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Density-Dependent Nematode Seasonal Multiplication Rates and Overwinter Survivorship: A Critical Point Model

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Abstract: Nematode multiplication rates Pf/Pi and overwinter survivorship (Pi2/Pf1) for *Meloidogyne incognita* were both adequately described by negative exponential models, indicating density dependence in each case. Density dependence of the multiplication rates is mediated by resource limitation and host damage; in survivorship rates it may be mediated by limitation of stored reserves or prevalence of antagonists. Parameters of multiplication rate models were crop specific and varied with host status and environmental suitability. Maximum multiplication rates (a) of nearly 1,000 were measured for tomatoes. Equilibrium densities were sensitive to tolerance of the nematode by the crop. Overwinter survival rates varied among locations where cultural practices and length of infestation time differed.

Key words: maximum multiplication rate, equilibrium density, cropping sequences, pest management, *Meloidogyne incognita.*

The importance of the relationship between crop growth or yield and preplant population densities of plant-parasitic nematodes has been well documented and defined (6,12,13). Justification for studies of this relationship is based on the need for anticipation of nematode damage in planning preplant nematode management strategies (3,4,6,11–13). Provided that adequate knowledge is available on cost-benefit effectiveness of management approaches, the predictions can be used for short-term optimization in nematode man-

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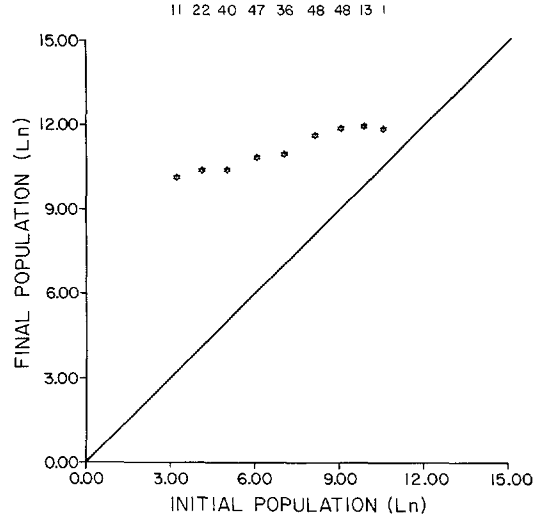

FIG. 1. The relationship between final and initial population densities of *Meloidogyne incognita* on tomatoes. Data set collected over 4 years in Orange County, California. Numbers of observations compacted into each data point depicted at top of figure.

agement (5,10). Such single season optimization may result in nematode population densities detrimental to subsequent crops, and optimization of cropping sequences should be considered (3,4). At least three pieces of information are necessary: 1) the relationship between crop yield and preplant nematode population density (Pi); 2) the expected multiplication of the nematode population during the cropping season; and 3) the overwintering survivorship of the nematode population. Preplant nematode densities and expected crop values may then be projected over several years (3,4). The information provides the basis for a linear programming approach to the selection of multiple cropping sequences, while allowing flexibility of management through annual biological and economic monitoring.

Analytical single-season models of nematode population increase, the relationship between final population density (Pf) and Pi, under a host crop have been developed (11,14–17) from the logic of the familiar logistic equation (1). The models redefine the rate of increase and carrying capacity of the logistic expression in terms of the maximum multiplication rate (a) (Pf/Pi at low population densities) and the equilibrium density (E), that initial population at which there is just sufficient food to maintain the population at the same level at the end of the growing season (14–16). In general, at higher Pi levels, resources become limited or the host is damaged so that the multiplication rate (Pf/Pi ratio) decreases (Fig. 1). The hypothesis is that the expected multiplication rate of a nematode population decreases with density, and the nematode density is associated with the limitation of food and space resources.

Also important in optimizing nematode management over a multiple year cropping sequence is the survival of nematodes between growing seasons (3,4,9). Data generated from the same experiments conducted for derivation of damage functions and multiplication factors may allow development of models for overwintering survivorship (rate of survival).

