by analysing the data of individual plots. TABLE 3 gives further a full nematode census based on soil sample examination of both trials.

Discussion: P. penetrans was the only known parasitic nematode present in large numbers when the experiment was started. One soil fumigation with DD increased the yield of red clover and potato noticeably for at least three years; however, the growth of oats and mangold was not influenced. This is explained by the fact that only the first mentioned crops are susceptible to damage by *P. penetrans*. DD has evidently not stimulated growth of the crops which are known

TABLE 3. Trial field LH. Nematode populations following four different crops, grown once (Trial I) and twice in succession (Trial II) in untreated soil ; means of two plots.

P. = *Pratylenchus*, pen. = *penetrans*, cr. = *crenatus*, neg. = *neglectus*; Pa. = *Paratylenchus*; T. = *Tylenchorhynchus*, mainly *dubius;* R. = *Rotylenchus*, mainly *robustus*; M. = *Meloidogyne hapla*; O. = other Tylenchida; S. = saprozoic nematodes

Preceding crops	Nematodes spring 1956 per 200 ml of soil (Trial I - preceding crops grown once)					Nematodes spring 1957 per 200 ml of soil (Trial II - preceding crops grown twice)						
	P.	Pa.	T.	O.	S.	P.	Pa.	T.	R.	M.	O.	S.
Red clover	675	200	410	345	2430	635 (pen. + cr.)	220	800	360	0	450	2545
Potato	155	30	150	260	2060	300 (pen.)	30	95	55	50	195	1665
Oats	220	120	260	390	2635	725 (pen. + cr.)	100	720	90	0	560	2730
Mangold	230	170	90	185	2155	530 (neg.)	2235	35	15	0	230	1635
Total of untreated plots	1280	520	910	1180	9280	2190	2585	1650	520	50	1435	8575
Total of treated plots	805	250	255	590	10695	1695	1105	925	90	15	285	8005

to be unsusceptible to damage by the nematode. The yield increase of susceptible crops was lower in 1955 than in 1956, due to a nearly normal development of the control plots in 1955 (*Table* 2).
The 1956 test crop of potato (*Fig.* 3a) showed marked crop rotation effects on the untreated soil, in fair agreement with the *Pratylenchus* infestations of the roots. Mangold was by far the most favourable preceding crop, followed by potato, oats and red clover (*Fig.* 4, c.f. also *Oostenbrink,* 1959). Yields on comparable treated plots, however, were still better and did not show a marked influence by the preceding crops (*Fig.* 3a, *Photo* 2). This is in agreement with the low *Pratylenchus* levels, with the red clover plots as an exception (*Fig.* 4). On treated soil red clover did not appear to be a less favourable preceding crop than the others in spite of a higher *Pratylenchus* density. It is highly probable that this can be attributed to a strong nitrogen effect, on the treated soil (c.f. page 196). The data of *Fig.* 4 indicate the dominant role of the nematodes: the correlation between the potato yield and the *Pratylenchus* density in the roots (which can have influenced each other mutually) is significant in spite of the forementioned nitrogen and eventual other "side effects" due to the different preceding crops and treatments. This correlation (r = —0,702, t = 3,39+) becomes, of course, distinctly more perfect when the clover plots are omitted (r = —0,885, t = 8,16++).
The 1957 test crop potato (*Fig* 3b) was for some unknown reason less heavily damaged than the 1956 crop. The yields on unfumigated soil were considerably higher in 1957 than in 1956, but they were somewhat lower on the fumigated soil. The effect of the fumigation was only slight, which is understandable because the *Pratylenchus* population had increased on the fumigated plots to a density which was 77 % of the unfumigated plots and because the nematode damage was slight. Small crop rotation effects were apparent in 1957, after two years' cultivation of the forementioned preceding crops, in unfumigated as well as in fumigated soil and red clover was now about equal to mangold as a preceding crop. Red clover was therefore an unfavourable preceding crop to potato on unfumigated soil in the year 1956, when marked effects of crop rotation and of soil fumigation were apparent, but it was not unfavourable to the same crop on the same soil in the next year. This is the second indication that the influence of red clover depends on whether the *P. penetrans* infestation or the nitrogen effect will turn the scale. The result may evidently vary depending on the infestation level of the soil and on the year.

