The common relation between population density and plant weight in pot and microplot experiments with various nematode plant combinations

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Summary – In 31 published and five unpublished experiments, curves according to the equation $y = m + (1 - m)0.95^{P/T-1}$ for $P > T$ and $y = 1$ for $P \leq T$ (Equation 3) were fitted to the relation between P and y, where P is the density at planting of various nematode species and y is the plant weight (expressed as a proportion of plant weight at nematode densities $P \leq T$) of various plant species at the end of the experiment. To compare basic patterns in these experiments, data sets were normalized with respect to m and T. Relative plant weights y were transformed to $y' = (y - m)/(1 - m)$ and nematode density scales were divided by T. Values of P/T were allocated to classes with regular intervals on a logarithmic scale. Averages of all y' values (Y') per class plotted against antilog of average log relative nematode density per class fitted almost exactly to a curve according to the equation $y' = 0.95^{P/T-1}$ for $1 < P/T < 100$ and $y' = 1$ for $P/T \leq 1$. It is concluded that Equation (3) for the relation between nematode density at the time of sowing or planting and relative plant weight during the first year after sowing or planting applies to a wide range if not to all combinations of nematode and plant species. This confirms Seinhorst's theory about plant growth reduction by nematodes for all these combinations. In only one of fifteen experiments with *Meloidogyne* species on host plants could an effect of population increase on relative plant weight be derived from the data. © Orstom/Elsevier, Paris

Résumé – *Relation générale entre densité de la population et poids des plantes lors d'expériences en pots et en micro-parcelles concernant différentes combinaisons nématode / plante* – Se fondant sur les résultats de 36 expériences (dont cinq non publiées) il a été établi des courbes correspondant à l'équation $y = m + (1 - m)0,95^{P/T-1}$ pour $P > T$ et $y = 1$, pour $P \leq T$ (équation 3), courbes ajustées à la relation entre densité à la plantation (P) de différentes espèces de nématodes et le poids de différentes espèces de plantes (y) - exprimé comme la proportion du poids aux densités $P \leq T$ - à la fin de l'expérience. Pour pouvoir comparer les schémas de base de ces expériences, les séries de données ont été normalisées en ce qui concerne m et T. Le poids relatif des plantes, y, a été transformé en $y' = (y - m)(1 - m)$ et les échelles des densités de nématodes divisées par T. Les valeurs de P/T ont été réparties en classes sur une échelle logarithmique. Les moyennes (Y') de l'ensemble des valeurs de y' pour chaque classe ont été alignées contre l'antilog du logarithme moyen de la densité des nématodes par classe ; ces moyennes s'ajustent exactement à une courbe d'équation $y' = 0,95^{P/T-1}$ pour $1 < P/T < 100$ et $y' = 1$ pour $P/T \leq 1$. Il en est conclu que l'Équation 3 concernant la relation entre densité des nématodes au moment du semis (ou de la plantation) et le poids relatif des plantes pendant la première année de croissance peut s'appliquer à un grand nombre sinon à la totalité des associations entre nématode et plante. Cela confirme, pour toutes ces combinaisons, la théorie de Seinhorst concernant la diminution de croissance des plantes sous l'influence des nématodes. Dans une seule des quinze expériences relatives à des espèces de *Meloidogyne*, un effet de l'augmentation de la population sur le poids de la plante a pu être mis en évidence à partir de ces données. © Orstom/Elsevier, Paris

According to Seinhorst's (1979, 1995*b*) growth model, the growth rates for plants of the same weight (and therefore of different age) at nematode densities P (r_p) and without nematodes (r_0) are related as follows:

$$r_p/r_0 = k + (1 - k)z^{P-T} \quad \text{for } P > T$$
$$r_p/r_0 = 1 \qquad\qquad \text{for } P \leq T \quad \text{and} \qquad (1)$$
$$r_p/r_0 = k \qquad\qquad \text{for } P \to \infty$$

assuming that at a given nematode density P, r_p/r_0 is constant throughout the growing period. The value of

k is independent of nematode density P and of time after planting, but may vary between experiments. T is the tolerance limit, the largest density P that does not cause growth reduction, and z is a constant smaller than 1. Cross sections orthogonal on the time axis of a three-dimensional model (Schomaker *et al.*, 1995) describing, at different values of k, the relation between total plant weight, nematode density, and time after planting are, from some weeks after planting, in close agreement with Equation (2),

$$y = m + (1 - m)z^{P-T} \quad \text{for } P > T \text{ and}$$
$$y = 1 \qquad\qquad\qquad \text{for } P \leq T \qquad (2)$$

in which z and m are constants smaller than 1. In most, if not all experiments, z^T could be considered to be 0.95. Then Equation (2) becomes

$$y = m + (1 - m)0.95^{P/T-1} \quad \text{for } P > T \text{ and} \qquad (3)$$
$$y = 1 \qquad\qquad\qquad\qquad \text{for } P \leq T$$

Recurrence in experiments of the basic pattern described in Equations (2) and (3) confirm Seinhorst's theory on growth reduction by nematodes, summarized by Seinhorst (1995*b*) as: 'The same happens later'. To compare these basic patterns in experiments with different nematode/plant combinations independently of the parameter values, the data from these experiments must be normalized with respect to the parameters m and T, which have different values for the various combinations.

