Agriculture, Ecosystems and Environment, 12 (1984/85) 285—299
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

POPULATION ASSESSMENT AND MANAGEMENT STRATEGIES FOR PLANT-PARASITIC NEMATODES[1]

HOWARD FERRIS

Department of Nematology, University of California, Riverside, CA 92521 (U.S.A.)

(Accepted for publication 4 September 1984)

ABSTRACT

Ferris, H., 1985. Population assessment and management strategies for plant-parasitic nematodes. *Agric. Ecosystems Environ.*, 12: 285—299.

Nematodes exhibit aggregative tendencies mediated by food distribution, feeding and reproductive behavior, and survival strategies. Determination of dispersion indices based on population mean and variance allows estimation of the sampling intensity required for prescribed population assessment precision. Critical point models of expected yield loss relative to pre-plant population density allow management decisions on a single season basis. Selection of optimal cropping sequence across several seasons requires further information on the expected multiplication rate of the population on a crop, and the overwinter survivorship of the population. Three critical point models then formulate the basis for a linear programming approach to cropping sequence selection, while allowing flexibility of management through biological and economic monitoring annually.

INTRODUCTION

In recent years, nematologists have earned the reputation of being the people who are giving pesticides a bad name. This reputation is somewhat justified in that chemicals introduced into the soil have slow degradation rates, reducing the buffer or sink capacity of soil. The problem is exacerbated by chemicals used as nematicides also appearing in residual amounts in stored food products after space fumigation. The net result is that the available arsenal of management tools for nematodes has diminished and, further, that the cost of the remaining management options is increasing. A few years ago it was possible to pre-plant treat a field with nematicide at a cost of $100(U.S.)/ha. The current cost would be in the region of $300(U.S.)/ha. The era of applying a nematicide treatment for insurance purposes is over; there is a need for a rational basis for nematode management decisions.

[1]This paper is a compilation of two papers presented at the 4th International Congress of Plant Pathology: (1) Crop losses caused by nematodes — concepts and approaches. (2) Nematode density and distribution relative to crop yield.

0167-8809/85/$03.30

Another consequence of the reduction in the number of nematicides is an increased interest in cultural controls and in the development of resistant varieties of agricultural crops. Cultural management of nematodes has often received merely lip service, and resistant varieties of processing tomatoes have been developed in California only within the last 3 years.

MODELS AND RATIONALE

The damage function

The basis for a rational approach to management decisions for nematodes lies in the notion that, as with most pests, there is some relationship between the numbers of the pest organisms and the yield or value of the crop (Seinhorst, 1965; Oostenbrink, 1966; Ferris, 1978; Ferris, 1982; Duncan and Ferris, 1983). For nematodes, it is convenient to use a critical point model of yield or crop values relative to pre-plant population densities (Fig. 1). The critical point models are of practical significance in that the management options to which they are to be applied are pre-plant decisions. It would theoretically be possible to make a more precise prediction of expected crop loss based on a multiple point model with more intensive assessment of the biological situation during the crop production period, or even a simulation model using input of either real time or historical weather data. However, these may be of less value in an applied sense. Also supporting the use of critical point pre-plant models is that the nematode population which is affecting the crop is present in the soil prior to planting. In other words, the timing is predictable. Further, the life cycle of the nematode is not explosive, only about three generations may be experienced during a single crop season.

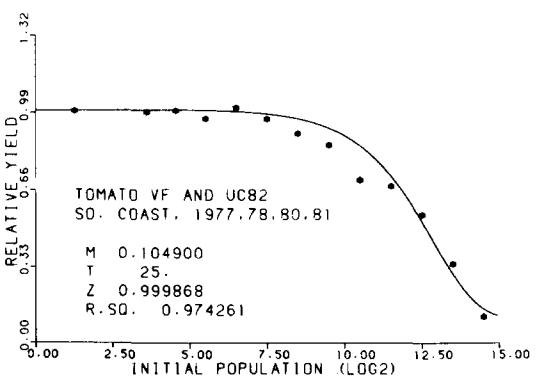

Fig. 1. The relationship between tomato yield and pre-plant population density (eggs and juveniles per 1000 g soil) of *Meloidogyne incognita* on a loamy sand in Orange County, California. The graph represents averages over a 4-year period. Data are described by the model $y = m(1-m)z^{P-T}$ (Seinhorst, 1965) where y = relative yield, m = minimum yield, T = tolerance limit, z is a constant reflecting nematode damage, and P is the initial population density.

