

The relationship between initial population density of potato cyst nematode *Globodera pallida* and the yield of partially resistant potatoes

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SUMMARY

The relationship between initial population density of *Globodera pallida* and yield was examined in five partially resistant and one non-resistant potato genotypes in a field trial. In the previous year, the experimental area had been manipulated using resistant and non-resistant potato genotypes to give plots with a range of initial population densities. The results showed that there were differences in the yield losses sustained by the different genotypes but that these were not related to their level of resistance. The data were examined using linear (Brown, 1969) and loglinear (Oostenbrink, 1966) regression models, an exponential model (Seinhorst, 1965) and an inverse linear model. The inverse linear model was found to summarise the data as adequately as the exponential model but with one less parameter.

RÉSUMÉ

Relation entre taux de la population initiale du nématode à kyste Globodera pallida et valeur de la récolte de pommes de terre partiellement résistantes

Un essai au champ a permis d'étudier la relation entre le taux de la population initiale de *Globodera pallida* et la valeur de la récolte chez cinq génotypes de pomme de terre partiellement résistants et un génotype non résistant. Les années précédant l'essai, le terrain avait été aménagé de façon à disposer d'un éventail de populations initiales. Les résultats ont montré des différences de récolte entre génotypes, mais ces différences ne sont pas liées au niveau de résistance. Les données ont été exploitées grâce à des modèles de régression linéaire (Brown, 1969) et loglinéaire (Oostenbrink, 1966), un modèle exponentiel (Seinhorst, 1965) et un modèle linéaire inverse. Ce dernier permet une définition des données aussi bonne que celle fournie par le modèle exponentiel, mais avec un paramètre en moins.

Potato yield is adversely affected by potato cyst nematodes (PCN). However, damage can be reduced by planting cultivars with different levels of tolerance (Trudgill, 1986) and resistance on a rotational basis. Nematicide trials to investigate tolerance differences have been conducted using resistant or partially resistant potato genotypes where yields from treated and untreated plots were compared (Trudgill *et al.*, 1983; Trudgill, Mathias & Tones, 1985; Whitehead *et al.*, 1984, 1987; Dale *et al.*, 1988). These trials identified tolerance differences but were not designed to study the relationship between initial PCN density (P_i) eggs/gm soil and yield loss.

Differences in tolerance to nematode damage are of particular importance in cultivars with resistance to PCN as these cultivars are most likely to be grown in infested soils. Strategies for maximising long-term yield can be investigated by modelling the interactions between P_i and yield. Equations relating the relationship between P_i and tuber or plant yield are an integral part of these models.

Three equations have been used in the literature to describe the effect of P_i on yield. Brown (1969) fitted a simple, linear yield loss model

$$E(Y) = a + b (P_i) \dots\dots\dots (1)$$

to field trial data for non-resistant cultivars. Here Y is the observed tuber yield and $E(Y)$ is its expected value for a given value of P_i . A variant of this model was suggested by Oostenbrink (1966) who regressed yield on $\log (P_i)$, giving the log-linear model

$$E(Y) = a + b (\log P_i) \dots\dots\dots (2)$$

Seinhorst (1965) introduced the exponential model

$$\begin{cases} E(Y) = Y_{max} [m + (1 - m)z^{(P_i - T)}] \text{ if } P_i > T \\ E(Y) = Y_{max} \text{ if } P_i \leq T \end{cases} \dots\dots\dots (3)$$

This equation has four parameters: Y_{max} , the expected yield in the absence of nematodes; T , the threshold for P_i below which no damage occurs; z , the rate at which increasing P_i decreases expected yield and m , the ratio of minimum ($P_i = \infty$) to maximum ($P_i = 0$) expected yield. Seinhorst justified the additional complexity by

providing these biological interpretations for the parameters. Equation (3) is difficult to interpret because tolerance depends on the three parameters m , T and z . We introduce a fourth equation, the inverse linear model

$$E(Y) = Y_{max} [1 - (1 - m) Pi / (c + Pi)] \dots\dots\dots (4)$$

giving fitted curves which are qualitatively like those from equation (3), in that they have sigmoidal shape when plotted against $\log(Pi)$. Equation (4) can be derived from the logistic equation