This is done by transformation of Equation (2) to

$$y' = \frac{y - m}{1 - m} = z^{P-T} \quad \text{for } P > T \text{ and}$$
$$y' = 1 \qquad\qquad\qquad \text{for } P \leq T \qquad (4)$$

Then, the value of y' at a relative nematode density $(P/T)_j$ $(j = 0 \text{ to } \infty)$ in n experiments $(i = 1 \text{ to } n)$ is the same in all experiments to which Equation (4) applies. Relative plant weights Y_{ij} at a given relative nematode density $(P/T)_j$ in the ith of n experiments, estimated by fitting a curve according to Equations (2) or (3) to the observed plant weights, can be considered as estimates of y' at that density. Moreover, if the relative minimum plant weight m_i was determined, Y_{ij} can be transformed to

$$Y'_{ij} = \frac{(y_{ij} - m_i)}{(1 - m_i)} \qquad (5)$$

which is an estimate of y' at relative nematode density $(P/T)_j$. The n transformed relative plant weights Y'_{ij} at a certain nematode density in all experiments are then estimates of the same y' at the same relative density $(P/T)_j$ and can be treated as replicates in a single experiment. Therefore, their average

$$\overline{Y}_j = \frac{1}{n} \sum_{j=1}^{n} Y'_{ij} \qquad (6)$$

is also an estimate of y' at relative density $(P/T)_j$. If the distribution of the transformed relative plant weights Y'_{ij} at each density can be treated as a normal distribution, the standard deviation of $\overline{Y}_j$ is $n^{-0.5}$ times that of the transformed relative plant weights.

The number n of transformed relative plant weights does not have to be the same at all relative nematode

densities P/T (as they would be for non-transformed relative plant weights), because all these relative plant weights represent estimates of z^{P-T} with the same value of z or $0.95^{P/T-1}$. Also, in general, the individual values of P/T in the ranges of relative nematode densities will not be the same in different experiments. To compare the results in a single graph, the values of P/T were divided into nematode density classes with the same class limits in the different experiments and a small ratio between these limits. The relation between log relative nematode density and plant weight within each nematode density class can then be treated as being linear. Instead of averages of Y'_{ij} per nematode density $(P/T)_j$ averages per relative density class j are calculated according to Equation (6). Not all experiments may be represented in every class, because the density intervals are larger than the class width and the lengths of the density ranges may be different. However, as above, differences in numbers of data per density class do not affect the quality of their averages as estimate of the theoretical value of y' for each of the classes. Average relative nematode densities per nematode density class is calculated as:

$$\overline{\left(\frac{P}{T}\right)}_j = \text{antilog} \frac{1}{r} \sum_{j=1}^{n} \left(\frac{P_i}{T_i}\right)_j \qquad (7)$$

with $(P_i/T_i)_j$ = the value of P/T from the ith experiment belonging in density class j and r_j = the number of observations in this class. With a class width of 1 to 1.4, as used below, the difference between the geometric mean according to Equation (6) and the arithmetic mean is very small.

If the deviations per nematode density class of the relation between the average relative nematode densities and average relative plant weights from Equation (4) are distributed randomly, then Equation (4) describes the relation between nematode density and relative plant weight accurately for most or all of the nematodes and plant species in the experiments, the results of which are summarised according to Equations (5) and (6). For Equation (4) to represent the actual relationship between relative nematode density and relative plant weight, the average relative plant weights per class should not deviate significantly from that according to Equation (4) in any class.

Materials and methods

To investigate whether Equation (4) accurately describes the relation between the population density at sowing or planting and the relative plant weight at some time after sowing or planting, data were used from 31 published and five unpublished experiments with *Pratylenchus penetrans* on *Daucus carota, Digitalis*

purpurea, Vicia faba, and apple seedlings. The five unpublished experiments were made in 10 cm wide, 30 cm deep cylindrical pots with 2 kg soil. To obtain twelve densities ranging from 0.1 to 200 eggs/g soil in the experiment with *D. purpurea,* twelve lots of partially sterilised sandy soil were spread out, inoculated separately by spraying with a suspension of the required number of nematodes, then mixed gently. Each lot of inoculated soil was then divided into five replicates of 2 kg and five replicates of non-inoculated partial sterilized soil were used as controls. All replicates were transferred to 2.5-dm³ pots in random order. For the experiments with *D. carota* and *V. faba,* 20 kg of partially sterilised soil was inoculated with a large number of nematodes, as described above. Then 10 kg of this inoculated soil was mixed with 10 kg non-inoculated partially sterilised soil. Half of the 20 kg mixture was mixed with another 10 kg of partially sterilised soil and so on until eleven nematode densities were obtained. Each lot of 10 kg inoculated soil was divided into ten portions of 1 kg, and each portion was mixed with 1 kg non-inoculated partially sterilised soil. The 100 portions of 2 kg thus obtained were transferred to 2.5-dm³ pots in complete random order. Per nematode density five pots were sown with

carrots and five pots with broad beans. After the seeds germinated, the number of seedlings was reduced to one per pot. For the published experiments, the reader is referred to the original articles for the methods used.

