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Relative susceptibilities of eleven potato cultivars and breeders' clones to *Globodera pallida* pathotype Pa 3, with a discussion of the interpretation of data from pot experiments

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Abstract

Curves according to the equation $Pf = M'(1 - e^{-aPi/M'})$ fitted well to the relations according to Seinhorst's (1993) model $Pf = y_e y_h M(1 - e^{-aPi/M})$ between initial egg densities of potato cyst nematodes (*Globodera rostochiensis, G. pallida*) Pi up to $5T_h$ (T_h = the tolerance limit of haulm weight) and Pf at the end of the growing season (a = maximum rate of reproduction, M, M' = different theoretical maximum egg densities). Variation of estimates of M', due to variation of the parameters of the submodels y_e and y_h for the effect of weight reduction of haulms (and, therefore, of roots) on cyst production and damage to root tissue on egg production, respectively, was small enough to be ignored relative to experimental error. Therefore, ratios of values of M', determined in simultaneous pot experiments with different potato cultivars, are reliable measures of the relative host status of these cultivars at initial egg densities Pi of these nematodes up to about $5T_h$. Variation between potato cultivars of growth reduction and damage to root tissue by the nematodes reduces the reliability of ratios of rates of relative susceptibility of these cultivars.

The ratios between the maximum rates of reproduction of *G. pallida*, pathotype Pa 3, on 8 out of 9 cultivars and one breeder's clone of potatoes and this rate on the susceptible cvs Bintje and Irene (relative susceptibilities rs_a) could be considered to be equal to the ratios of maximum population densities M' on these cultivars (relative susceptibilities $rs_{M'}$) (relative susceptibilities independent of initial egg density). The latter ratios were 0.59 times the first (relative susceptibilities negatively correlated with initial egg density) in one cultivar and one breeder's clone. Relative susceptibilities rs_a and $rs_{M'}$ of the tested cultivars and breeders clones suggest the existence of continuous ranges of both relative susceptibilities between 0.50 and 0.15 with, in a great majority of cases, $rs_a = rs_{M'}$.

Introduction

Potato cultivars that are partially resistant against *Globodera pallida* pathotypes Pa 2 and Pa 3 are grown in short rotations with non-host crops on infested soil to keep crop losses small by keeping potato cyst nematode densities small over a number of cropping cycles. The expected frequency distribution of egg densities at the times of planting of a potato cultivar with a given 'relative susceptibility', grown in a given rotation with non host crops, is derived from the frequency distributions of rates of reproduction on this cultivar at given egg densities at planting with the help of a stochastic model. The rates of reproduction are considered to be the products of the rates on a fully susceptible cultivar in the field and the 'relative susceptibility' of the partially resistant cultivar [Seinhorst *et al.*, 1994] ('susceptibility' and 'resistance' used in the sense, traditional in nematology, of 'goodness as a host', not as that of 'sensitivity to growth reduction'). Relative susceptibilities of partially resistant cultivars are determined in pot experiments as ratios between final egg densities, obtained on the cultivar to be tested and on a fully susceptible cultivar, both at the same initial egg densities [Seinhorst, 1984, 1986]. According to Phillips [1984], Seinhorst [1984] and Seinhorst and Oostrom [1984] relative susceptibilities of a number of potato cultivars in pot experiments were the same over ranges of egg densities of *G. pallida* at planting up to those causing a notable reduction of final plant weight. Values determined at a single (preferably small) egg density at planting then suffice for advice according to the stochastic model. However, the reduction of the size and quality as a food source of the root system of the plants attacked by nematodes and its effect on final nematode densities may be different in different potato cultivars and this difference may also vary between experiments. This could result in different ratios between final egg densities on a partially resistant cultivar and the susceptible reference at nematode densities larger than the tolerance limit of the potato cultivars. In Materials and Methods the theoretical magnitude of this variation is demonstrated with the help of Seinhorst's [1993] model. The egg densities at planting up to which it still can be ignored are determined.

According to Seinhorst [1984] the ratio between the (relatively large) maximum egg densities of *G. pallida* pathotype Pa 3 on cvs Astarte and Multa on the one and on cv. Ehud on the other hand was smaller than that between the maximum rates of reproduction on these cultivars in the same experiment. Such differences could also exist between fully susceptible cultivars and more resistant ones than those mentioned above. For a suitable prediction of the effect of such cultivars on population density over a number of rotation cycles the dependency of the relative susceptibility on initial egg density of the relevant potato cyst nematode pathotype must be taken into account. To investigate, whether differences between relative susceptibilities at different initial nematode egg densities occur in commercially grown cultivars that are partially resistant to *G. pallida* pathotype Pa 3, rates of reproduction of this pathotype of nine cultivars and two breeder's clones at a range of initial egg densities were compared in a pot experiment with those on the fully susceptible cvs Bintje and Irene.