The objective of this paper is to explore the relationship between host status, nematode density, and nematode multiplication rate and inter-season survivorship.

MATERIALS AND METHODS

Data: Experiments conducted over several years in southern California have studied the relationship between various crops and preplant population densities of *Meloidogyne incognita* (Kofoid and White) Chitwood. At several sites, the same plots were used over a series of years. The standard experimental design was 30–60 4-row plots (approximately 5 m long, 25-m^2 area) for each crop at each location. The treatment imposed on each plot was a different Pi level achieved by differential cropping and low dosages of nematicides. Standard commercial cultural and irrigation practices were applied. Besides crop yield measurements, Pi and Pf values were determined as the mean population extracted from two 2.5-cm-d, 12-core soil samples taken 30 cm deep. Soil samples were taken in the plant beds to assess population levels experienced by the plants. Preplant samples were removed approximately 2 weeks before planting, and post-harvest samples were taken immediately following harvest. Population densities of root-knot nematodes are expressed as the total of eggs and second-stage juveniles per 1,000 grams soil, corrected for stage-specific efficiency of the elutriation–sugar flotation sieving (2) extraction technique employed. The relationship of Pf in the fall to Pi the subse-

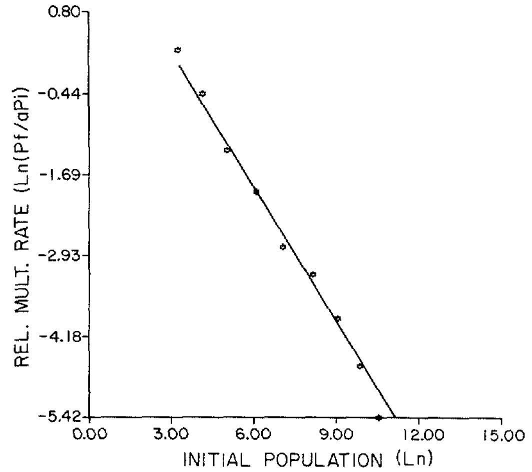

FIG. 2. Relative multiplication rate (Pf/Pi) (log scale) in relation to Pi for *Meloidogyne incognita* on tomatoes. Same data set used as in Figure 1.

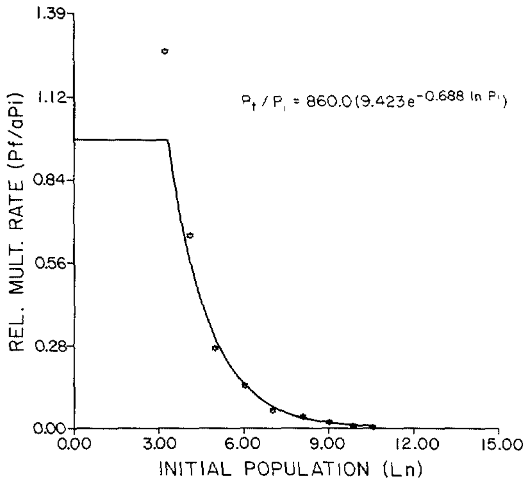

FIG. 3. Relative multiplication rate of *Meloidogyne incognita* in relation to Pi, according to the model: $Pf/Pi = ace^{-b \ln Pi}$ or $Pf/Pi = acPi^{-b}$. Values for *Meloidogyne incognita* on tomatoes: $a = 860$, $c = 9.4$, $b = 0.688$. Orange County, California.

quent spring provides a data base for study of overwinter survival, including any density-dependent influences on survivorship.

Models: Data from experimental plots indicate a strong density dependence of the multiplication factors (Fig. 2) and suggest a negative exponential relationship between the factor and natural log (ln) Pi. It has become convention to express Pi data graphically on a $\log_2$ scale; however, in the interests of standardization and avoiding confusion, a natural log scale may be preferable. Accordingly, the model $Pf/Pi = ce^{-b \ln Pi}$ was selected as descriptive of the data, where c is a scaling factor, b a rate determining variable, and e is the base of the natural logarithm. Since $e^{\ln Pi} = Pi$, the model may be rewritten as $Pf/Pi = cPi^{-b}$, so that $Pf = cPi^{1-b}$.