Partially sterilized soil was obtained by steaming soil to kill all pathogens present, after which the soil was allowed to 'recover' (enabling fungi to grow on the dead organic material) before nematodes were applied. Without this recovery period, the nematodes added to the soil would not have survived.

The data from all experiments were transformed according to Equation (5) and presented in Figs 1, 2, 3, and 5. Tables 1, 2, 3, and 4, associated to these figures, give the details on nematode species; plant species; estimated values of tolerance limits T, assuming that $z^T = 0.95$, and relative minimum plant weights m in curves according to Equations (2) and (3); and references to the original publications. For almost all published experiments, estimates of T and m were given in the original publications. These estimates are also mentioned in Tables 1, 2, 3 and 4. Before combining all results, estimates of T and m these experiments were ckecked and in some cases slightly adjusted. If T and m were not given in the original
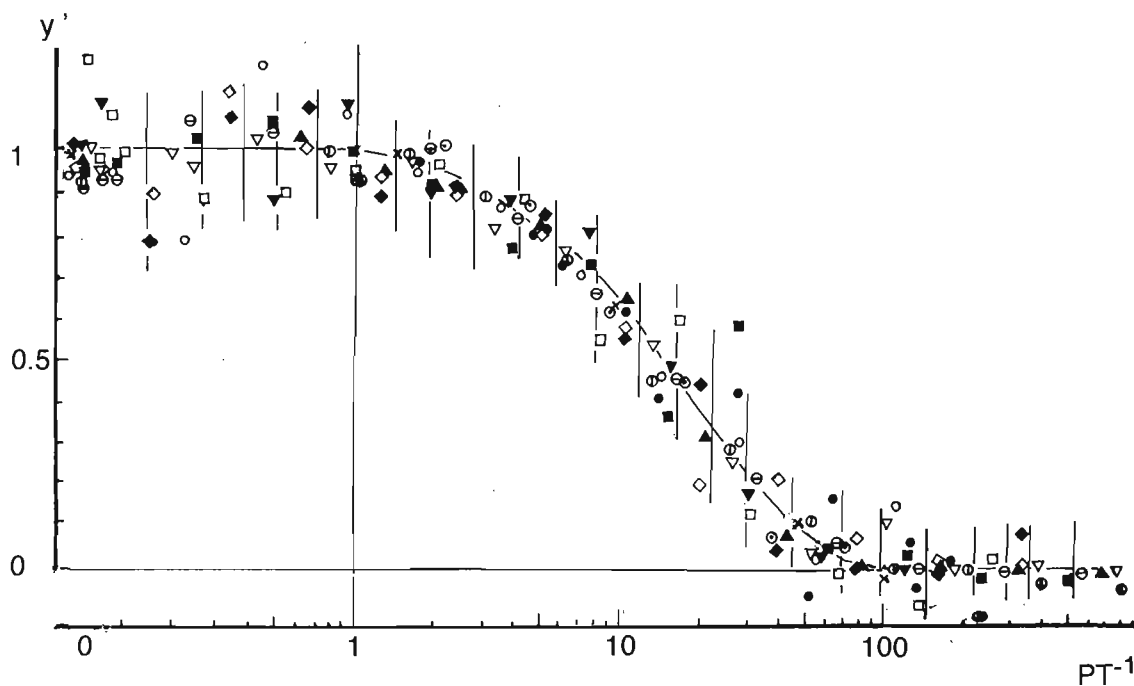