Materials and methods

Set up of the experiments

The experiments were done in 10 l pots filled with a mixture of silver sand (60 %), crushed ceramic material (30 %) and clay powder (10 %), to which 1 g NPK (12:10:18) fertilizer was added per kg. A cylindrical piece of tuber with a single sprout was planted at 5 cm depth. The pots were inoculated by injecting egg suspensions uniformly distributed into 20 narrow channels from top to bottom of the 20 cm deep pots. The pathotype Pa 3 population used was the more virulent one, indicated by Seinhorst and Oostrom [1984] as 'Dutch', also as 'Rookmaker' and by Seinhorst [1986] as Pa 3 (1), to distinguish it from the less virulent Pa 3 (2). It was maintained on cv. Irene. The range of egg densities used was 0.5, 1, 2, 4, 8, 16 and 32 eggs/g soil. Of each cultivar there was one pot per egg density. The moisture content of the potting medium was kept between 10 and 15 % of its dry weight. The pots were placed in a randomized fashion on a greenhouse bench at 15° to 24 °C. The experiments were ended four months after planting by cutting off the above ground parts of the plants and stopping the watering of the pots. Final egg densities were determined in 500 g of the well mixed dry contents of the pots or a larger quantity of soil, if necessary for the collection of about 300 cysts/pot. Egg suspensions were made by crushing these cysts [Seinhorst, 1988; Seinhorst and den Ouden, 1966]. Eggs were counted in samples from these suspensions containing about 300 eggs.

Method of analysis of the results of the pot experiments

The relation between egg density at planting, *Pi*, and that at the end of the experiment, *Pf*, in pots inoculated with egg suspensions, is expected to be that described by Seinhorst (1993, 1994) in the equation:

$$Pf = y_h y_e M(1 - e^{-aPi/M}) \qquad (1)$$

with

$$\begin{aligned} &y_h = m_h + (1 - m_e)0.95^{x_h} \text{ with}\\ &x_\mathrm{h} = Pi\ T_h^{-1} - 1 \text{ for } Pi > T_h \text{ and}\\ &y_h = 1 \text{ for } Pi < T_h \end{aligned} \qquad (2)$$

(relative haulm weight before senescence set in, expressed as a proportion of haulm weight at $Pi < T_h$).

$$\begin{aligned} &y_e = m_e + (1 - m_e)0.9^{x_e} \text{ with}\\ &x_\mathrm{e} = Pi\ T_e^{-1} - 1 \text{ for } Pi > T_e \text{ and}\\ &y_e = 1 \text{ for } Pi < T_e \end{aligned} \qquad (3)$$

(the number of eggs/cyst in the final population, expressed as a proportion of the number at $Pi < T_e$).

a (= $Pf\,Pi^{-1}$ for $Pi \to 0$) is the maximum rate of reproduction.
M (= Pf for $Pi \to \infty$, if $y_e = 1$) is the theoretical maximum egg density if the nematodes would not damage the plants.
T_h = the density Pi below which haulm weight is not affected.
m_h = the minimum relative haulm weight.
T_e = the density Pi below which the egg content of the cysts in the final population is not affected by attack of the plants by the nematodes.
m_e = the minimum relative egg content of the cysts of the final population.

In general T_h is of the order of 1.8 eggs/g soil in the field and in the 10 l pots with one haulm as used in the experiments discussed below. T_e ranged from 1.7 to 5.3 eggs/g soil and m_e from 0.25 to 0.87 in pot experiments with pathotype Pa 3 on various cultivars [Seinhorst, 1993]. In the same experiments m_h ranged from 0.25 to 0.7 (unpublished data).

The host status of a partially resistant potato cultivar relative to a fully susceptible reference without interference by the (variable) growth reduction and damage to the root tissue caused by the nematodes is characterized by two ratios: that between the values of a and that between those of M for curves according to eq. (1), fitted to the relations between initial and final egg densities on the two cultivars (the relative susceptibilities rs_a and rs_M). To determine M, values of the parameters in eqs (2) and (3) must be derived from haulm weights and from numbers of eggs/cyst at medium to large initial egg densities. However, for predictions of the effect of growing partially resistant potato cultivars in a rotation with non host crops on population densities only final densities at small to lower medium initial ones (little or no growth reduction) are required. Seinhorst [1984] and Seinhorst and Oostrom [1984] found acceptable to good fits of curves according to the simplified arbitrary equation:

$$Pf = M'\,(1 - e^{-aPi/M'}), \qquad (4)$$

fitted to the relations between Pi up to about 10 eggs/g soil ($5.5T_h$) of *G. pallida* pathotype Pa 3 and Pf in experiments with susceptible and partially resistant potato cultivars in 10 l pots. The host status of a cultivar relative to a fully susceptible reference can then again be characterized by two ratios: that between the values of a (the relative susceptibility rs_a) and that between those of M' (the relative susceptibility $rs_{M'}$). for curves according to eq. (4), fitted to the relations between initial and final egg densities on the two cultivars. The susceptibility of a cultivar relative to that of a reference at a given Pi then is the ratio of Pf according to eq. (4) on the first and that on the latter cultivar at this Pi. However, contrary to M, M' is a hybrid parameter. It is not only a measure of the suitability of a cultivar as a host of the nematodes but is also affected by its sensitivity to growth reduction (represented by y_h and eq. (2)) and to damage to the root tissue by the nematodes (represented by y_e and eq. (3)). The parameters of eqs. (2) and (3) do not only vary between cultivars in the same experiment but the ratios between values of the same parameter for two cultivars may be different in different experiments. Therefore, values of M' and $rs_{M'}$ determined in pot experiments are only acceptable as measures of susceptibility (host status) and of relative susceptibility, if the variation of M' due to variation of the effects of growth reduction and of damage to root tissue by the nematodes (variability of the parameters of eqs (2) and (3)) is small. To investigate the possible magnitude of this variability, relations between Pi and Pf/a according to eq. (1) were calculated for various values of M/a with all combinations of T_h = 1.8 eggs/g soil, T_e = 1.8, 4 and 5 eggs/g soil, m_h = 0.3, 0.6 and 0.75 and m_e = 0.3 and 0.6. Those for T_h = 1.8 eggs/g soil combined with T_e = 4 eggs/g soil, $m_h = m_e = 0.3$ and $m_h = m_e = 0.6$ ($m_h m_e$ = 0.09 and 0.36) are given in Fig. 1, because a similar variation of the products of m_h and m_e occurred between cultivars in the pot experiment.

Curves according to eq. (4) were fitted to the resulting sets of relations between *Pi* and *Pf/a* according to eq. (1). Those for *M/a* = 2.5, 4, 6, 12 and 25 eggs/g soil, are given in Fig. 1. These curves fitted almost exactly to relations between *Pi* and *Pf/a* according to eq. (1) at *Pi* up to 8 eggs/g soil ($4.4T_h$) with both $m_h = m_e = 0.3$ and $m_h = m_e = 0.6$. The fitted curves underestimated the actual value of *Pf* at *Pi* = $2.2T_h$ and overestimated it at $4.4T_h$ both by only 1 to 2 %. The (non-linear) relations between *M/a* and *M′/a* for $m_h = m_e = 0.3$ and $m_h = m_e = 0.6$ are given in Fig. 2. Ratios $M'_{0.6}/M'_{0.3}$ between *M′/a* for $m_h = m_e = 0.6$ and that for $m_h = m_e = 0.3$ are about 1.1 at all values of *M/a* investigated. Of all the combinations of parameters tested only ratios between *M′* for T_e = 4 eggs/g soil and $m_h = m_e = 0.6$ and *M′* for T_h = 1.8 eggs/g soil, m_h = 0.3 and m_e = 0.6 or smaller were considerably larger than 1.1 but combinations of these extremes will probably occur rarely. The range of variation of estimated values of *M′* of 10 % of the average is equivalent to a coefficient of variation of 2.5 %. If this c. v. also applies to the susceptible reference cultivar this will add a c. v. of not more than 3.5% to the