Another modeling approach was tested for prediction of nematode multiplication factors. In the explanatory critical point model of Seinhorst (13) ($y = m + (1 - m)Z^{Pi-T}$ for $Pi > T$, $y = 1$ for $Pi \leq T$) for the relationship between crop growth and Pi, expected growth is a function of the proportion of root undamaged by the nematode population; m is minimum yield at high nematode densities, Z is a damage rate parameter and a function of nematode virulence, and T is the tolerance limit. Obviously, the undamaged proportion of the root is also an indicator of the resources available to the nematode population, either for new infection sites, or, through its relationship to crop growth, the food available to the nematode population. The proportion of undamaged root system may be a useful indicator of nematode multiplication during a crop season. It would be satisfying to use the same model to explain nematode multiplication as that used to describe crop growth relative to Pi. I attempted to use this model to describe nematode multiplication where yield of

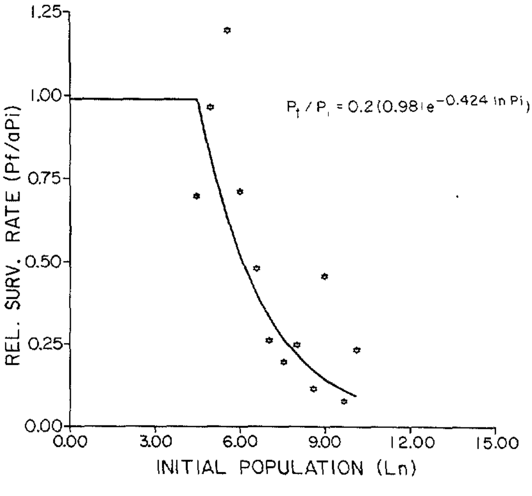

FIG. 4. Overwinter survival of *Meloidogyne incognita* in relation to fall population densities, according to the model: $Pi2/Pf1 = ce^{-b \ln Pf1}$ or $Pi2/Pf1 = c\,Pf1^{-b}$, constrained by a maximum value of 0.15, where $c = 0.98$ and $b = 0.424$. Tulare County, California.

nematode population is considered the relative magnitude of its increase through the growing season (Pf/Pi).

Empirical observations of overwintering survivorship data from experimental plot locations (Fig. 4) also indicate a negative exponential relationship, in this case to the natural log of the final population for the previous year. Consequently, this model was applied to the data. In this case, the relationship is $Pi2/Pf1 = ce^{-b \ln Pf1}$, where Pf1 is the population entering the overwinter period and Pi2 is the population surviving. Then, $Pi2/Pf1 = cPf1^{-b}$ and $Pi2 = cPf1^{1-b}$.

Analyses: Measurements of nematode multiplication and survival rates from experimental plots are subject to the same kinds of errors as measurements used for the development of damage functions (7). Consequently, in examining nematode multiplication factors, it is convenient to minimize the expected and observed variability by compacting the data sets into logarithmic density classes (7). There can logically be no nematode reproduction calculated when $Pi = 0$; however, such an estimate may result from sampling error or from a population below the detectable level. A positive final population, often found in such plots, would indicate an infinitely large multiplication factor. Hence, all data points with $Pi = 0$ were eliminated from the data set. The reproduction factors are calculated by determining the average Pf for all plots with Pi falling within a density class. The average of the Pi values within a density class represents the initial density estimate for that class. The multiplication factor is calculated as Pf/Pi.

The negative exponential models for both multiplication rates and survivorship were fitted to the data sets by linear regression techniques after log transformation. Regression of ln(Pf/Pi) values against ln Pi allows solution for an intercept value (ln c) and a slope (b) from the equation: $\ln(Pf/Pi) = \ln c - b \ln Pi$. Parameters of the Seinhorst (13) damage function model for seasonal multiplication rates were determined by the algorithm developed by Ferris et al. (8) for fitting the model to yield and Pi data.