Nematode distribution

To make use of critical point models, however, we need to deal with the reality of biological distributions (Fig. 2). In one study (Goodell and Ferris, 1980), distribution of the genus *Helicotylenchus* was highly correlated with fine-textured soil, while that of *Meloidogyne* was more general in a 7-ha field (Fig. 2). If the perceived nematode problem for the crop was *Helicotylenchus*, the appropriate approach would be stratification of the field to determine the population density adequately. The variability in these distribution patterns is initially intimidating, but it is important to reflect that the yield of a crop is the sum of individual plant yields across the total plant population which constitutes that crop. The crop is subjected to the same non-uniform nematode distribution which is being sampled and assessed.

Consider the microdistributional attributes of a nematode population, particularly relative to its life history and feeding strategies. The root-knot nematode, a sedentary endoparasite, deposits eggs in masses resulting in intense aggregation. An ectoparasitic nematode invests some of its assimilated energy into movement, reducing the amount available for production of offspring. Further, since eggs are deposited individually as the nematode moves through the soil, a somewhat less aggregated distribution results. However, nematode microdistribution is primarily mediated by the distribu-

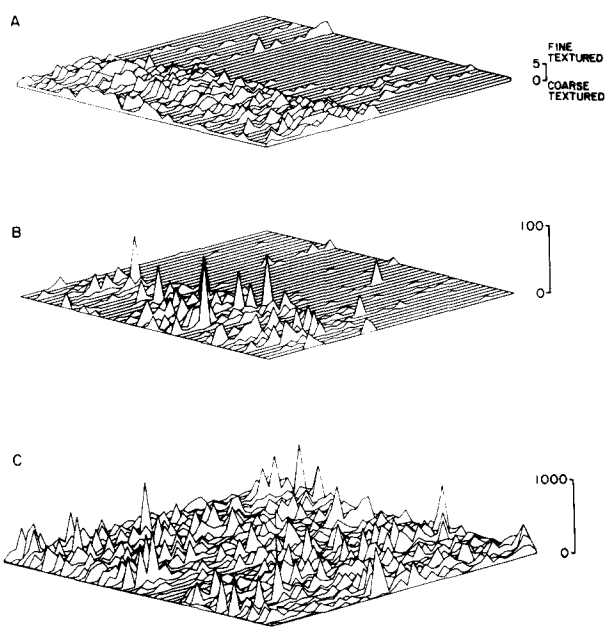

Fig. 2. Three-dimensional projection of population-density distribution in 200 g of soil relative to edaphic conditions: (A) soil texture; (B) *Helicotylenchus digonicus*; (C) *Meloidogyne arenaria*. Field area 7 ha, host crop alfalfa (from Goodell and Ferris, 1980).

tion of its food sources; for plant-parasitic nematodes, the spacing and morphology of the plant root system is a primary determinant.

In a study of the temporal aspects of the distribution and density of nematodes in the root system of a grape vine (Ferris and McKenry, 1974) the nematode distribution was most consistent in the vine row and variable between rows as a result of cultural practices and availability of food sources (Fig. 3). The soil-inhabiting component of the population was at greatest numbers during the autumn and winter, and moved into the root system during the summer as the nematode passed through its life cycle. The timing of a nematode population assessment would have to consider the phenology of the nematode and crop interaction. Similarly, the position at which the sample was taken for population assessment should be such as to minimize variability in the sampling process.

The result of these biological and edaphic sources of variability is an aggregated distribution (Goodell and Ferris, 1980). Single cores of soil taken from a field, will have a high frequency of zero or low numbers of nematodes in them. A few of the samples will have extremely high numbers

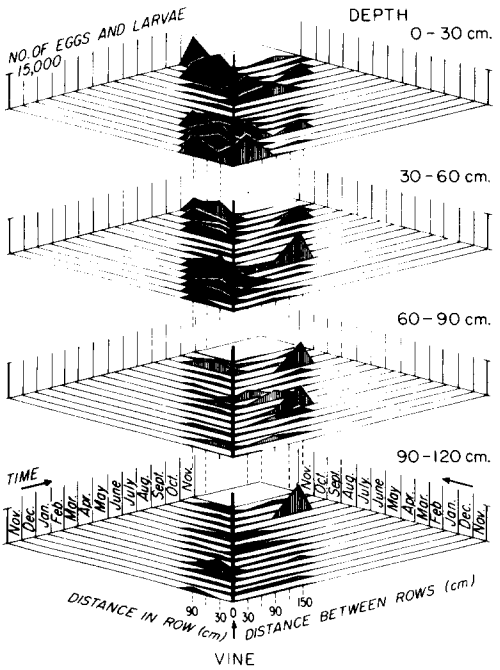

Fig. 3. Spatial distribution of *Meloidogyne* spp. on grapevine roots from November 1972 to November 1973. Each plane represents a 30-cm depth interval from the soil surface. Points plotted are the average of the number of nematodes in 500 cm^3 of soil from the upper and lower 15 cm of each depth interval. The solid black line represents the position of the vine, points to the left are samples taken in the row, and points to the right are samples taken between rows. The closest set of axes is the first sampling date, and the furthest set is the last sampling date.