Red clover *as a test crop* on both trials in 1957 responded to the preceding crops in much the same way as potato 1957. Moderate rotational effects appeared with mangold as a good preceding crop. Clover was, however, not a good preceding crop to itself; the influence of the nitrogen effect has evidently been outweighed by the higher level of *P. penetrans* and/or other nematodes parasitic to clover or by some other adverse factor.

The yield differences of the crops in this experiment can therefore, apart from the above mentioned nitrogen effect, largely be explained by the assumption that the influence of *P. penetrans* was decisive. The nematode figures of *Table* 2 and of *Fig.* 4 are in general accordance with this assumption. Two further complications, however, become apparent when the nematode populations extracted from the soil are studied.
Table 3 shows first that the *Pratylenchus* density in the soil, contrary to the root infestation recorded in *Fig.* 4, disagrees with the yield loss unless correction is applied with respect to the species. The sample examination in the spring of 1957 revealed that the population was not purely *penetrans,* but that other *Pratylenchus* species had come to the fore on the mangold, oats and clover plots. 20 specimens identified to species proved to be all *penetrans* on the plots with two years of potato, but they were all *neglectus* (*Rensch*) on the mangold plots and they were a mixture of *penetrans* and *crenatus* on the oats and clover plots. This information came too late for splitting-up the *Pratylenchus* populations of 1957 and earlier years quantitatively into species. It shows nevertheless, that the *penetrans* numbers on the mangold, oats and clover plots in the spring of 1957 were lower than the total *Pratylenchus* numbers recorded in *table* 3. This must also hold for the *Pratylenchus* populations extracted in 1956 from the soil (*Table* 3, Trial I). The figures of *Table* 3 are therefore not detailed enough to support or to contradict the correlation between yield loss and *penetrans* infestation. Root extraction demonstrated this correlation clearly (*Fig.* 4), because potato is an efficient host for *P. penetrans* and not for the other *Pratylenchus* species in the mixture.
Table 3 shows further that the population density of *Paratylenchus-, Tylenchorhynchus-, Rotylenchus-* and *Meloidogyne* species have also been influenced by the preceding crops. *Meloidogyne, M. hapla Chitwood,* is a potential parasite of the test crops potato and red clover, and its appearance may have contributed to their yield deficits in 1957 on the plots where potato was grown in the previous years. The other genera are evidently not promoted by potato and are not known as parasite of this crop, but they may have been of some significance with respect to the growth of red clover.

D. *Arable land VMO at Overloon*

Potatoes showed increasingly poor growth on several fields of this arable farm since 1932. The sandy loam of the field under consideration was infested with *Pratylenchus* (*penetrans* + some *crenatus*), *Tylenchorhynchus* (mainly *dubius*), *Paratylenchus, Rotylenchus* (mainly *robustus)* and minor concentrations of some other root-infesting nematode species, in addition to saprozoic nematodes. In 1954 potato showed poor growth, which was attributed to heavy infestation by *P. penetrans,* the only known root parasite in this soil which was proven pathogenic to potato. Three field experiments were started here:

1. Soil fumigation with a heavy dose of DD in the autumn of 1954 caused a nearly full kill of all plant parasitic nematodes in two strips of this field. In 1955 rows of 41 crops were grown twofold on treated and untreated soil. Several woody crops, several potato varieties (including all varieties used in the experiments under B, C and D) and red clover showed poor growth on the untreated soil in this year; growth improvement by the soil fumigation was marked in these crops. This was also the case with cereals and grasses in this field. Several crops of the Chenopodiaceae and Cruciferae, however, did not show favourable response. In 1956 nine crops were

sown or planted again, tworeplicate, on small plots of the same soil. The influence of the soil treatment became again visible among other crops in red clover (PHOTO 3).

2. In 1955 a crop rotation experiment was started on an adjacent part of the field. In this year eight crops were grown on plots of 18 sq. metres with four replicates. The crops were oats, rye, mangold, potato, rose (*Rosa canina* L.), swede (*Brassica napus napobrassica* (L.) RCHB.), white clover (*Trifolium repens* L.) and grass (*Lolium multiflorum* LAM.). On two replicate series potato, variety *IJsselster,* was grown as a test crop in 1956. On the other two replicates the crops of 1955 were again grown in 1956, followed by potato, variety *IJsselster,* as a test crop in 1957. The growth of the eight preceding crops was fairly good in 1955 except for that of rose which was poor. In 1956 growth of rose was relatively better; growth of potato and the cereals was less good than in the previous year and the white clover crop was very poor. TABLE 4 demonstrates the influence of one year's culture of the different crops on the mixed nematode population, according to soil sample examination in the spring of 1956. Essentially the same differences were found after two years' culture of these crops. FIG. 5 shows the regressions of the yield of the subsequent potato crops, 1956 and 1957, on the pre-cropping populations of *Pratylenchus* (in 1957 *P. penetrans* only) in the soil. It became necessary to determine *P. penetrans* especially in 1957, since at that time *P. crenatus* came to the fore on some of the plots.