To standardize the models for different crops, it is convenient to divide through by the maximum multiplication rate (a) (14), so that Pf/Pi is expressed as a relative multiplication factor (f) on a 0–1 scale: $f = Pf/aPi = (c/a)Pi^{-b}$. The best estimate of the maximum multiplication factor (a) occurs at low Pi. Since the (a) value provided by the lowest population density class in the data set (Figs. 2, 3) is subject to experimental and measurement error, (a) is estimated by the model prediction for the lowest Pi observed in the data set. Alternatively, (a) can be calculated at that Pi value identified as the tolerance level in the host-plant damage function. The rationale would be that this is the population level at which there is first evidence of resource limitation. In the linear (logarithmic) form of the model, the intercept value (ln c) is corrected to the relative scale by subtracting the predicted estimate of (ln a) at the lowest ln Pi. The (c) value in the exponential model is determined by c/a. The slope parameter (b) is not affected by the adjustment for maximum multiplication rate. For all population densities below the lowest observed Pi, the relative multiplication rate is assumed to be 1.0 (Figs. 2, 3). This rationale, of course, assumes that underpopulation phenomena (18) do not exist in the data set. Such phenomena (depressed reproduction due to scarcity of mates) are not a problem with parthenogenetic species.

The equilibrium density (E) (14) is, like (a), an indicator of host status of the crop to the nematode and of nematode pathogenicity on the crop. By definition, it is that Pi for which $Pf/Pi = 1.0$. Then, $1.0 = cE^{-b}$ in the model unadjusted for maximum multiplication rate, so $E = c^{1/b}$.

Since survivorship values are implicitly on a 0–1 scale, it is inappropriate to correct for any maximum survival in establishing parameters of survivorship models. However, the nature of the negative exponential model is such that as Pf1 approaches 0, Pi2/Pf1 approaches infinity. Therefore, it is necessary to constrain the upper range of the proposed model to the highest survivorship (max) observed in the data set.

Model parameters for seasonal multiplication rates and overwinter survivorship were derived for several experimental locations over several years to determine their stability. Data from a series of crops at each location were useful in that they provided a wide range of Pf values at the

TABLE 1. Parameters of a negative exponential model for crop season population increase of *Meloidogyne incognita*: $f = acPi^{-b}$ for $Pi > T$, $f = a$ for $Pi \leq T$.

Crop	Location	Soil	a*	c†	b‡	r^2§	E‖	T¶
Processing tomatoes	Orange County	Loamy sand	860	9.4	0.688	0.99	207	25
Processing tomatoes	Kern County	Sandy loam	990	23.4	0.828	0.95	245	35
Processing tomatoes	Riverside County	Silt loam	544	108.8	1.056	0.85	210	84
Green beans	Orange County	Loamy sand	709	5.7	0.630	0.92	164	15
Bell pepper	Orange County	Loamy sand	599	28.2	0.797	0.99	226	65
Cantaloupe	Orange County	Loamy sand	586	1.0	0.665	0.96	46	0
Blackeye beans	Kern County	Sandy loam	21	6.8	0.590	0.94	23	25

* Maximum seasonal multiplication rate.

† Scaling factor of negative exponential model.

‡ Rate determining variable for effect of increase in ln Pi.

§ Coefficient of determination for model fit to density-class data sets.

‖ Equilibrium density (Pi when Pf/Pi = 1.0).

¶ Tolerance limit in damage function: $y = m + (1 - m)Z^{Pi-T}$.

end of a cropping season, allowing an appropriate fit of the survivorship model. On a single crop, Pf values are often high, and data may be scarce for survival at low Pf values.