of nematodes. Such distributions are frequently described by the negative binomial. Again, it is important to remember that the crop is also growing in the face of this aggregated distribution pattern. The nematode population assessment problem is one of magnitude and proportion. The Society of Nematologists and various other sources (Barker and Campbell, 1981; Ferris et al., 1981) recommend that one sample of 12—20 soil cores be used to represent a 2-ha section of otherwise uniform field. In practice the area of field sampled may be somewhat larger; often around 4 ha or more. It is important to remember that sampling costs money and the amount of money to be invested in this process should be relative to the information expected from it. In California, the average cost of a soil sample for assessment of a nematode population is currently about $20 (U.S.) through commercial laboratories. One sample of 12—20 cores for 2 ha of field represents about 1 two-millionth of that field sampled, providing a perception of the expected population assessment precision given the distribution pattern.

Sampling tools used for nematode population assessment are generally core samplers or augers. There is considerable potential for improvement of this technology and for mechanization. Perhaps the problem has not been brought before the engineering community with sufficient emphasis.

Sampling intensity and assessment precision

The relationship between precision and intensity in assessing populations of plant parasitic nematodes is described by

$$n = (t_\alpha/d)^2 \frac{s^2}{\bar{x}^2} \qquad \text{(i)}$$

This general relationship indicates that the number of samples (n) required to measure a population with specified precision (d) is a function of the mean ($\bar{x}$) and variance (s^2) of that population. It is also a function of a probability parameter (the standard normal variate z, or its t approximation) (Karandinos, 1976; Wilson and Room, 1982). The precision parameter is expressed as the acceptable proportional range of the population assessment. If it is required to measure the population within 10% of its true value, $d = 0.1$. If d has a value of 0.1, its component contribution to the sampling intensity is 100 (i.e., $1/d^2 = 100$). In other words, precision is costly in terms of sampling intensity (Ferris, 1984).

A problem with projecting the required sampling intensity for a specific field situation from eqn. (i) is that the variables we are attempting to measure are components of the equation. Both the population mean and variance are determinants of required sampling intensity. There are too many unknowns for use of the equation in its present state. Some of these may be reduced if there is a predictable biological relationship between them. Such a relationship between the variance and mean of the population is conceivable, based upon aspects of the biology. The population distribution can be described by the negative binomial (Goodell and Ferris, 1980;

Barker and Campbell, 1981). The relationship between variance and mean in a population described by this distribution (Karandinos, 1976) is

$$s^2 = \bar{x} + \bar{x}^2/k \qquad \text{(ii)}$$

The k-value, or index of dispersion of the negative binomial distribution and presumably a biologically descriptive parameter, should allow prediction of the variance. However, from eqn. (ii), $k = \bar{x}^2/(s^2 - \bar{x})$, the k-value is dependent upon the magnitude of the nematode population to be measured. Thus, it is probable that the k-value will vary through time with the population. It may only be valuable for predicting the variance if the expected change in the k-value through time is known.

The relationship between variance and mean can also be described by Taylor's power function ($s^2 = a\bar{x}^b$) (Taylor, 1961; Taylor, 1971; Taylor et al., 1978; Barker and Campbell, 1981). The parameters a and b are descriptive of the exponential relationship between variance and mean, such that b can be considered an aggregation parameter and a, according to Taylor, a function of sample size. If we solve this equation for b ($b = (\ln s^2 - \ln a)/\ln \bar{x}$), the dispersion is not a direct function of the mean, but a function of the log of the mean. This may make it less sensitive than the k-value of the negative binomial to population change. However, this logic can be misleading since b is an exponent in the variance to mean relationship, and the relationship may be extremely sensitive to small changes in the exponent. Solving the variance to mean relationship for a, $a = s^2/\bar{x}^b$, might indicate an influence of population size on the a value.