$$E(Y) = Y_{max} [1 - (1 - m) \exp(kx + C) / (1 + \exp(kx + C))] \dots\dots\dots (4a)$$

where $x = \log(Pi)$, $C = \ln(c)$ and the scale parameter k is given the value 1 . The parameters have biological interpretations: Y_{max} is the expected yield at $Pi = 0$; c determines the rate at which increasing Pi decreases expected tuber yield; and m gives the ratio of minimum ($Pi = \infty$) to maximum ($Pi = 0$) expected yield as for the Seinhorst model. Note that tolerance is expressed in only two parameters, c and m .

This paper describes an analysis of data from an experiment in which a field population of PCN was manipulated to give a range of Pi . The tuber yields were analysed by fitting each of the four equations above to the data. The suitability of these equations for describing the relationship between Pi and yield loss is discussed.

Materials and methods

The trial was on a loamy sand site in East Lothian Scotland, infested with *Globodera pallida*. The site was uniform and level, apart from a slight depression at one corner. In a preliminary year (1984) the trial area (54.9 m by 27.3 m) was located along one edge of a heavily infested area and was divided into two parallel blocks of nine plots. Sampling showed that the initial pre-planting population density (Pi) of *G. pallida* gradually decreased along and across the trial area. Each plot was 6.1 m long \times 13.65 m wide (fifteen rows). In each of the blocks one plot of each of nine genotypes of potato was planted.