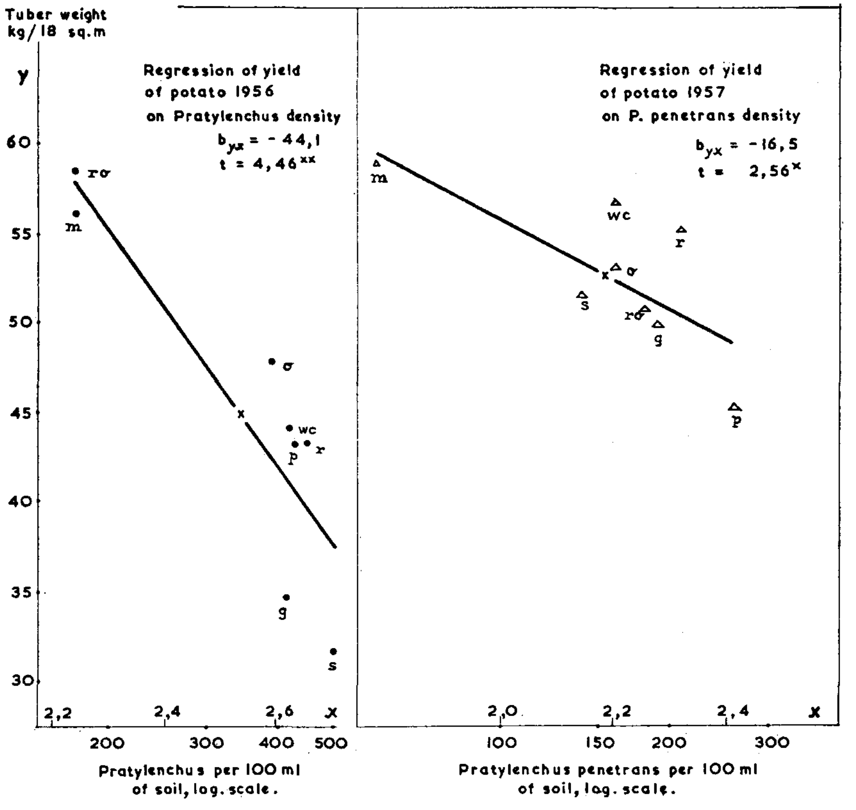
3. In another adjacent part of the same field soil treatments with different nematicides were applied in the autumn of 1955. Potato, variety *IJsselster,* was grown as a test crop in 1956 and again in 1957. Part of the results have been published

TABLE 4. Trial field VMO. Nematode populations following eight different crops P. = *Pratylenchus,* mainly *penetrans*; Pa. = *Paratylenchus*; T. = *Tylenchorhynchus,* mainly *dubius*; R. = *Rotylenchus,* mainly *robustus*; O. = other Tylenchida; S. = saprozoic nematodes

Crops in 1955	Nematodes spring 1956 per 100 ml of soil						Potato yield 1956 kg/18 m²
	P.	Pa.	T.	R.	O.	S.	
Mangold (*Beta vulgaris alba* DC.)	175	230	180	55	140	1515	56,1
Rose (*Rosa canina* L.)	175	20	160	20	185	2015	58,5
Oats (*Avena sativa* L.)	390	55	750	45	180	1830	47,9
Grass (*Lolium multiflorum* Lam.)	415	315	1115	65	195	2405	34,6
White clover (*Trifolium repens* L.)	420	85	185	60	175	2660	44,0
Potato (*Solanum tuberosum* L.)	430	20	250	15	175	2015	43,3
Rye (*Secale cereale* L.)	450	60	675	30	190	1740	43,3
Swede (*Brassica napus napobrassica* (L.) Rchb.)	505	25	655	45	155	1455	31,6
L.S.D. 95 % [1]	112	161	340			466	7,41
99 %	169	241	510			699	11,11
F.-value [1]	9,89++	3,74++	8,68++	0,99–	0,89–	6,36++	11,9++

[1] c.f. TABLE 1.