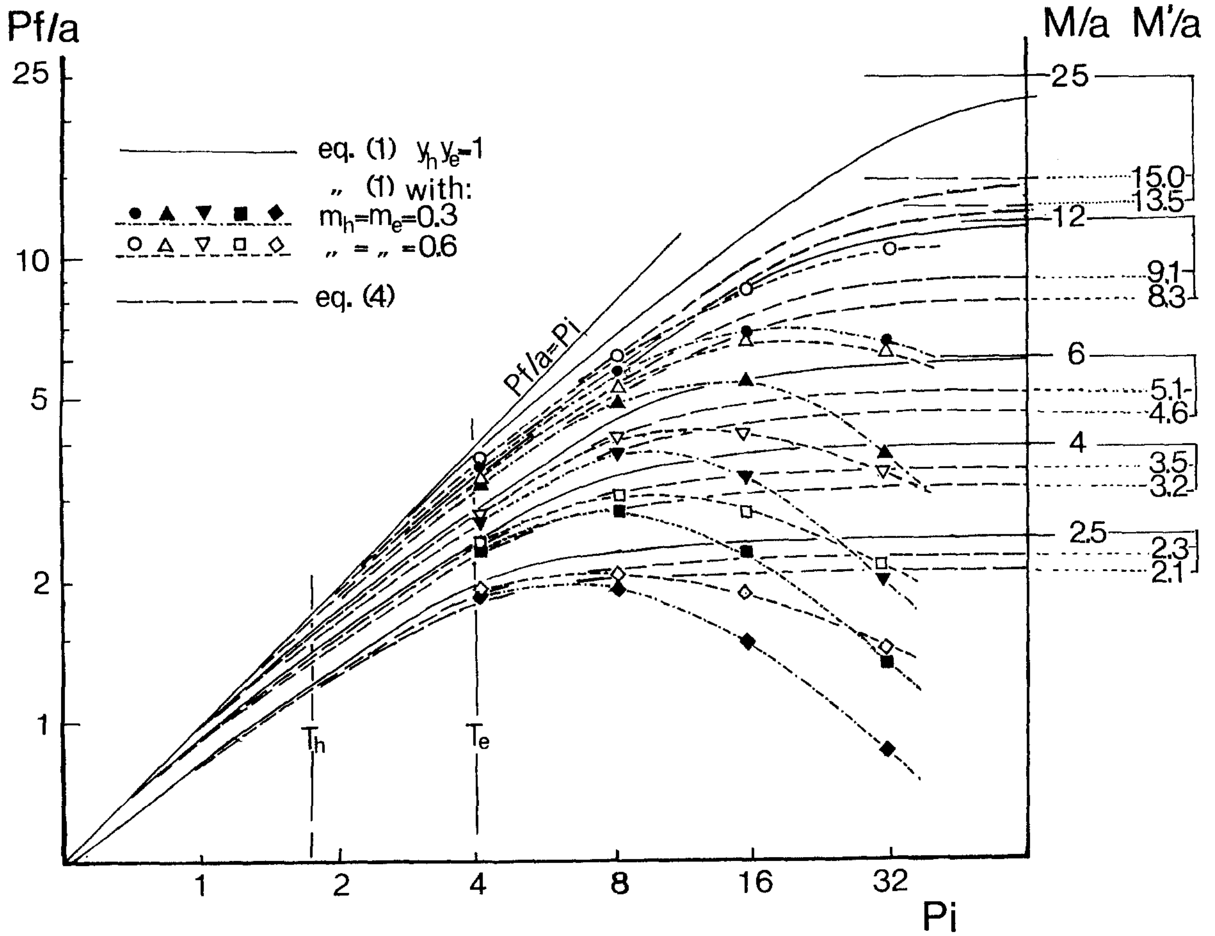

Fig. 1. Relations between *Pi* and *Pf/a* (eggs/g soil) according to eq. (1) for T_h = 1.8 eggs/g soil, T_e = 4 eggs/g soil, $m_h = m_e$ = 0.3 and 0.6 and different ratios *M/a*, with curves according to eq. (4) fitted to *Pf/a* values at *Pi* up to 8 eggs/g soil. *M/a* and *M′/a* in eggs/g soil.

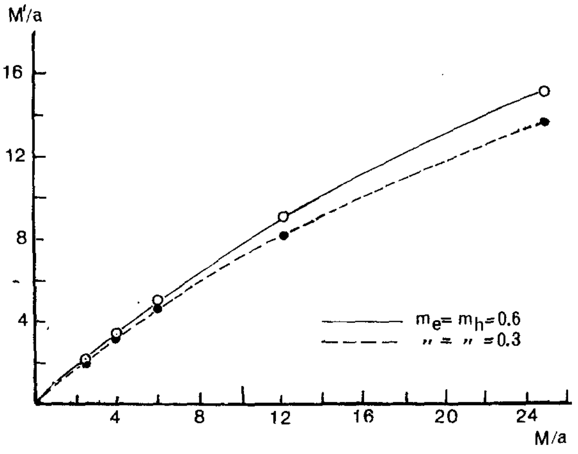

Fig. 2. Relations between M/a (eq. (1)) and M'/a (eq. (4)) for $m_h = m_e = 0.3$ and 0.6. M/a and M'/a in eggs/g soil.

experimental error of the estimate of $rs_{M'}$. This variability will generally remain hidden as a (relatively small) component of the much larger experimental error of the estimates of M'. Therefore, the possible variation of M'/a relative to M/a does not affect the value of $rs_{M'}$ of a cultivar materially, if measured in different experiments with different ratios M/a and M'/a, if this cultivar and the reference have the same ratios M/a.

Because of the non-linear relation between M/a and M'/a (Fig. 2) different estimates of $rs_{M'}$ will be obtained for a cultivar with a smaller or larger ratio M/a than that for the susceptible reference, in experiments with different values M/a for the reference, even if the products $y_h y_e$ at the same Pi are the same for both cultivars. Values of $rs_{M'}$ for a partially resistant cultivar with $rs_M/rs_a = 0.5$ were calculated with the help of Figs. 1 and 2 for $M/a = 4$, 12 and 24 eggs/g soil for the susceptible reference cultivar, $m_h = m_e = 0.3$ and $m_h = m_e = 0.6$ (Table 1). According to this Table there is a weak positive regression of rs_M/rs_a upon M/a if $rs_{M'} < rs_a$. As a consequence there will be a weak negative regression of rs_M/rs_a upon M/a if $rs_{M'} > rs_a$. With the help of Figs. 1 and 2 $rs_{M'}$ at any value of M'/a can be derived from that at a given value of this ratio. However, as M'/a cannot be predicted for a given field and year, a difference between $rs_{M'}$ and rs_a slightly increases the uncertainty of the prediction of population development, when a cultivar with this characteristic is grown.