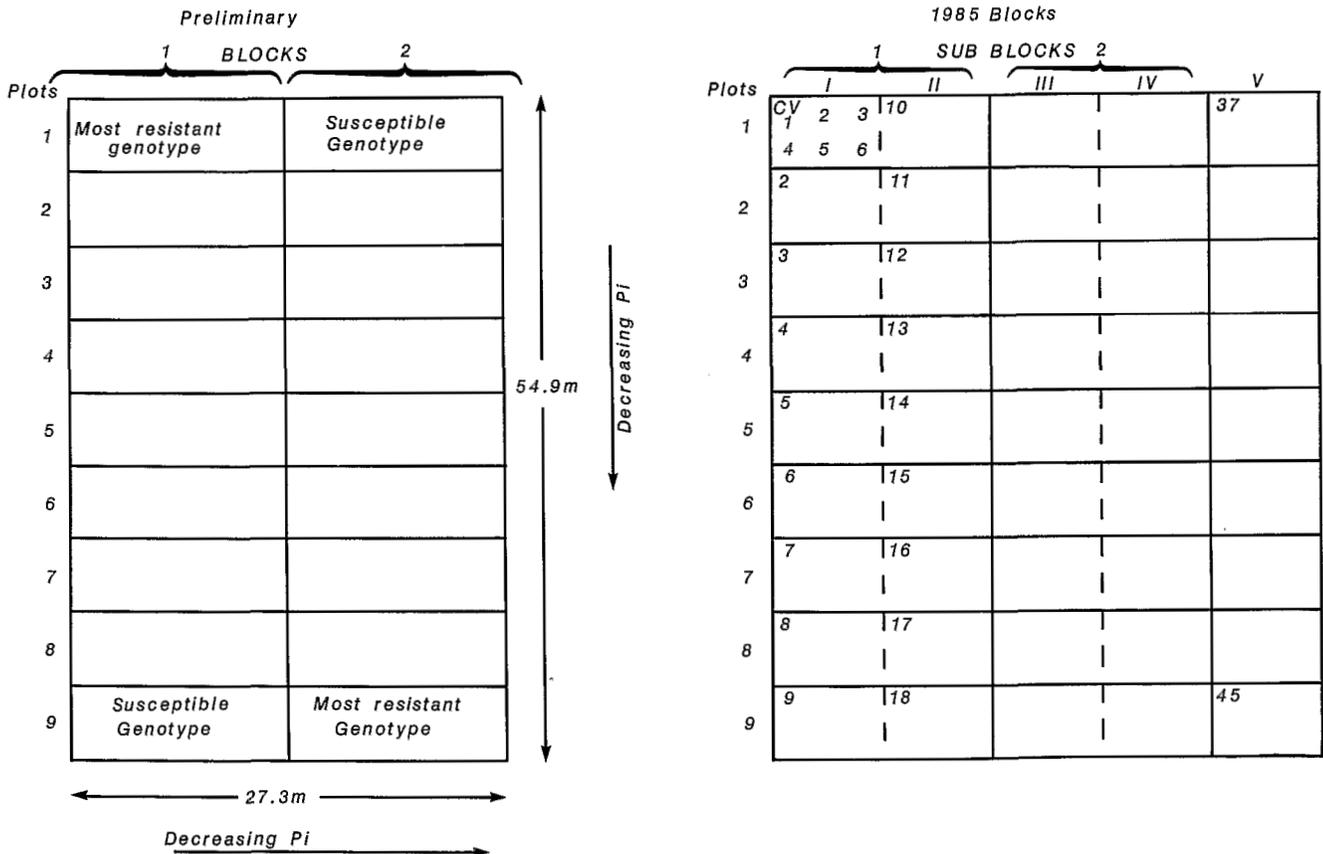


Fig. 1. Experimental design in 1985 and 1986.

Two of the genotypes (Maris Piper and an early maturing breeders' clone 11242) were non-resistant and seven were breeders' clones, derived from *Solanum vernei* which allowed between 20 % and 90 % reproduction of *G. pallida* females (Phillips, unpubl.) when compared to non-resistant genotypes.

The potatoes were planted in a systematic order from the least to the most resistant in one block and in the reverse order in the other (Fig. 1). The tubers were planted 38 cm apart in rows 92 cm wide. Weed, aphid and blight control were according to local farm practice. Prior to harvest the block corners were marked by measurement and by pits filled with a distinctive gravel. The tubers were lifted by machine.

In 1985 the corners of the site were accurately located and plots received N:P:K (15:15:21) fertiliser at 1 t ha⁻¹ incorporated overall.

Observations on plant growth and female PCN on the roots in 1984 indicated a trend from high to low infestation across the blocks and consequently these blocks were split lengthwise to give four sub-blocks. None of the genotypes planted in the preliminary year left very low population densities. Hence a further area along one side of the original 1984 site was used to produce a fifth sub-block. This area had been used to grow cereals in the preliminary year, so it had a low infestation of *G. pallida*. Each sub-block was divided into 9 plots 6.1 m long by 6.8 m wide. Thus the trial, as a whole, consisted of 45 plots each with 6 sub-plots; 270 sub-plots in total (Fig. 1). Rows superfluous to the experimental rows were used to provide inner and outer guards and a central tractor path.

Six potato genotypes were planted within each plot. Planting areas (sub-plots) were 3.05 m lengths of two adjacent rows, and genotypes were allocated to planting areas at random. The six potato genotypes were: Maris Piper (non-resistant to *G. pallida*), Fiona and 12243 (with low levels of resistance), Morag and 11233 (with moderate resistance), and Vantage (with high resistance).

The seed tubers had been chitted to have sprouts approximately 1 cm long. Great care was taken in selecting equal weights of healthy tubers for each sub-plot and in accurate spacing (38 cm) during planting on 17 April. Irrigation was not applied as the summer of 1985 was exceptionally wet. The haulm was destroyed on 23 September and at harvest on 8 October the central six plants in each of the two rows (from a total of 12 per row) were hand dug and the total weight of tubers recorded. In nine plots at one end of the trial a proportion of the tubers had rotted. The yield data from these areas were not included in subsequent analysis.

Immediately after planting, a sample of 30 cores (2 cm radius × 12 cm length) of soil (weighing approx. 1 kg) were taken from the centre of each sub-plot. The soil samples were air dried and the cysts extracted in a Schuilling centrifuge. The eggs and juveniles were

extracted from the cysts using the modified Bijloo method (Seinhorst & Den Ouden, 1966).

An analysis of variance was performed on the estimated P_i s to examine the effect of the preliminary year. It proved necessary to log transform the P_i to make variance independent of mean value.