Fig. 1. Relations between nematode density at sowing or planting P/T_j and relative plant weight Y_{ij}'. Curve according to Equation (4). References to symbols and associated values of parameters T and m are summarized in Table 1. In the graph Y_{ij} and P/T_j are indicated as y' and PT^{-1} respectively.
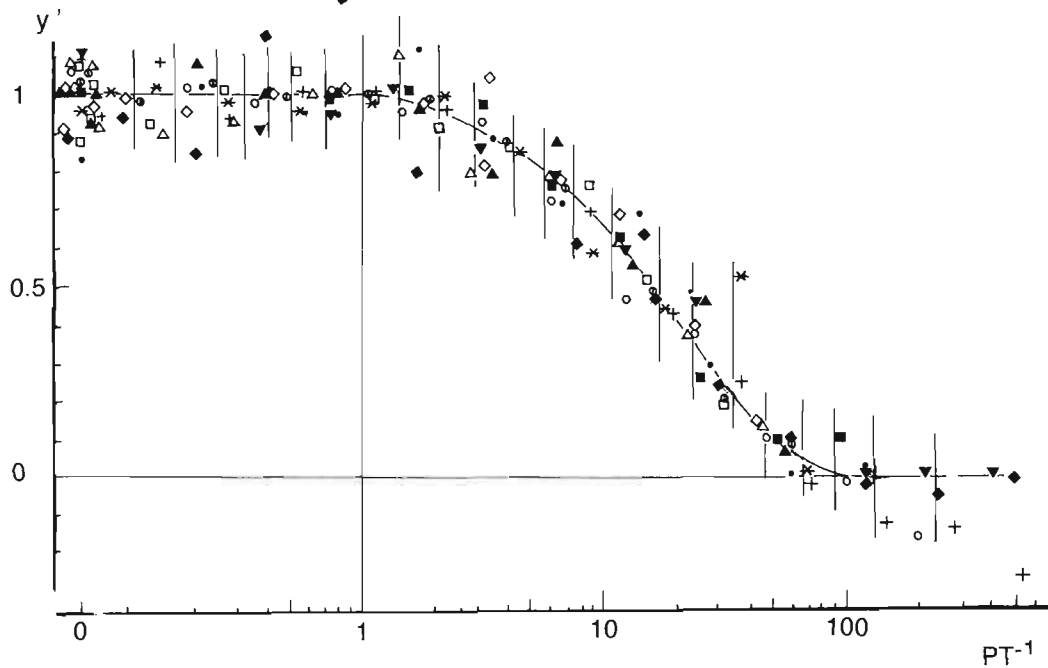
Fig. 2. As Fig. 1. References to symbols and associated values of parameters T and m in Table 2.
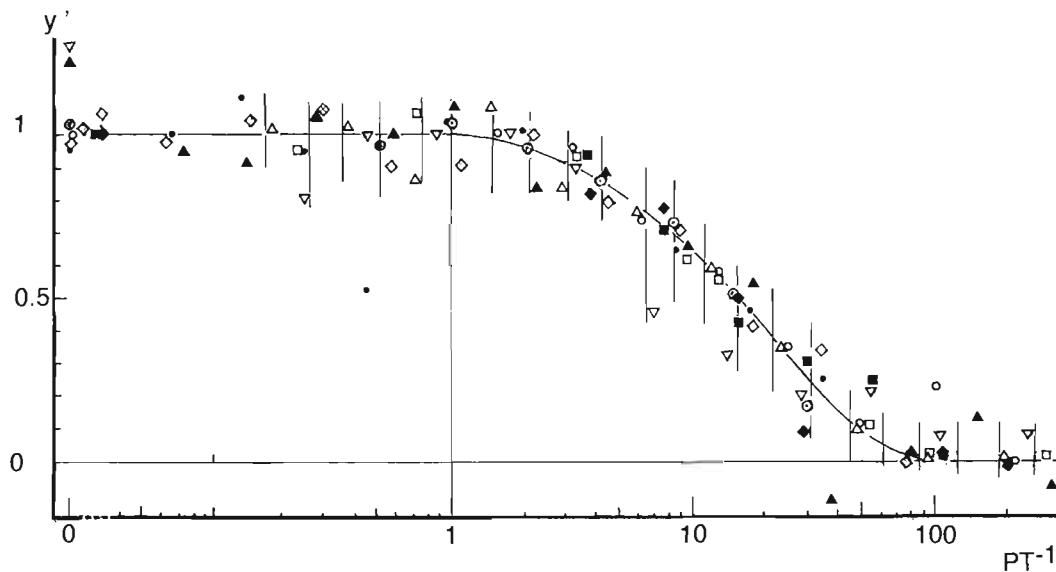

Fig. 3. As Fig. 1. References to symbols and associated values of parameters T and m in Table 3.

article they were estimated for the first time. No pre-determined scheme was followed for the distribution of the different experiments among the first three