The conclusion from the theoretical considerations can be, that not only ratios of maximum rates of a reproduction a of a potato cyst nematode pathotype on different potato cultivars but also those of M' on these cultivars, both derived by fitting curves according to eq. (4) to the relation in pot experiments between initial and final egg densities of the nematodes at initial egg densities up to about $5T_h$, are good estimates of relative susceptibilities rs_a and $rs_{M'}$ of these cultivars at small and at medium egg densities at planting, respectively. Therefore, conclusions on relative susceptibilities of the investigated cultivars are based on values of a (rs_a) and of M' ($rs_{M'}$) for curves according to eq. (4) fitted to measured Pf values at Pi up to 8 eggs/g soil ($4.4T_h$).

Results

The relations between initial and final egg densities on the various cultivars and clones are demonstrated in Figs. 3 and 4. Those on cvs Bintje and Irene can be considered to be the same. A curve according to eq. (4) with a maximum rate of reproduction a of 43 times and a maximum egg density M' of 160 eggs/g soil ($M'/a = 3.7$ eggs/g soil)

Table 1. Effect of value of M/a on value of $rs_{M'}$ of a partially resistant cultivar with $rs_M/rs_a = 0.5$ for $m_h = m_e = 0.3$ and $m_h = m_e = 0.6$

	Reference cultivar		Partially resistant cultivar		
$m_h = m_e$	M/a	M'/a	M'/a	rs_M/rs_a	rs_M/rs_a
0.6	4 eggs/g	3.5 eggs/g	1.9 eggs/g	0.5	0.54
	12 " "	9.1 " "	5.1 " "	0.5	0.56
	24 " "	14.8 " "	9.1 " "	0.5	0.56
0.3	4 " "	3.2 " "	1.75 " "	0.5	0.55
	12 " "	8.3 " "	4.6 " "	0.5	0.55
	24 "" "	13.3 " "	8.3 " "	0.5	0.62