FIG. 5. Field VMO. Yield of potato 1956 and 1957 plotted against pre-cropping populations of *Pratylenchus* (in 1957 *P. penetrans* only). Potato 1956 followed eight different crops of 1955, potato 1957 followed the same crops grown twice, in 1955 and 1956 (m = mangold, ro = rose, o = oats, g = grass, wc = white clover, p = potato, r = rye, s = swede).



(BESEMER and OOSTENBRINK, 1957), but additional data are of value here. The three most successful treatments were DD-60 ml/sq.m, Vapam, 50 ml/sq.m. and EDB 10 vol % — 120 ml/sq.m. (Vapam = sodium N-methyldithiocarbamate dihydrate, EDB = ethylenedibromide). They left 1—4 % of the *Pratylenchus* populations alive and improved the tuber yield of the 1956 crop considerably, viz. with 53—68 % of the yield on untreated plots. In 1957 pre-cropping *Pratylenchus* populations of the treated plots were still only 0—16 % of the untreated control. The 1957 potato crop yielded more than the 1956 crop. It hardly showed any effect of the treatments, yield increases were only 2—9 % of untreated. This was due to the fact that in this year the control plots were nearly healthy.

Discussion: The fact that Chenopodiaceae and Cruciferae were equally good on both, untreated and treated soil of the first mentioned fumigation experiment indicates that no general soil deficiency was present in this field. It is reasonable sure that the poor growth of woody crops, potatoes and red clover in 1955 and 1956 are caused by the heavy *P. penetrans* infestation. The poor growth of cereals and grasses may be due to the other root infesting nematodes in this soil, of which at least two species are known as parasites of Gramineae, viz. *T. dubius* and *P. crenatus.*

The rotation experiments 1955—1957 support the results of trial field LH described under C. Potato showed marked rotational effects in 1956, with rose and mangold as the best preceding crops, in close association with the *Pratylenchus* figures (b_{yx} = — 44,1 kg of potatoes on 18 m^2 per tenfold increase of the *Pratylenchus* population, which was mainly *P. penetrans*; c.f. *Fig.* 5). It is possible that the low yields following swede and grass are partly due to another factor. In 1957 the test crop potato developed better and the influence of the preceding crops, now grown twice in succession, was much less (b_{yx} = — 16,5; c.f. *Fig.* 5). It is concluded that damage to potato on this soil was much more severe in 1956 than in 1957. Consequently marked effects of crop rotation and soil fumigation appeared in 1956 and not in 1957. The soil treatment experiment under 3 shows convincingly that the 1957 potato crop on the untreated soil was not damaged, in contrast to the same plant on the same soil in 1956. This confirms the data under C.

The marked influence of the preceding crops on some other nematode groups is illustrated in *Table* 4. These nematodes have probably not been of much influence to the test crops potato; their host-parasite relationships are briefly discussed on page 207.

E. *Arable land OS at Sappemeer*

On this field arable crops were grown in the years before 1955 and difficulties were not observed. In 1955 half of the field was grown with potato and the other half with sugarbeet. In 1956 rose, *Rosa canina* L., was sown on both halves. This crop was fair after beet but it was a complete failure after potato, with a sharp and straight border between both halves, c.f. PHOTO 4. Root samples, taken on 19. July 1956, revealed that the roses on the potato plot harboured 19.500 *Pratylenchus,* mainly *penetrans,* per 10 g of roots and those on the beet plots 7.350.

Discussion: The heavy infestation and the negative relation between infestation rate and damage indicate that *P. penetrans* is the cause of this crop rotation effect. It demonstrates that serious damage may occur in roses when they are grown on arable land infested with *P. penetrans.*

F. *Survey results*

Four sets of data furnish information on the distribution of *P. penetrans*:

a. Thousands of plant samples from various nurseries of woody crops, ornamental plants and strawberries, sent for different purposes by advisory and field inspection officers over a period of ten years, revealed the occurrence of the nematode in about half of these crops.

b. The "Bedrijfslaboratorium voor Grondonderzoek" examined 355 soil samples from 271 fruit orchards on river clay in the centre and on lighter soils in the south-eastern part of the country. 74 % of the samples were infested, 24 % harboured more than 50 specimens per 100 ml of soil. The percentage of infested fields was nearly as high on the river clay as on lighter soils; the population density, however, was on an average lower. About the same results were obtained in a recent survey by the "Rijkstuinbouwconsulentschappen" in the river clay area (unpublished report).