graphs. The nematode density scales in the graphs were divided into classes, starting from $P_{ij}/T_{i.} = 1$ with further class limits 1, 1.41, 2, 2.82 etc. (ratio between
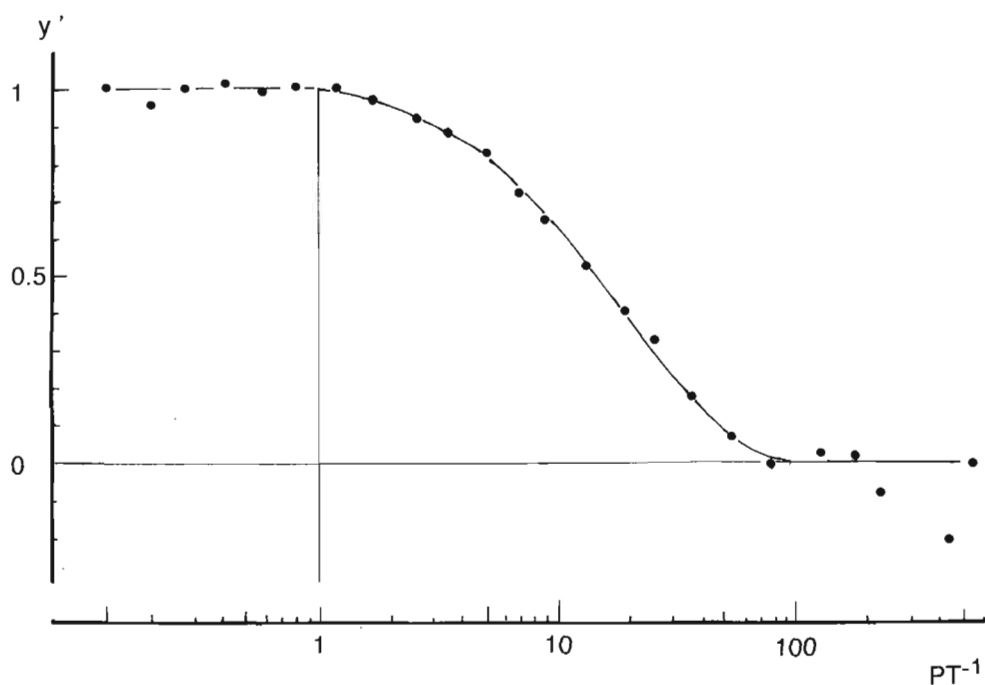
Fig. 4. *Relation between average* (P/T)j *(j = density class) and relative plant weights per experiment* Y'$_{ij}$, *transformed according to Equation (6). In the graph* $\bar{y}_j$ *and* P/T$_j$ *are indicated as* y' *and* PT^{-1} *respectively.*
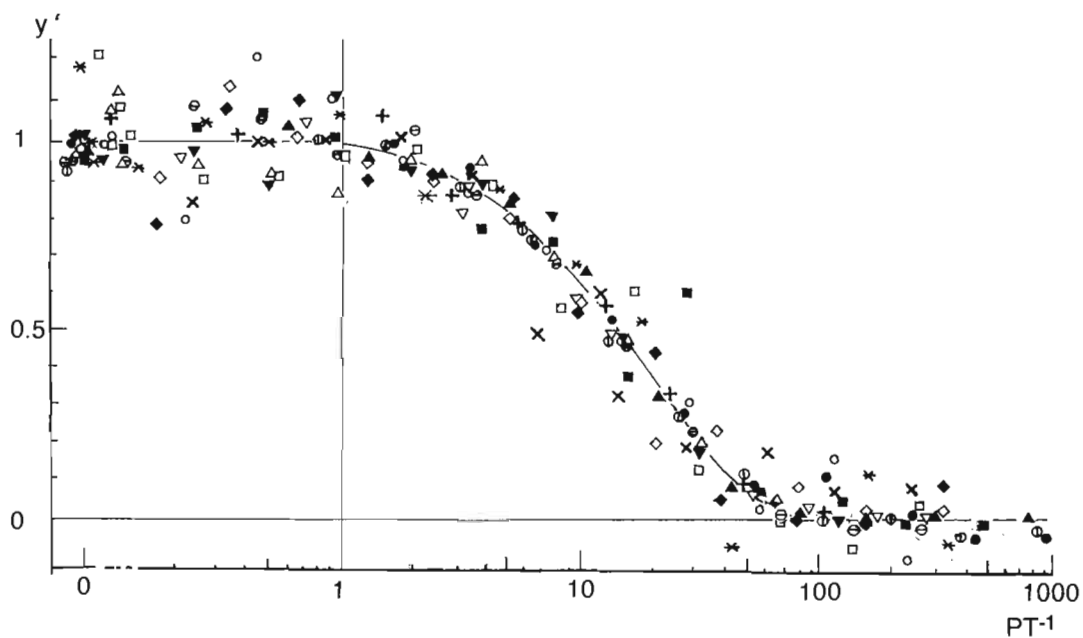

Fig. 5. *Relation between initial density of eggs and second stage juveniles of* Meloidogyne *species* P/T$_j$ *and the relative weight* Y$_{ij}$ *of different plant species some time after sowing or planting. Curve according to Equation (4). References to symbols and associated values of parameters* T *and* m *are summarized in Table 4. In the graph* Y$_{ij}$ *and* P/T$_j$ *are indicated as* y' *and* PT^{-1} *respectively.*

Table 1. *Details of experiments, visualised in Fig. 1, on the relation between nematode density at planting and plant weight at the end of the experiment: nematode plant species; original and new estimates of the tolerance limit* T *and minimum yield* m *according to Equation (3), and the author(s) of the experiments.*

Symbol	Nematode species	Plant species, cultivar	Original publication			T nem./g soil	m
			T nem./g soil	m	Reference		
●	*Heterodera avenae*	*Triticum sativum*	-	-	Meagher & Brown (1974)	0.3	0
○	*Meloidogyne incognita*	*Beta vulgaris*	1.1	0.1	Di Vito *et al.* (1981)	1.1	0.1
▽	*Xiphinema index*	*Vitis vinifera*	0.17	0.05	Di Vito *et al.* (1985)	0.15	0.05
▲	*M. incognita*	*Cucumus melo*	0.19	0	Di Vito *et al.* (1983)	0.19	0
▼	"	*Nicotiana tabacum*	2	0	"	2	0
□	"	*Helianthus annuus*	1.85	0.25	Sasanelli & Di Vito (1992)	1.85	0.25
■	"	*Brassica oleracea*	0.5	0.05	"	0.5	0.05
◇	"	*Capsicum annuum* (susceptible)	0.74	0.1	Di Vito (1986)	0.74	0.1
◆	"	*Capsicum annuum* (resistant)	0.74	0.4	"	0.74	0.4
⊕	*M. javanica*	*Oryza sativa*	0.26	0	Di Vito *et al.* (1996)	0.18	0.04
⊖	"	*Oryza glaberrima*	2.68	0	"	2.2	0.035
×	*Tylenchorhynchus dubius*	*Lolium perenne*			Den Toom (1988)	1.6	0.6
⊙	*Longidorus elongatus*	*Fragaria vesca*	0.2[1])	0.3	Seinhorst (1966)	0.09[2])	0.3