The parameters in the yield equations were estimated using maximum likelihood, assuming normal errors and equal variances. Hypotheses about the parameters were tested by simultaneously fitting each equation to data for all six genotypes with some of the parameters either fixed at values of interest or constrained to take the same value for a number of genotypes. The goodness of fit of equations to the data was assessed graphically and by partitioning the residual sum of squares into a component for pure error and a component for model lack of fit. The estimate of pure error variance was obtained from differences between residuals in plots with P_i which differed by less than 0.05 (l_n eggs/g soil) after fitting the log-linear model.

Results

The mean pre-planting population density (P_i) of *G. pallida* for each of the 36 sub-blocks, based on individual sub-plot estimates, ranged from 1.95 to 173.2 eggs/g soil. Analysis of these data indicated large differences between plots depending on the potato genotype grown in the first year ($F_{8,8} = 39.4$).

The tuber yield ranged from 0.7 to 33.3 kg/plot (Table 1). In the lightly infested plots, clones 11233 and 12243 yielded the least and Morag the most. However, in heavily infested plots, 12 243 had a much higher yield than any other genotype and thus had the highest yield averaged across all plots. There was some indication of a plot effect over and above the effect of P_i . However, because the size of the plot effect was small it was subsequently ignored and tuber yield considered as a function of genotype and P_i alone.

Table 1

Relative susceptibility, together with mean, lowest and highest yields (kg/plot) from six potato clones grown in plots with different initial population densities of *G. pallida*

Clone	Susceptibility	Mean	Lowest	Highest
Maris piper	100	13.1	0.7	29.2
Fiona	51	10.5	1.1	27.0
12243	56	18.7	14.9	23.8
Morag	21	12.6	1.1	33.2
11233	14	9.5	1.0	25.1
Vantage	10	11.7	3.9	24.0

The pure error estimate of residual mean square was 7.3 (60 d.f.). The corresponding sum of squares has been

subtracted from all residual sums of squares quoted (Table 2).

Table 2

Goodness of fit tests for each of the four models

Model	d.f.	SS	F
Linear	126	3 266	3.5
Loglinear	126	965	1.1
Exponential (Seinhorst, T = 0)	120	954	1.1
Inverse linear (m = 0)	126	954	1.0
Pure error	60	440	

Fitting the linear model (Equation 1) to the data gave a residual sum of squares of 3266 (126 d.f.), indicating a significant lack of fit ($F_{126,60} = 3.5$). This was confirmed by plots of the residuals against P_i showing considerable bias.

The log-linear model (Equation 2) gave a residual sum of squares of 965 (126 d.f.) indicating a good fit to the data which was supported by the lack of fit test ($F_{126,60} = 1.1$). The slope parameter (Table 3) can be held constant across five of the genotypes ($F_{4,60} = 1.7$) but not across clone 12243 as well ($F_{1,60} = 94$). However, there is no guarantee that this model will give positive predicted yields for high values of P_i , and the fitted curve is unbounded at $P_i = 0$.

Table 3

Parameter estimates (and S.E.s in brackets) derived from regressing yield on P_i for six potato genotypes

Clone	b	a
Maris Piper	- 6.00 (0.57)	32.7 (2.0)
Fiona	- 5.03 (0.40)	27.5 (1.4)
12243	- 1.05 (0.25)	22.8 (0.9)
Morag	- 5.53 (0.51)	30.5 (1.8)
11233	- 5.09 (0.33)	26.6 (1.2)
Vantage	- 4.65 (0.28)	27.1 (1.0)

Numerical difficulties were encountered when trying to estimate the parameters in the exponential model (Equation 3). The fitted values were sensitive to changes in z , since the best fits are obtained when z is close to its maximum value of l . This was overcome by estimating a transformed parameter, z_i , where $z_i = \exp(z)/(1 + \exp(z))$. The same transformation was used to estimate m_i . Equation 3 is also over parameterised, there being a range of parameter values which give rise to curves that fit equally well to the data. In order to make progress, the value of T was fixed at zero eggs/g soil and conditional estimates of the remaining parameters were made. The best estimates are given in Table 4. For the

most tolerant clone, 12243, the estimates of m and z were very highly correlated. The values of m and z appeared to be constant across the other five genotypes ($F_{8,60} = 1.0$). Furthermore, either m ($F_{1,60} = 2.5$) or z ($F_{1,60} = 0.0$) can be held constant across all varieties, but not both ($F_{2,60} = 113$). Residual plots and the lack of fit test ($F_{120,60} = 1.1$) indicate a good fit.