RESULTS

The empirical negative exponential model adequately described data sets tested. As an example, the relationship between Pf/Pi and Pi for processing tomatoes at the University of California South Coast Field Station, Orange County, California, for data collected over a 4-year period, exhibits a classic example of the effects of resource limitation on nematode multiplication (Fig. 1). Each point represents the mean of several observations (denoted in the figure) within a logarithmic series density class (7) to minimize effects of sampling and experimental error. When Pf/Pi values are calculated for this data set and log transformed to allow determination of the parameters of the negative exponential model, an excellent fit results (Fig. 2) and reveals the declining influence per nematode with increasing population densities in the arithmetic form of the model (Fig. 3).

Host status and environmental effects on seasonal multiplication rate were standardized to a 0–1 scale by dividing the model by the maximum multiplication rate (a) observed at the damage function tolerance limit. The (a) value would be used as a multiplier in the model:

$$Pf/Pi = acPi^{-b}$$

The other parameters of the model, c and b, were calculated for a series of crops in Kern, Orange, and Riverside counties. The model was used to determine equilibrium density estimates for these crops (Table 1). The negative exponential model was also an adequate descriptor of nematode overwintering survivorship relative to ln values of the population entering the winter period (Fig. 4). The parameters of this model were determined for different data sets and locations to determine their stability across years and locations (Table 2).

Although the Seinhorst model (13) applied to nematode reproduction rates is philosophically appealing, the fit of the

TABLE 2. Parameters of a negative exponential model for overwinter survival of *Meloidogyne incognita*: $f = acPi^{-b}$ such that Pi2/Pf1 is the minimum of max and f.

Location	Winter	Max*	c†	b‡	r^2§
Orange County	1980–81	0.16	2.13	0.267	0.44
Kern County	1981–82	0.70	14.8	0.608	0.74
Tulare County 1	1983–84	0.31	6.64	0.561	0.61
Tulare County 2	1983–84	0.15	0.98	0.424	0.73

* Maximum observed survivorship in data set.

† Scaling factor of negative exponential model.

‡ Rate determing variable for effect of increase in ln Pf1.

§ Coefficient of determination for model fit to density-class data sets.

model to the data was not satisfactory, especially at higher population densities. The Seinhorst model is, in fact, exponential in form, as determined by defining $Z^{-T} = c$ and $Z = e^{-b}$. Then:

$$y = m + (1 - m)ce^{-bPi}$$

and the values (c) and (b) determined by linear regression techniques. This is especially straightforward for $m = 0$ as with the multiplication data. However, use of either this linear regression approach or the curve-fitting algorithm (8) produced parameters which were unsatisfactory predictors of nematode reproduction unless the initial population data were log-transformed, as in the empirical negative exponential model.

DISCUSSION

Parameters of the negative exponential model for nematode multiplication rates were influenced by crop species, environmental suitability, and geographic location (Table 1). For processing tomatoes, maximum multiplication rates (a) and equilibrium density (E) reflected the favorable host status of this crop (14,16) and can be used as benchmark high values for consideration of the other crops. The (a) values were sensitive to soil texture, being highest in coarse-textured soils and in warm climate regions (Kern County). Since (a) values were measured at the population density indicated by a damage function algorithm (8) to be the tolerance limit (T) (13), the (c) value or Y-axis intercept of the model is an analytical constant rather than a biological indicator of host status. The (b) value, or slope-determining parameter of the model, is of greater consequence. Higher (b) values indicate greater density dependence of nematode multiplication, that is, greater impact per additional nematode on the decline of the nematode multiplication rate. In tomatoes the (b) values differed somewhat with environment, being highest in finer-textured soil and lowest in coarse-textured soils. For other good hosts (green beans, bell pepper, and cantaloupe), (a) values were similar to those for tomatoes. However, equilibrium densities varied according to the tolerance of the plant to the nematode. Bell pepper is tolerant to *M. incognita* and exhibited a high equilibrium density, whereas cantaloupe is intolerant, suffering damage at low population densities, resulting in a low equilibrium density. Cowpea cultivar California Blackeye 5 is a very poor host of *M. incognita,* with low (a) and (E) values. The magnitude of these parameters indicates, however, that the nematode population will increase on this variety when at low Pis.