1) For $z^T = 0.9$ 2) For $z^T = 0.95$

Table 2. *Details of experiments, visualised in Fig. 2, on the relation between nematode density at planting and plant weight at the end of the experiment: nematode plant species; original and new estimates of the tolerance limit* T *and minimum yield* m *according to Equation (3), and the author(s) of the experiments.*

Symbol	Nematode species	Plant species, cultivar	Original publication			T nem./g soil	m
			T nem./g soil	m	Reference		
●	*Heterodera goettingiana*	*Pisum sativum*	3.5	0.3	Di Vito *et al.* (1978)	3.4	0.28
○	*H. avenae*	*Avena sativa*	1.4	0.27	Seinhorst (1981)	1.4	0.27
⊕	"	"	0.85	0.05	"	0.85	0.05
★	"	"	0.35	0.6	"	0.35	0.6
+	*Tylenchorhynchus dubius*	*Lolium perenne*	1.8	0.18	"	1.6	0.22
□	*Pratylenchus penetrans*	*Vicia faba*	-	-	unpublished	6.2	0.43
◇	"	*Daucus carota*	-	-	"	1.4	0.49
△	"	*Digitalis purpurea*	-	-	"	5.6	0.16
▲	"	*Malus*	-	-	"	1.5	0.44
■	*H. ciceri*	*Cicer arietinum*	1.34	(av.) 0.26	Greco *et al.* (1993)	1.3	0.16
▼	*H. carotae*	*Daucus carota*	0.8	0	Greco & Brandonisio (1980)	0.7	0
◆	*H. trifolii*	*Trifolium repens*	0.7	0.12	Seinhorst (1981)	0.7	0.12

Table 3. Details of experiments, visualised in Fig. 3, on the relation between nematode density at planting and plant weight at the end of the experiment: nematode plant species; original and new estimates of the tolerance limit T and minimum yield m according to Equation (3), and the author(s) of the experiments.

Symbol	Nematode species	Plant species, cultivar	Original publication			T nem./g soil	m
			T nem./g soil	m	Reference		
●	*Heterodera avenae*	*Avena sativa*	1	0.6	Greco & Brandonisio (1987)	1	0.6
○	*Meloidogyne incognita*	*Solanum melongena*	0.054	0.1	Di Vito *et al.* (1986)	0.054	0.05
△	"	*Coffea arabica*	2.09	0.4	Vovlas & Di Vito (1991)	1.4	0.4
▽	*M. javanica*	"	1.34	0.4	"	1.15	0.4
▲	*M. incognita*	*Lycopersicum esculentum (resistant)*	0.55	0.7	Di Vito *et al.* (1991)	0.5	0.7
□	*M. artiella*	*Cicer arietinum*	0.13	0.1	Di Vito & Greco (1988a)	0.13	0.1
■	*H. trifolii*	*Trifolium repens*	-	-	Hidding *et al.* (1963)	0.8	0
◆	*M. hapla*	"	-	-	"	0.08	0.4
◇	*Pratylenchus penetrans*	*Vicia faba*	-	-	(unpubl.)	1.3	0.43
⊙	*M. javanica*	*Helianthus annuus*	0.45	0	Di Vito *et al.* (1996)	0.25	0.43

Table 4. Details of experiments, visualised in Fig. 5, on the relation between nematode density at planting and plant weight at the end of the experiment: nematode plant species; original and new estimates of the tolerance limit T and minimum yield m according to Equation (3), and the author(s) of the experiments.

Symbol	Nematode species	Plant species, cultivar	Original publication			T nem./g soil	m
			T nem./g soil	m	References		
●	*Meloidogyne incognita*	*Solanum melongena*	0.054	0.05	Di Vito *et al.* (1986)	0.054	0.05
○	"	*Beta vulgaris*	1.1	0.1	Di Vito *et al.* (1981)	1.1	0.1
△	"	*Lycopersicum esculentum (susceptible)*	4	0	"	4	0
▲	"	*Cucumus melo*	0.19	0	Di Vito *et al.* (1983)	0.19	0
▼	"	*Nicotiana tabacum*	2	0	"	2	0
□	"	*Helianthus annuus*	1.85	0.25	Sasanelli & Di Vito (1992)	1.85	0.25
■	"	*Brassica oleracea*	0.5	0.05	"	0.5	0.05
◇	"	*Capsicum annuum (susceptible)*	0.74	0.1	Di Vito (1986)	0.74	0.1
◆	"	*C. annuum (resistant)*	0.74	0.4	"	0.74	0.4
+	"	*Coffea arabica*	2.09	0.4	Vovlas & Di Vito (1991)	1.4	0.4
×	*M. javanica*	"	1.34	0.4	"	1.15	0.4
⊕	"	*Oryza sativa*	0.26	0	Di Vito *et al.* (1996)	0.18	0.04
⊖	"	*Oryza glaberrima*	2.68	0	"	2.2	0.04
⋆	*M. incognita*	*Lycopersicum esculentum (resistant)*	0.55	0.7	Di Vito *et al.* (1991)	0.5	0.7
▽	*M. artiella*	*Cicer arietinum*	0.13	0.1	Di Vito & Greco (1988)	0.13	0.02

the upper and lower class limits $2^{0.5}$). The same was also done for densities $P_{ij}/T_i < 1$. Average values per nematode density class j of relative plant weights Y_{ij}, in the different experiments according to Equation (6) and of antilog's average log $(P_i/T_i)_j = (P/T)_j$ (Equation (7)) were calculated and plotted in Fig. 4.