Table 4

Estimates of Y_{max} and the transformations of parameters m, z (with S.E.s in brackets) from the exponential equation ($T = 0$) derived from fitting curves to yield as a function of P_i for six genotypes of potatoes

Clone	Y_{max}	$Log_e [m/(l - m)]$	$Log_e [z/(l - z)]$
Maris Piper	27.9 (1.9)	- 2.39 (1.71)	3.57 (0.27)
Fiona	24.3 (1.3)	- 1.79 (0.47)	3.35 (0.21)
12243	21.3 (0.6)	- 1.04 (8.11)	5.76 (2.59)
Morag	27.5 (1.7)	- 1.46 (0.37)	3.18 (0.24)
11233	24.2 (1.19)	- 1.68 (0.32)	3.09 (0.20)
Vantage	24.8 (0.97)	- 1.13 (0.32)	3.14 (0.17)

The inverse linear model (Equation 4) gave a slightly better fit to the data than equation 3 (Tables 2 & 5). Constraining m to be zero did not result in a significant lack of fit ($F_{6,60} = 0.3$), whereas it did result in a substantial simplification of the model. Furthermore, the value of a could be held constant across all genotypes except clone 12 243 ($F_{3,60} = 1.1$) but could not be held constant across all 6 in ($F_{1,60} = 232$). Again, residual plots and the lack of fit test indicated a good fit ($F_{126,60} = 1.0$).

The fitted curves from the log-linear, exponential and inverse linear models for the most tolerant (clone 12243) and the most intolerant genotypes (Maris Piper) are shown in Figs 2 and 3.

Table 5

Estimates (with S.E.s in brackets) of parameters Y_{max} and c from the inverse linear equation ($m = 0$) derived from fitting curves to yield as a function of P_i for six potato genotypes

Clone	Y_{max}	c
Maris Piper	29.7 (2.2)	22.1 (3.9)
Fiona	25.5 (1.4)	21.1 (2.9)
12243	21.4 (0.5)	397.5 (87.8)
Morag	28.5 (1.9)	21.0 (3.4)
11233	25.0 (1.6)	25.8 (2.6)
Vantage	25.5 (1.3)	16.5 (2.1)