A further logical step in the analyses described is the application of ranges and confidence intervals to the parameter estimates. Since the estimates are derived from linear regression approaches, such ranges are readily determined, either graphically or by calculation, by applying confidence bands to the model. Since the models presented are developed from data sets in which variability has been minimized by collapsing population levels into density classes (7), ranges associated with the current estimates are very small (note high r^2 values). At least in part, the purpose of this paper is to demonstrate the development and utility of the application of critical point models of nematode population processes to nematode management decisions. At this time, it seems inappropriate to enter into the literature narrow ranges on parameter estimates when these ranges are a function of the experimental design, sampling methodology, and analytical technique employed.

Data sets for overwintering survivorship were smaller and somewhat less conclusive (Table 2). Maximum survivorship measured in Orange County was 0.16, compared with 0.7 in Kern County. Since there are few low Pf1 values in the data sets, the maximum survivorship estimates are determined by extrapolation and their reliability and the statistical significance of differences will only be revealed by further experimentation and experience. Maximum survivorship at other locations was variable even during the same winter. There are several possible explanations. One is that the Orange County locations have a long history of root-knot nematode infestation, whereas the nematode was introduced to field plots only 1 year earlier in the Kern County location. Survivorship values possibly reflect the relative buildup and establishment of populations of nematode antagonists in these locations. At the Tulare County 2 location, a winter spinach crop was grown, requiring several cultural operations which probably reduced nematode survival.

The density dependence of survivorship is exhibited by the magnitude of the (b) value. The (b) value was higher in Kern County than in Orange County, indicating a greater density effect on survival. This may substantiate the biological antagonist hypothesis, since the antagonists would become more prevalent in areas with higher population densities and long-standing infestations, such as the Orange County location. Survivorship was intermediate at the Tulare County 1 location at low Pi, but the (b) values were high, indicating greater density dependence. Here, yet another interpretation is possible. The Tulare County 1 field is in a rotation of cotton and cowpeas. The cowpea variety planted is a poor host of the cotton race of *M. incognita*, and population increase occurs only at low Pis. At higher Pis, the overwintering population was produced at high competitive stress and may have had low levels of food reserves, resulting in reduced survivorship.

The lack of fit of the Seinhorst yield model (13) to seasonal population multiplication rates is interesting. The model is essentially a negative exponential relationship with nontransformed Pi values, as opposed to the multiplication rate model proposed here with ln Pi values ($Pi^{-b} = e^{-b \ln Pi}$). The underlying rationale of the Seinhorst model is that it reflects growth relative to resource availability. However, the rate of population growth is apparently more strongly influenced by increasing nematode density than is the rate of plant growth. Empirically, this is reflected by the need to log transform the Pi values to achieve satisfactory fit of the negative exponential form of the multiplication rate model. Both (Z) and (T) values in the Seinhorst model were considerably lower for nematode multiplication data than for yield data. Apparently the plant is able to partition the majority of available resources to its own growth processes and maintenance needs, which is of ultimate benefit to the parasite in prolonging the food source. Despite alteration of the plant physiology, as population densities increase, the nematode apparently receives a progressively smaller proportion of the product than does the plant. Of course, other density-dependent factors may also prevail and contribute to the greater impact of nematode density on multiplication rates than on plant growth. For example, space availability in roots may result in deterioration of infection sites or deleterious accumulation of waste products around individuals. Also, biological antagonists may be favored at higher nematode population densities.

The fit of the negative exponential model to both seasonal nematode multiplication and overwinter survivorship promotes a high level of confidence in this model for projecting expected nematode population development and decline on a field scale. Such models, along with damage functions, can be used for optimizing cropping sequences for nematode management (3,4) by allowing projection of the magnitude and influence of Pi levels in subsequent years and the cumulative loss due to nematodes over a multiple-year cropping sequence.

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