Results and conclusions

Fig. 4 demonstrates an excellent fit of the relation between actual values of Y_j' and average $(P/T)_j$ to the values of y' at these nematode densities according to $y' = 0.95^{P/T-1}$ (Equations [3] and [4]) for average $(P/T)_j = 1$ to 100 and $y' = 1$ for average $(P/T)_j \leq 1$. The poorer fit for average $(P/T)_j > 100$ is probably partly due to Seinhorst's (1981) 'second mechanism of growth reduction' which refers to mechanical damage to the root system at high population densities, the general relation of which is not known. It may, therefore, be concluded that Equations (2), (3), and (4) give a proper description, during the first growing season after sowing or planting, of the relation between relative weight and population densities from 0 to 100 T for a wide range of nematode and plant species (Figs 1, 2, 3), thus confirming Seinhorst's (1979, 1986) theory about growth reduction for these nematode and plant species. Apparently, deviations of actual relative plant weights in separate experiments from those according to Equation (3) with properly estimated values of T and m are generally due to experimental error, although some deviations at population densities > 30 T are most probably caused by Seinhorst's 'second mechanism of growth reduction'.

The confirmation of the constancy of the value of $z^T = 0.95$ emphasizes the need to investigate the mechanism by which the plant counteracts the effect on growth of nematode densities up to T.

EXPERIMENTS WITH *MELOIDOGYNE* SPECIES

A good fit of a curve according to Equation (4) to the relation between initial nematode density and relative plant weights was also obtained for almost all experiments with *Meloidogyne* species (Fig. 5, data and references in Table 4). A deviation of the relation between initial nematode density and total plant weight several months after planting from the relation estimated according to Equation (4), due to a rapid increase of population density of these species, was described on theoretical grounds by Seinhorst (1995b) and illustrated in his Fig. 4. This deviation could only be derived from the data in one experiment, *viz.*, the description by Di Vito *et al.* (1991) of the relation between initial density of second stage juveniles of *M. incognita* and relative weights of the fruits of susceptible tomatoes. An alternative interpretation of the data is given in Fig. 6. The interpretation by a single curve according to Equation (3) in

Fig. 1 of Di Vito *et al.* (1991) is replaced by one, that is the product of a reduction by :

1) The initial nematode population according to Equation (3) with $T_1 = 0.43$ second stage juveniles/g soil and $m_1 = 0.7$, as for the resistant tomatoes, with no or only a small second generation.

2) The second generation produced by this initial population, again according to Equation (3) but with T_2 at the initial density of approximately 0.065 second stage juveniles/g soil and $m_2 = 0.85$ (Seinhorst 1995a, b)

3) The 'second mechanism of growth reduction' (Seinhorst, 1981) at $P > 4$ second stage juveniles/g soil ($62T_2$).

The curve drawn in Fig. 6 for the reduction in point 3) is arbitrary because no general relation between nematode density and the effect of the 'second mechanism' is known. The large values of m possibly resulted from the age of the plants at the start of the experiment, which can be interpreted as a 'delay of attack' resulting in an increase of m (Seinhorst, 1995a). The first two reductions of fruit yield (both due to the 'first mechanism of growth reduction' which causes growth retardation) are proportional to the reduction of total plant weight. Most probably the largest densities of the first generation already reduced the relative plant weight to less than 0.7 by the 'second mechanism of growth reduction' and plants died off after attack by the second generation. The new interpretation of the data results in a much smaller estimated experimental error than the original interpretation. An acceptable fit is still obtained for $m_2 = 0.9$ and $m_1 = 0.5$, therefore assuming that m_1 is smaller than for resistant plants. The economic differ-
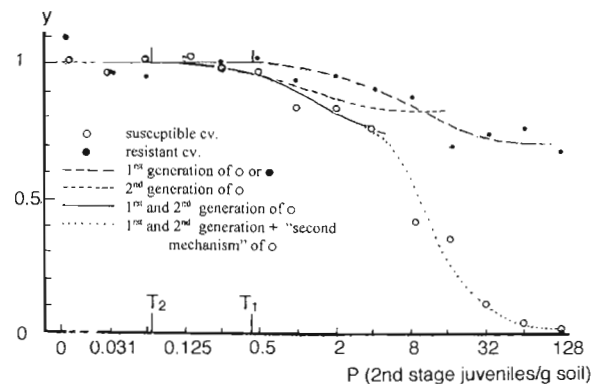

Fig. 6. *Re-interpretation of data from experiments on the relation between initial population density of 2nd stage juveniles of* Meloidogyne incognita *and fruit yield of susceptible and resistant tomato plants by Di Vito* et al. *(1991).* y = *fruit weight divided by estimated fruit weight in the absence of nematodes. Curves are according to Equation (3), except the (arbitrary) dotted line.*

ence between the interpretation by Di Vito *et al.* (1991) and the interpretation of Fig. 6 is a crop loss of 5% at $P = 0.43$ second stage juveniles/g soil according to the latter and no loss according to the former interpretation.