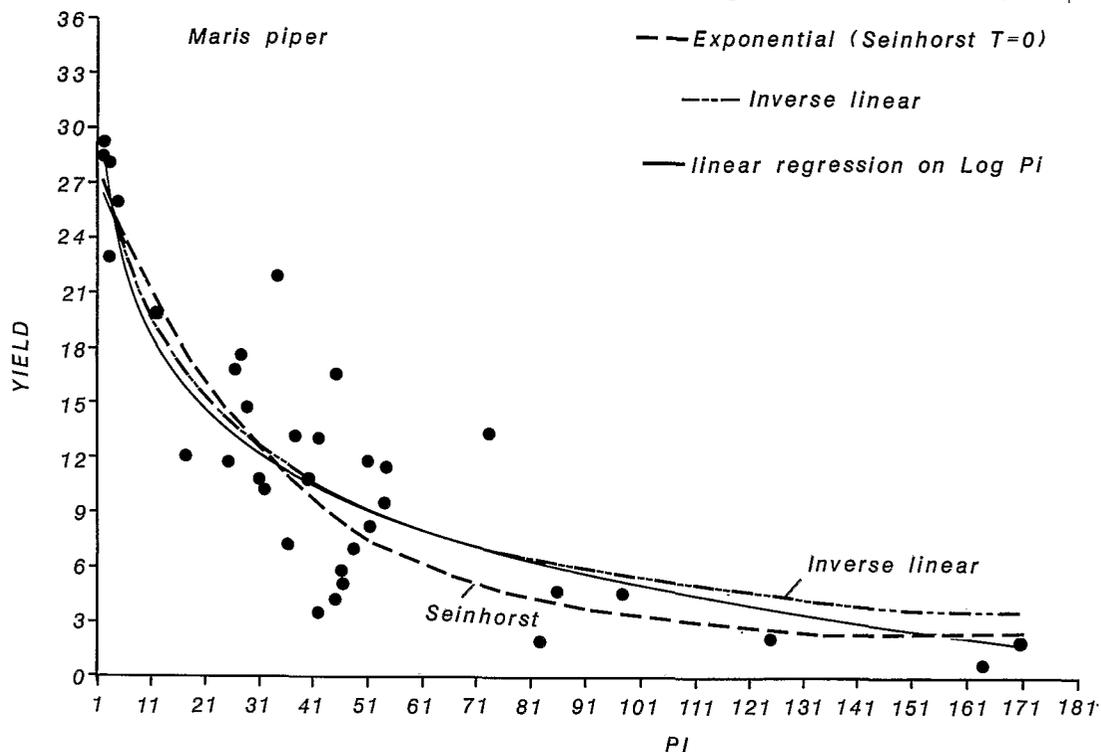


Fig. 2. Unconstrained fits of yields as a function of P_i for potato genotype clone 12243 grown in field plots infested with *G. pallida*.

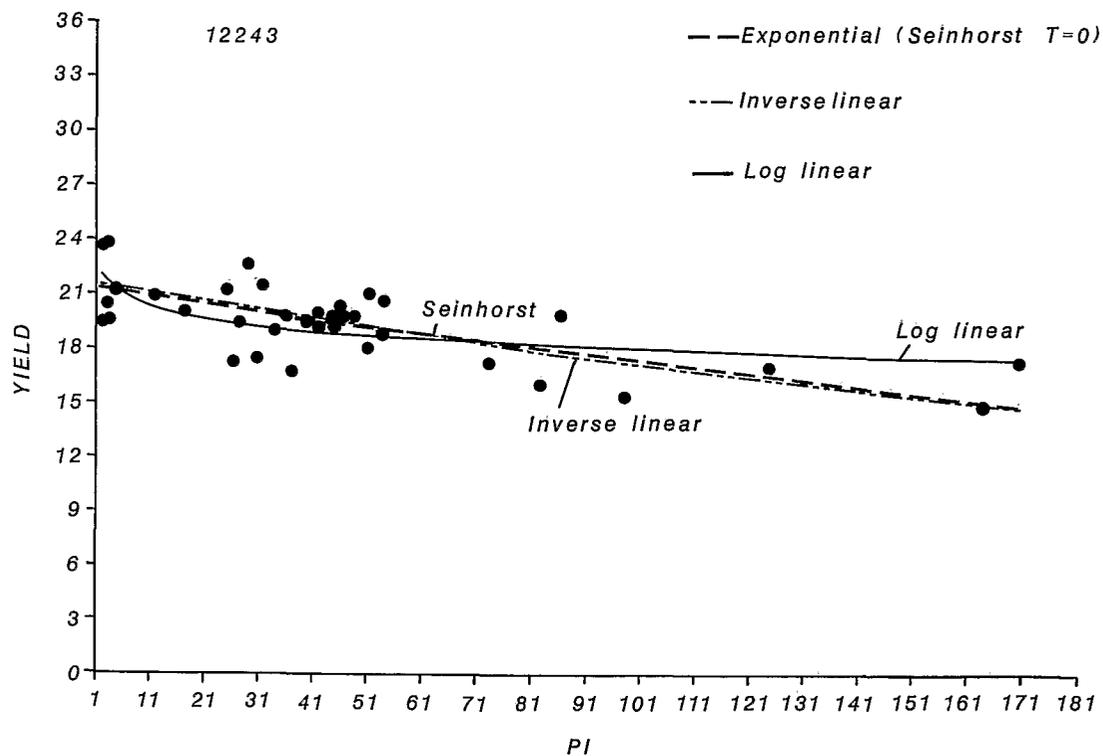


Fig. 3. Unconstrained fits of yield as a function of P_i for potato genotype Maris Piper grown in field plots infested with *G. pallida*.