c. Peaty sand soil in the Veenkoloniën, on which potatoes are regularly grown, harboured noticeable populations in 58 % of the fields according to the examination of 295 random root samples taken in the period 1956—1958 inclusive. Another species, *P. crenatus,* was present in nearly 100 % of the same samples.

d. Soil samples from all fields of 48 arable farms in different parts of the country, examined by the forementioned Bedrijfslaboratorium, revealed an infestation on 77 % of the farms or in 34 % of the fields ; 9 % of the fields harboured more than 100 *P. penetrans* per 100 ml of soil. The peaty sand soil in the Veenkoloniën was more, and the clay soil was less generally infested than the sand, silt and loam soils in the rest of the country. C.f. TABLE 5.

TABLE 5. Occurrence of *Pratylenchus penetrans* on arable farms of which all fields were examined by the "Bedrijfslaboratorium voor Grond- en Gewasonderzoek" in the period 1957—1960 incl.

Soil type and area	Number of farms		Number of fields		
	Examined	Infested	Examined	Infested	Heavily infested
Peaty sand (Veenkoloniën of Groningen, Drenthe and Overijssel)	18	17 (= 94%)	316	135 (= 43%)	40 (= 13%)
Sand, silt and loam (Nine different provinces)	26	18 (= 69%)	318	94 (= 30%)	23 (= 7%)
Clay (Gelderland and Zeeland)	4	2 (= 50%)	72	14 (= 19%)	0 (= 0%)
Total	48	37 (= 77%)	706	243 (= 34%)	63 (= 9%)

* Heavily infested means > 100 *P. penetrans* per 100 ml of soil.

Discussion : The forementioned data indicate that *P. penetrans* is fairly widespread, though it is not omnipresent even in favourable biotopes (as appears to be the case with *P. crenatus*). It is therefore probable that *P. penetrans* has not yet reached its potential distribution area and that it is still spreading. The nematode evidently prefers lighter soils. It does not reach dense populations in clay soil, though it does occur there in orchards as well as in arable farms. It is fairly safe to conclude that more than 50 % of the fields are noticeably infested in nurseries of perennial plants, in fruit orchards and on arable land in the Veenkoloniën as well as locally on other light to medium soils. The category "sand, silt and loam soils" of *Table* 5 is probably a representative average for light and medium soils in the country. This means that on these soils 69 % of the farms or 30 % of the fields are infested. 9 % of all fields comprise population densities which will often cause failures in susceptible crops. The marked population increases on efficient hosts and the great susceptibility to damage of several crops not included in this study, make it probable that the nematode is of practical significance on many lighter infested fields as well.

3. General discussion and conclusions

The present experiments stress known data about the parasitic potencies of *P. penetrans* and its host-parasite relationships and allow a more quantitative insight into the significance of this nematode in the practice. The data are obtained from widely different trial fields. All fields were infested with more than a hundred *P. penetrans* per 100 ml of soil. We know from earlier inoculations, that these populations can cause serious growth deficits in the test crops apple and rose, potato and red clover. The weight of the nematode factor can not be determined exactly by field trials in which other factors may also be included, but the regression lines and further observations discussed hereafter indicate that *P. penetrans* was the main cause of the growth differences observed. The symptoms of poor growth illustrated in PHOTO's 1, 2, 3 and 4 are therefore probably typical for *P. penetrans* damage.

FIGS. 1, 2, 4 and 5 record the yield or growth evaluation of the test crops, indicating growth deficits, plotted against the *Pratylenchus*, if possible the *penetrans* levels (logarithmic scale as used by LOWNSBERY and PETERS (1955) and by JONES (1956) with respect to *Heterodera* infestations). The data suggest a rectilinear relationship and in FIGS. 1, 4 and 5 straight lines are calculated and drawn. This linear relationship is in accordance with our earlier results on *P. penetrans* (OOSTENBRINK, 1956a), and also with the general concept of root eelworm damage explained by JUSTESEN and TAMMES (1960). LOWNSBERY and THOMASON (1959) suggested that the linear relation between the logarithm of initial population density and growth deficit of the infested plant is perhaps generally valid. There is, however, no certainty that the transformation to the logarithmic scale is most suitable. It must in fact be considered normal that the line is more horizontal with both very heavy and very light nematode infestations. The fact, however, that a direct relationship between *Pratylenchus* density and growth deficit of the test crops *can* be made visible in all trials, indicates that the nematode must be a major cause of the growth differences observed. Other growth factors and the technique, as discussed later, introduce great variability in rotation experiments: only a dominant factor will show up consistently as is the case in these trials.