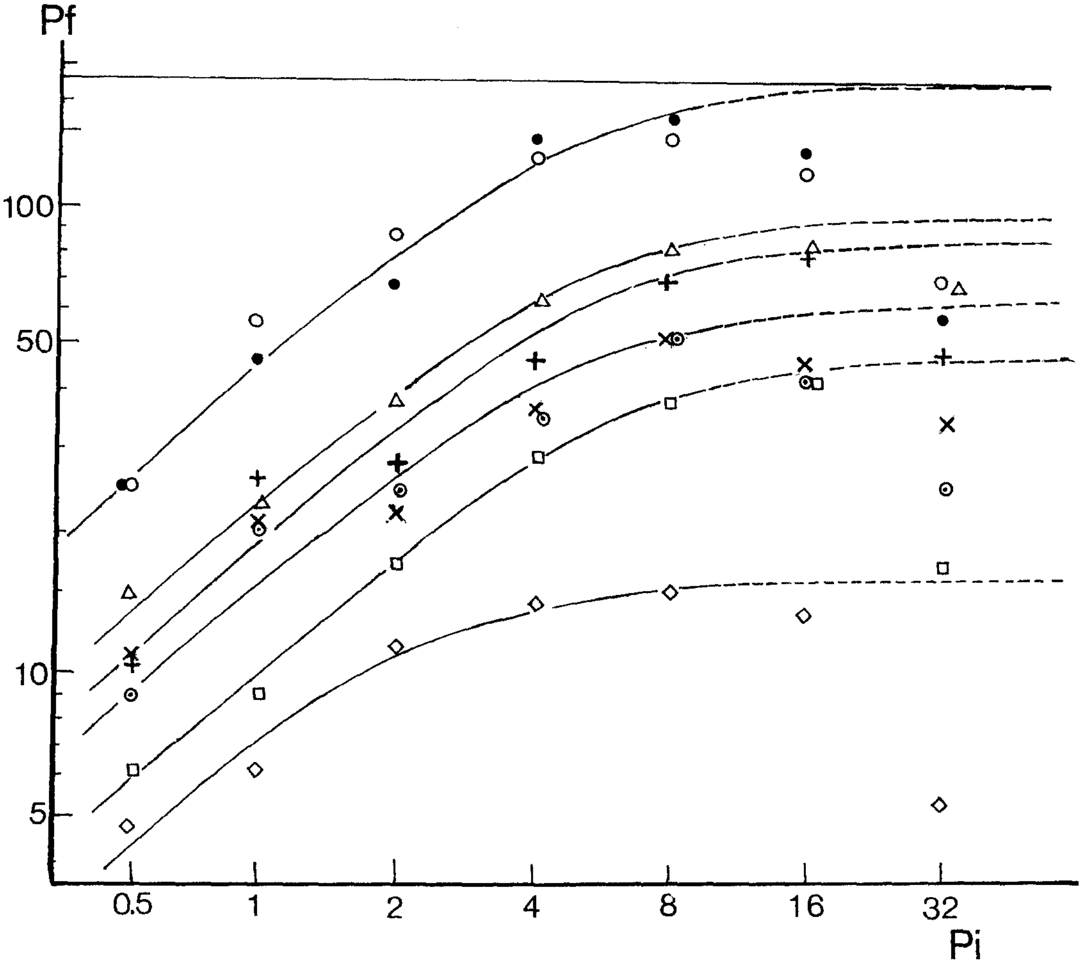

Fig. 3. Relations between initial and final egg densities (*Pi* and *Pf*) of *G. pallida* pathotype Pa 3 on eight potato cultivars in single pots per cultivar and egg density *Pi*. See Table 2 for the meaning of the symbols. *Pi* and *Pf* are in eggs/g soil. All curves are according to eq. (4): $Pf = M'(1 - e^{-aPi/M'})$.

fitted well to the data. Curves according to eq (4) with ratios M'/a of 2.1 (clone Karna 77/281) and 2.2 eggs/g soil (cv. Activa) and between 3.4 and 4.1 eggs/g soil in the remaining eight cultivars and one breeder's clone were fitted to the actual relations between Pi and Pf at Pi up to at least 8 eggs/g soil. The relations between $Pi > 8$ eggs/g soil and Pf can be considered to fit to curves according to eq. (1) with m_h and m_e both between 0.3 and 0.6 (Compare Fig. 5 with Fig. 1). The ratios rs_a and $rs_{M'}$ between the values of a and M' for the various cultivars and those for cvs Bintje and Irene, all as for the curves according to eq. (4) fitted to the data in Figs. 3, and 4, are given in Table 2.

Discussion and conclusions

The relative susceptibilities rs_a and $rs_{M'}$ of the nine cultivars and two breeder's clones to *G. pallida* pathotype Pa 3 (1), ranged from 0.15 to 0.51 and from 0.08 to 0.51, respectively. The ranges of values listed in Table 2 suggest, that, contrary to Seinhorst's [1986] supposition, there is a continuous range of relative susceptibilities between the largest and smallest values. According to the curves in Figs. 3 and 4 and Table 2 rs_a was only slightly smaller or larger than $rs_{M'}$ in eight of the 10 partially resistant cultivars and one breeders' clone. The coefficient of variation of the ratios $rs_{M'}/rs_a$ of the first nine partially resistant cultivars

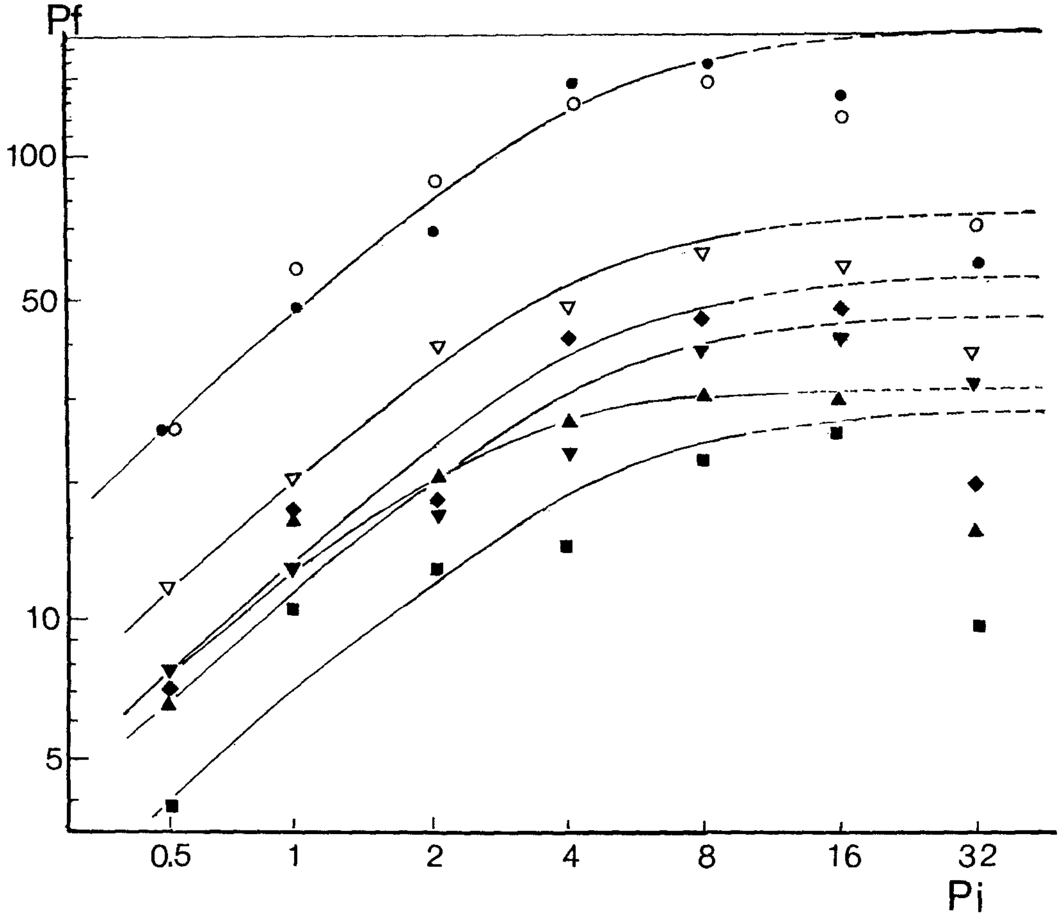

Fig. 4. As Fig 3 for the two references and the remaining five cultivars.