To make use of any of the descriptions of the variance to mean relationship, we need information on their stability, relative to time and to sample unit size, for individual nematode species. The magnitude of the parameters of Taylor's power function can be determined by log—log transformation of variance and mean data and using linear regression to determine intercept (log a), and slope (b-value). We find the expected exponential relationship between variance and mean with sample data from small plot studies (Fig. 4) and linearizing the relationship provides an a-value estimate of 0.04 and b-value of 2.2 for *Meloidogyne incognita.* To explore the stability of these parameters, we undertook an intensive sampling study in a field near Bakersfield, California, which was coming out of a cowpea crop in September, 1982. Population distributions were followed through a fallow period during the winter, and through a cotton crop in 1983. The strategy was to establish a 25 × 25 grid pattern of the field, so that a single soil core was removed at each grid intersection. Grid intersection points were 6.7 m apart. The field was sampled at approximately monthly intervals in the same pattern with the grid placed so that repeated sampling sites were within 0.5 m of each other. Nematode species identification and population counts were made for individual soil cores.

Computer software was developed to remove and arrange cores in a specified pattern from the data base to determine the variance and mean associated with repeated samples of specified size. If variance and mean

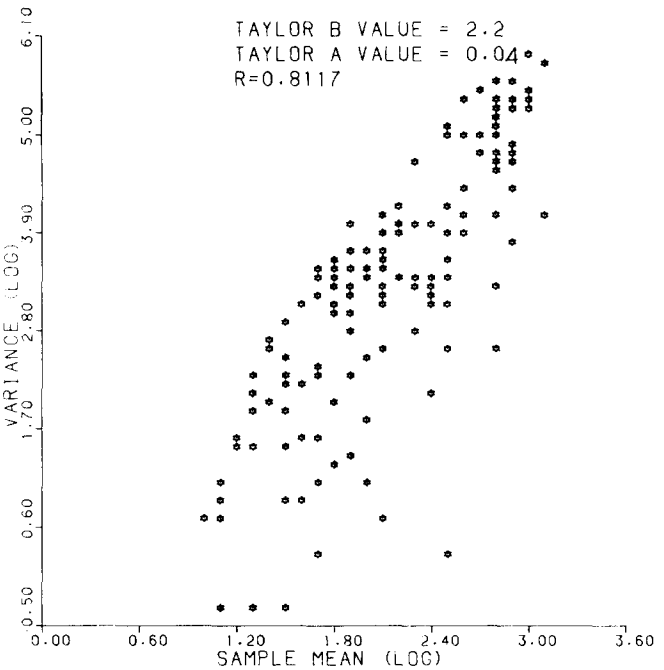

Fig. 4. The relationship of log variance to log mean of *Meloidogyne incognita* population densities for 1 kg soil samples from 25-m^2 field plots. Mean and variance calculations based on two samples of 12 cores each.

relationships are based upon two samples of a single core each, and the procedure is repeated 100 times, a wide range of estimates of variance and mean are obtained. As sample unit size is increased, repeated estimates of variance and mean represent a narrower range. A linear regression through a data set distributed over a wide range provides reliable, repeatable estimates of the y-axis intercept (log a in Taylor's power function). Confidence in the estimation of the a-value diminishes as sample unit size increases and greater extrapolation is necessary to the y-axis. At large sample unit sizes, the confidence in the slope drawn through the tightly clumped repeated estimates of mean and variance diminishes. In plotting the predicted a-value against sample unit size (Fig. 5), the two are related by a strong exponential relationship ($r^2 = 0.99$) up to about six cores, becoming more variable when data from higher sample unit sizes are included. Extrapolation of the relationship to greater sample unit sizes is appropriate and is compatible with the mean of repeated estimates of the a-value at these levels.

The graphs of the relationship between a-value and sample unit size for each sampling period fall into two main groups (Fig. 5). The lower group is for those sample dates through the overwintering period and prior to cotton planting. These samples were removed from fallow ground with no regard to previous or future crop spacing. The higher group of a-value predictors are for those samples taken after planting the cotton crop, when

cores were removed from the root zone of a cotton plant. Presumably the attractiveness or aggregation pattern associated with nematodes around the cotton roots affected the distribution. The relationship for the final sample period is omitted from these data since it showed greater variability and higher population densities. For applied purposes, the mean a-value relative to sample unit size was determined for each of the two groups of samples. Thus, for *M. incognita* in this single field situation an average through the lower set of curves in Fig. 5 projects the expected a-value relative to sample unit size during the overwintering period and an average through the upper set represents the expected a-value relative to sample unit size during the cotton crop season. Given these estimates of a, it is possible to estimate the b-value better by linear regression, forcing the line through log a for data sets from different sampling periods. The b-value rapidly stabilized as sample unit size increased whereas the k-value of the negative binomial was more sensitive to sample unit size.