Two other observations stress the significance of the nematode factor. The susceptible crops showed their unusual poor growth in all trials notwithstanding a quite different cropping history of the fields. This was e.g. the case with potato on the nursery soil and with woody crops on the arable soil. The only known common growth factor was *P. penetrans*, and there is little chance that an other common adverse factor of all these crops could accidentally be present in all soils. It appeared further that soil fumigation with DD or other nematicides fully restored the productivity of the soil for some years with respect to the susceptible crops. This is considered a strong indication that the poor growth was due to nematode damage (CHRISTIE, 1959; OOSTENBRINK, 1956b). The known side effects of these fumigants (slight increase of pH and of available nitrogen) can not have interfered with the results. Other direct growth-increasing properties of DD have not been found with certainty and are surely not of general significance. The fumigant did not at all stimulate growth on the nonsusceptible crops (c.f. TABLE 2). There are a few sickness problems in this country about which statements were made that they are not nematode damage and can nevertheless be cured by nematicides, but none of these cases has adequately been proved and careful observations have shown that parasitic nematodes are associated with each of these problems [1]. The striking curative effect of

[1] These problems are: a. non-specific sickness in pears replanted on apple soil in association with *Pratylenchus penetrans* (in litt., Versl. Tuinbouwk. Onderz. 1956: 124), b. carrot sickness in Voorne, which problem comprises damage by *Rotylenchus robustus* and other nematodes, as well as the so-called tailed carrot problem ("staartpeen") which can *not* be solved by DD-treatment (*Meded. Dir. Tuinb. 22* (1959), 620—625), c. sickness symptoms in some flower bulbs in the Noordoostpolder in association with *Hemicycliophora sp.* (*Jaarverslag IPO. 1959*, 118) and d. poor growth in meadows in association with a complex of rootinfesting nematodes (Phytonematology in Western Europe, stencilled report Alabama Polytechnic Institute 1957, p. 7).

the treatments with nematicides, therefore, support the view that the growth differences in our experiments were largely due to nematode, in this case mainly *P. penetrans,* damage.

The relationship between growth deficits and population density of *P. penetrans,* therefore the slope of an eventual regression line and the absolute values, appear to vary markedly and results of different experiments must therefore not be superimposed. Test crop and soil fertility will normally influence the curve, and this appears also to be the case in the same crop on the same soil with such complex factors as the technique and the growing season. Longer incubation of the samples changed the slope and the position of the regression lines of Trial KW (FIG. 1). It is clear from Trials VMO and LH that potato was heavily damaged by *P. penetrans* in 1956 and not in 1957 and that the lines of these years must for that reason, be quite different (FIG. 5). Favourable growing seasons seem to reduce the difference between lightly and heavily attacked plants in this case ; these results are in contrast to those obtained by JONES (1956) on *Heterodera schachtii* infestation of beet. Other effects of different preceding crops and treatments, therefore other growth factors, may influence the relationship on one soil and not on the other by introducing variability (FIG. 4 ; c.f. also OOSTENBRINK, 1956 a, who described *P. penetrans* damage in apple which was aggravated by "specific sickness" in one field and not in the other). It is therefore unreasonable to expect a constant relation between *P. penetrans* density and yield deficits in practice, in spite of the marked damage which this nematode causes in general. This is probably also true for many other host-nematode relationships.