Discussion

There are marked differences between the potato genotypes in the degree of yield loss sustained in heavily infested soil. However, as found by others (Trudgill & Cotes, 1983; Alphey & Phillips, 1988; Dale *et al.*, 1988); there was no obvious relationship between differences in tolerance of damage and the level of resistance to *G. pallida*. Non-resistant Maris Piper was intolerant as was moderately resistant cv. 11233. Vantage, the most resistant cultivar, was moderately tolerant whereas clone 12243, the least resistant genotype, was very tolerant.

Analysis of the data has shown that the relationship between tuber yield and untransformed P_i can not adequately be approximated by a straight line. All of the other three equations considered fit reasonably well to the data. However, the linear regression of tuber yield on $\log(P_i)$ must be recognised as being an approximation because of its undesirable asymptotic properties. Although allowance could be made for these defects, we feel it is better to use equations which naturally incorporate the asymptotic properties required of the model.

The exponential model of Seinhorst (Equation 3) is well established in the literature, but the four parameters could not be estimated simultaneously using our data despite the wide range of P_i considered. Estimating three of the parameters conditional upon the value of a fourth is a somewhat unsatisfactory way of proceeding, because the values taken by the three parameters will depend on the value at which the fourth is held. Thus conclusions drawn about constancy of parameter values across potato genotypes will always be open to dispute. We chose to fix $T = 0.0$ because this removes the discontinuity in the first derivative. Such a feature is undesirable, because it indicates an abrupt change in the nature of the relationship for which there is no empirical evidence. Both parameters z and m can be held constant across five of the genotypes, and either can be held constant across all six. However, holding both of the parameters constant across all six genotypes gave a much worse fit. Thus there is insufficient information in the data to tell whether it is z or m or both which differ between the genotypes used, so the model must retain at least two tolerance parameters.

The attractive feature of the inverse linear (Equation 4) is that it needs only two parameters, and satisfies the necessary shape constraints at high and low PCN densities. Since the value of m can be fixed at zero, the simplified expression.

$$E(Y) = Y_{max}/[1 + (P_i/c)] \dots\dots\dots (5)$$

is available. This equation is particularly appealing as tolerance is expressed by a single parameter. It would be interesting to know how the tolerance parameter depends on environmental factors.

The data collected in this experiment can best be discussed in the light of the fits obtained from Equations

(3) and (4). Of the six genotypes, five appeared to have identical tolerances, whereas the sixth was considerably more tolerant. This latter clone yielded least at low P_i but had the greatest yields for P_i higher than 11 eggs/g soil.

Whether or not the data support the hypothesis that PCN can reduce tuber yields to nothing is debatable. Fitting Equations (3) and (4) led to different conclusions. This can be accounted for by the different rates of approach to the asymptote assumed by the two equations. Equation (3) assumed yield approaches its asymptote exponentially as P_i increases, and so the asymptote is almost reached within the range of P_i observed. Extrapolation indicates that little further change is possible. Thus a non-zero asymptote is highly plausible. However, the inverse linear relationship of Equation (4) approaches zero much more slowly as P_i increases. In this case a much greater decrease in expected yield occurs when the fitted curves are extrapolated beyond the highest observed P_i , so the data appear to be compatible with the hypothesis that tuber yields have an asymptote at zero.

There is evidence that the degree to which tolerance of PCN is expressed, whether measured by rate of yield loss, proportional yield loss or minimum yield, varies with the environment in which the crop is grown. From a number of trials at different sites in different years, Dale *et al.* (1988) have shown that genotypes do differ in their tolerance but that its expression is subject to genotype \times environment interactions: differences between sites were independent of P_i . Trudgill (1987) showed that fertiliser influenced the degree of yield reduction due to PCN. Seinhorst (1982) estimated the values of m in different trials conducted in a wide range of environments and acknowledged that the value of m differed. Trudgill (1986) has reviewed other environmental factors including soil type, nutrient status and other husbandry practices which may interact with damage by PCN and affect the extent of yield losses.

If predictive models of the effect of PCN on yield are to be developed they will have to incorporate parameters that not only reflect the level of the nematode population but also the genotype of potato and the environment in which it is to be grown. Combining such a model with one for estimating the population dynamics of the nematodes would provide a powerful means of developing integrated control strategies utilising partially resistant cultivars for the management of PCN compatible with producing economic yields.

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