The pattern described above could be expected to fit also to the results of the experiments with *M. incognita* on susceptible and resistant tomatoes of Di Vito *et al.* (1983). However, there are too few observations at very small initial egg densities to estimate the weight of susceptible tomatoes in the absence of nematodes. If there was any effect of the second and later generations on relative plant weight of the susceptible tomatoes it cannot be distinguished from experimental error and would have resulted in a value of *m* of at least 0.9.

The four relative weights at zero to one egg/g soil of susceptible tomatoes in the experiment of Di Vito *et al.* (1981) varied from 0.8 to 1.2 and did not supply any information on possible effects of the second and later generations on plant weight.

Contrary to what might be expected, root knot nematodes did not affect plant weight in the experiments of Table 4, and Figs 5 and 7 in the same way as
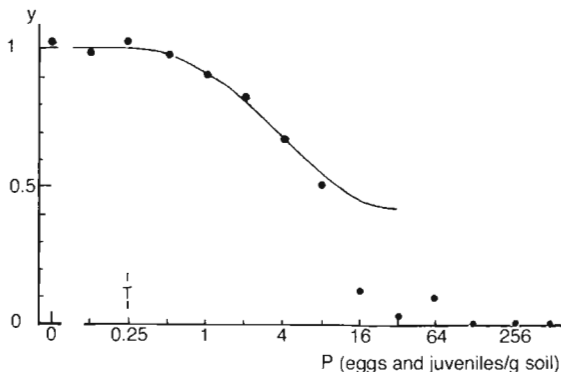

Fig. 7. Re-interpretation of data from experiments on the relation between initial population density of 2nd stage juveniles of Meloidogyne javanica *and top weight of sun flower (*Helianthus annuus *by Di Vito* et al., *1996).* y = *top weight divided by estimated top weight in the absence of nematodes. Curve according to Equation (3).*

in Fig. 6. The data fit closely to a relation according to Equation (4). There is no indication of an effect of a second generation with a much smaller value of *T* than for a first generation and a fairly large value of *m* (0.7 to 0.9). Moreover, $T = 0.2$ or more eggs/ g soil in eleven of the fifteen experiments with susceptible plants and, therefore, about the same as for resistant plants without a sizeable second generation. The only possible expla-

nation is that, by the time reproduction had increased population density considerably, the plants had become insensitive to the new nematodes, presumably because for these nematodes, *m* increased until it was too close to 1. Seinhorst's (1995*a*, *b*) experiments with oat cyst nematode on oats show that a very small *m* for a first generation attacking shortly after sowing can go together with a very large *m* for a later generation (or after a considerable delay of the start of the first attack). This might have occurred in the experiments mentioned in Table 4 and Fig. 5. If also, as with the tomatoes, *m* for the growth reduction caused by the 'first mechanism' was large, then only the 'second mechanism' (reducing the capacity of the plant to take up water, with as a result increase of dry matter content and ultimately wilting and death; Seinhorst, 1981) remains as a cause of small plant weights. However, then the relation between nematode density and plant weight can be expected to depart from the relation according to Equations (2), (3), and (4), which is not the case in the experiments summarized in Table 4. Apart from the experiment of Fig. 6, an effect of the 'second mechanism' could only be derived from the relation between initial egg density of *M. javanica* and the total plant weight of sunflower (*Helianthus annuus*) in an experiment by Di Vito *et al.* (1996). In Fig. 7 the data from this experiment were re-interpreted, resulting in $T = 0.25$ eggs and juveniles/g soil and $m = 0.43$ for the reduction of plant weight by the 'first mechanism' according to Equations (2), (3), and (4) with an additional reduction of plant weight by the 'second mechanism' at densities > eight eggs and juveniles/g soil, whereas there is no evidence of weight reduction by the second and later generations. Experimental error is considerably smaller according to the new interpretation than according to the original one, fitting a single curve according to Equation (3) to the data.

It seems improbable, that there is either no effect of the 'second mechanism' or that all reduction at more than about four eggs/g soil is due to it without departure of the relation between initial nematode density and plant weight from one according to Equations (2), (3), and (4). A third mechanism that could affect the relation between nematode density and plant weight is growth stimulation by small nematode densities. However, it could hardly be expected to exceed a few percent weight increase, too little to compensate a sizeable weight decrease by a second generation. Average relative plant weights per class of nematode densities, calculated as for Figs 1 to 3, did not reveal any effect of growth stimulation.

Although the relation between root knot nematode density and plant weight in the different experiments is not understood, the available information could be considered sufficient for agronomic purposes. This means that one may assume that the results of these

experiments are reproducible - apart from a correction for incapacitation in some experiments of a large percentage of the inoculum by the hypochloride treatments (Di Vito *et al.*, 1986, 1991) - and that these results will also apply in the field. But then it is assumed without explicit proof, that, from about three weeks after sowing or planting, plants (except egg plant; see Table 4) become insensitive to growth reduction by the 'first mechanism' resulting from attack by root knot juveniles of the second and later generations but remain sensitive to such growth reduction by juveniles of the original population still present in the soil. This is the paradox derived from the data of an experiment with repeated inoculation with *Heterodera avenae* eggs of soil with oat plants (Seinhorst, 1995b). The problem is certainly worth further investigation for both theoretical and practical reasons (effect of delay of attack that is not explained by the increased size of the plant).

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