in Table 2 was 6.5 %. However, $rs_{M'}$ of the remaining cultivar and breeder's clone was only $0.59rs_a$ (average $M'/a = 2.2$ eggs/g soil against 3.7 eggs/g soil in the other cultivars: see Fig. 5). The small differences between the ratios $rs_a/rs_{M'}$ of the first eight cultivars and one breeder's clone in Table 2 suggest, that these differences are due to experimental error and variation due to differences between values of m_h and m_e for the different cultivars. A better presentation then is that of Fig. 5. Here, the ranges of values Pf/a per cultivar were plotted against initial egg densities Pi., fitting those of the ten cultivars and one breeder's clone with $rs_a/rs_{M'}$ = about 1 to a curve according to eq. (4) with ratio $M'/a = 3.7$ eggs/g soil (Fig. 5A) and those of one cultivar and one breeder's clone with $rs_a/rs_{M'} = 0.6$ and 0.56 to a curve with $M'/a = 2.2$

Table 2. Relative susceptibilities of 11 potato cultivars and two breeders' clones to pathotype Pa 3 of *Globodera pallida*

Symbols Figs 1–3	Cultivar	rs_a	$rs_{M'}$
○	Bintje	1	1
●	Irene	1	1
△	Pansta	0.51	0.51
▽	Producent	0.44	0.41
+	Promesse	0.42	0.47
⊙	Karna 77/270	0.35	0.34
×	Proton	0.35	0.34
◇	Santé	0.29	0.30
□	Atrela	0.00	0.25
▼	Elles	0.25	0.25
■	Darwina	0.15	0.15
△	Activa	0.30	0.18
◇	Karna 77/281	0.16	0.09