Adverse growth factors of the same importance as *P. penetrans* (such as specific sickness in woody crops, c.f. OOSTENBRINK, 1956a), have not been encountered in these trials. At least two other factors, however, have incidentally caused noticeable yield differences, viz. the nitrogen effect of clover and adverse influences apart from *P. penetrans.*

FIGS. 3, 4 and PHOTO 2 of Trial LH indicate that red clover increased the *P. penetrans* infestation and at the same time improved soil fertility. In 1957 *P. penetrans* damage to potato was slight in general and damage to potato on the clover plots was apparently compensated by the nitrogen effect ; c.f. FIG. 3b. (Damage to red clover as a test crop was not compensated, c.f. FIG. 3c and d). In 1956, however, *P. penetrans* damage to potato was more severe and was compensated only on the fumigated plots, but not on the untreated soil (FIG. 3a, compare also plot c, B with c, A in FIG. 4). This may be due to the heavy infestation on the untreated plots in spring 1956. It is, however, probable that on these plots nitrogen fixation by the roots of the 1955 red clover crop has also been less efficient : there were fewer nitrogen nodules than on the fumigated soil. This may be a consequence of the heavier nematode infestation. This phenomenon was noted earlier in field observations and it was proved to exist in nematode-infested peas. Nodulation and nitrogen fixation were progressively suppressed here by inoculation of *Heterodera goettingiana* larvae in peas ; the infected plants lost their potency for nitrogen fixation and their normal protein content decreased. This already occurred at inoculation levels of nematodes which did not yet cause deficits of plant weight and total yield (OOSTENBRINK, 1955b).

Impaired nitrogen fixation in legumes as a consequence of nematode infestation may be widespread in practice, since these plants are often infested by root-infesting nematodes.

Adverse influences not attributed to *P. penetrans* are noted in potato plots of Field LH II and in apple on former rye plots of Field KW. Both can be due to other rootinfesting nematodes, viz. to *Meloidogyne hapla* and to *Tylenchorhynchus dubius* respectively, but no conclusive data can be given without further experimental evidence.

The variability in the regressions and correlations do not exclude the possibility that other fertility factors could have been of importance on incidental plots, but they have not been noticed with certainty.

The TABLES 1, 3 and 4 demonstrate the complexicity and dynamics of the nematode population in general and indicate several plant-nematode relationships apart from *P. penetrans*. Five cases are listed here as follows:

a. Grass, red clover, oats, rye and swede were efficient hosts of *Tylenchorhynchus dubius* (TABLES 1, 3 and 4).
b. Red clover was an efficient host of *Rotylenchus robustus* (TABLE 3).
c. Potato built up a noticeable population of *Meloidogyne hapla* more rapidly than red clover, mangold and oats (TABLE 3).
d. Mangold and grass were efficient hosts of *Paratylenchus* sp. (TABLES 3 and 4).
e. Mangold suppressed *P. penetrans* and *P. crenatus* in comparison to other arable crops, but it appeared to be a very efficient host of *P. neglectus* (TABLES 1, 3, 4).

These cases confirm and extend cases e - i in issue II of this series (OOSTENBRINK, 1961). Some of these relationships may have been of significance to the forementioned test crops as indicated. Most of them, however, are associated in the first place with crops not included as test plants in this study.

The practical aspects of the data may be summarized as follows:

a. *P. penetrans* must be considered an important cause of poor growth in many crops of tree seedlings, potatoes and red clover. About one third of all fields on light and medium soils and about one half of the fields in nurseries and fruit orchards and in the Veenkoloniën harbour this nematode; 9 % of all fields examined were heavily infested. Three control methods are suggested by the trial results.

b. The high significance of the regressions of the yields of susceptible crops on *P. penetrans* populations indicate the value of soil sample examination as a basis for advisory work, in spite of the fact that the relation between nematode density and damage is variable. In this way cultivation of susceptible crops in heavily infested fields, and therefore failures as illustrated by PHOTO 4, can be avoided. It is not advisable to cultivate woody crops in fields with more than 50, or potatoes and red clover in fields with more than 100 *P. penetrans* per 100 ml of soil.

c. Soil disinfection with nematicides suppressed the sickness symptoms, i.e. rotation effects, on both trials where this treatment was applied. This treatment will normally cure *P. penetrans* damage for some years. (C.f. BESEMER and OOSTENBRINK, 1957; MEIJNEKE, 1959). Its application will, however, be restricted to valuable crops until the costs of treatment decrease.

d. The data confirm earlier results that beet or mangold, sown plum, apple and rose are favourable; whereas, potato, oats, rye and red clover are unfavourable preceding crops on soil infested with *P. penetrans*. The nitrogen effect of red clover may sometimes compensate the rise of the nematode level under this crop. It is therefore advisable to avoid cultivation of the forementioned arable crops, except beet, in infested nurseries of tree crops. It is also advisable to grow beet prior to potatoes or red clover on heavily infested arable land. Perhaps the cultivation of red clover should be omitted on infested soil.

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