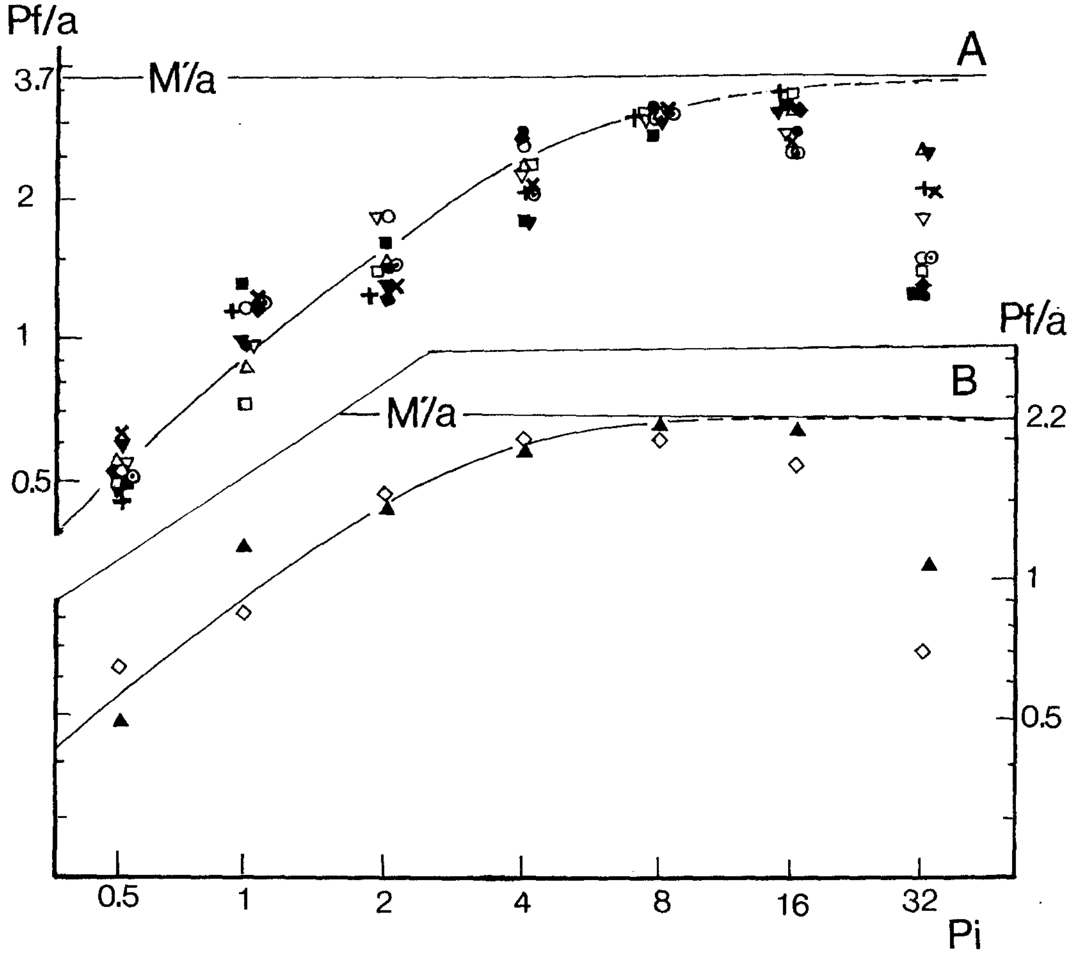

Fig. 5. Relation in the cultivars of Figs. 3 and 4 between initial egg density *Pi* (eggs/g soil) and *Pf/a* (eggs/g soil). A: cultivars with ratio *M'/a* = 3.4 eggs, B: cultivars with ratio *M'/a* = 2.2. eggs.

eggs/g soil (Fig. 5B). An approximate estimate of the coefficient of variation of rates of reproduction in single pots at *Pi* between 0.5 and 8 eggs/g soil was derived from the ranges of values per initial egg density of *Pf/a* in Fig. 5A divided by *Pf/a* according to the curve, assuming that their distribution was symmetrical relative to this curve. The ratio between the largest and smallest values of this range then was 1.8. If this range comprises 95 % of the observations (4s) the coefficient of variation is 14 % per pot. With an equal contribution of the rates observed at *Pi* = 0.5 to 8 eggs/g soil to the variability of $rs_{M'}/rs_a$ the coefficient of variation of the latter would have been $(14^2/5)^{1/2}$ % = 6.3 %, which is to be compared with the 6.5%, derived above from the data in Table 2.

The greater variability at *Pi* = 16 and 32 eggs/g soil in Fig. 5A and at *Pi* = 32 eggs/g in Fig. 5B than at smaller initial egg densities can be ascribed to differences between cultivars in parameter values of the relations between initial egg density and haulm weight and between the first and numbers of eggs/cyst (eqs. (2) and (3)) [Seinhorst, 1993]. As a result, ratios between final egg densities on different cultivars at initial densities > 4*T* may vary more between experiments than those at smaller initial egg densities. Relative susceptibilities determined at large initial densities are, therefore, unreliable.

Fig. 5 confirms Phillips' [1984] supposition, that in general rs_a and $rs_{M'}$ of partially resistant cultivars are (about) the same. However, there are exceptions in which $rs_a > rs_{M'}$. In cv. Activa and the clone Karna 77/281 $rs_{M'}$ is $0.59rs_a$. This difference is too large to be caused by a difference in the final sizes of the plants of these almost equally productive cultivars. Calculating Pf values, assuming $M/a = 4.2$ eggs/g soil and tolerance limits $T_h < 2$ eggs/g soil and $T_e < 4$ eggs/g soil did not result in Pf/a values at up to $Pi = 8$ eggs/g soil similar to those in Fig. 5B for cv. Activa and the clone Karna 77/281. Therefore, small tolerances to the nematodes is not the cause of the small value of M'/a. A cause could be that in these cultivars the exclusion mechanism regulating the intraspecific competition of the nematodes [Seinhorst, 1993] affects a larger proportion of the food source than in the other ones, which, due to the absence of competition, does not affect the maximum rate of reproduction.

With none of the tested cultivars could differences in percentage hatch between the cultivars have been the cause of the difference in relative susceptibility [Mugniéry and Balandras, 1993; Trudgill, 1993]. Such a difference would result in a difference in numbers of juveniles around root tips at initially the same egg density in the soil and a corresponding difference in rate of reproduction as far as due to this difference in percentage hatch. However, the maximum egg density per unit weight of root and, therefore, also that of curves according to eq. (1), fitted to the data in Figs. 3 and 4, is determined entirely by the space available for the nematodes in the roots. Therefore, it is, not affected by the maximum rate of reproduction of a nematode population. A smaller hatching rate in one cultivar than in another would result in a larger value of M/a in the first than in the second cultivar. However, the only deviation from the value of M/a of the reference cultivars Bintje and Irene was a smaller value of M/a in one cultivar and one breeder's clone.

As a good cropping advice system must be based on knowledge of both rs_a and rs_M, which may differ, relative susceptibilities should be determined at ranges of initial egg densities. The results of the experiments reported here indicate that reliable estimates of rs_a and $rs_{M'}$ can be obtained with six initial egg densities between $0.25T$ and $8T$ in six pots per cultivar, provided the pot to pot coefficient of variation of reproduction rates is not larger than 14%. This requires hardly more effort to obtain estimates of both rs_a and $rs_{M'}$, than for obtaining an equally accurate estimate of the relative susceptibility at a single density.

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