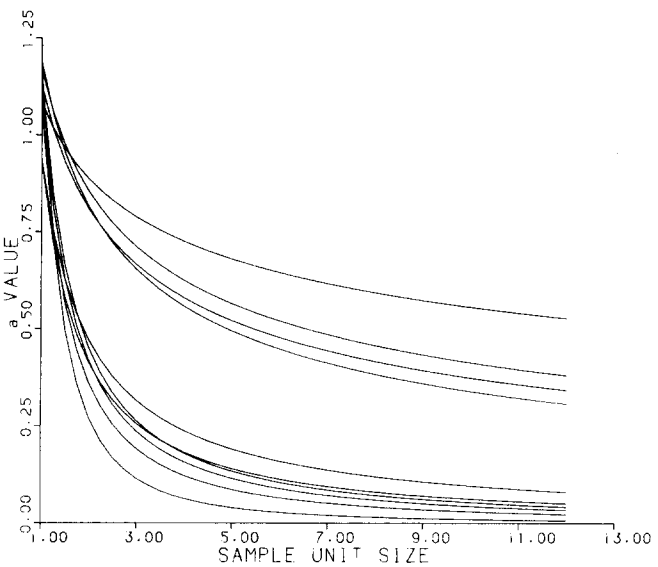

Fig. 5. Relationship of Taylor a-value to sample unit size (number of cores) for *Meloidogyne incognita*. Graph represents 10 sampling periods spanning a single year.

With the removal of possible artefact from the assessment of a- and b-values for different data sets, the stability of the b-value of the exponential relationship and the k-value of the negative binomial over time can be determined (Fig. 6). The population density in the field reduced following the final disking of the cowpea crop. This was followed by a linear decline of the population through the fallow overwintering period. The time scale is expressed on a physiological time (degree-day (DD)) basis, reflective of the fact that metabolic rates affecting survival and population change are temperature-dependent. After planting the cotton crop, the population in

the soil remained at a low level through the first generation and then increased to the end of the growing season, approximately 4100 DD from the start of the experiment. The k-value of the negative binomial exhibited its expected dependence upon population density, dropping following the destruction of the cowpea crop, fairly constant through variable during the winter period, appearing to drop in the early part of the cotton crop, and then increasing again with the population increase at the end of the cotton crop. The b-value of the exponential relationship, however, stayed constant although different for the overwinter period and for the subsequent crop period.

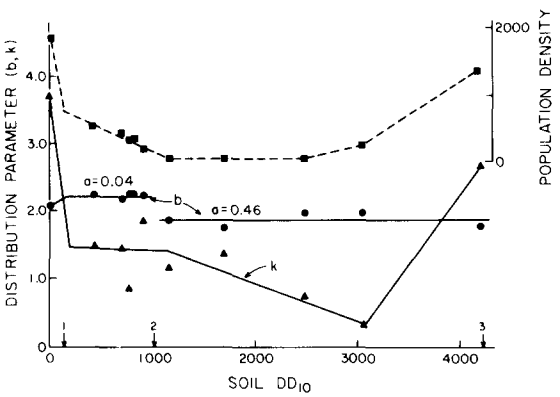

Fig. 6. Variation through time (1 year) of population density (■) of *Meloidogyne incognita* and distribution parameters (▲ = negative binomial k-value; (●) = a and b of Taylor's power function). Each measurement based on 100 samples of 12 soil cores.

The stability of the Taylor constants for distribution is encouraging and promotes their use for variance to mean consideration in sampling intensity precision relationships. Again, the apparent stability of the b-value may be misleading since the variance to mean relationship is very sensitive to small variations in this value.

Consider again the relationship between sampling precision and sampling intensity (eqn. i), and the contribution of the various components of this relationship upon the sampling intensity prediction. The variance to mean relationship ($s^2/\bar{x}^2$) component varies in our data in the range from 1 to about 4. The t_α value has a minimum of 1.96, is dependent upon sampling intensity, but may have a value of approximately 2, providing component contribution to the sampling intensity of 4. The precision level (d) however, is a problem in this relationship. A precision requirement for an assessment within 10% of the true mean sets $d = 0.1$, a multiplier component of 100 in the sampling intensity relationship. Barker and Campbell (1981) recommended that for management decisions it would be necessary to measure the population within 5% of its true value. Thus, $d = 0.05$ and the contribution to the sampling intensity is a multiplier of 400! We have used simulation

studies from a population distribution data base (Fig. 7) and determined the influence of number of samples and sample unit size (cores) on the deviation of the population assessment from the true mean (Goodell and Ferris, 1981). A large number of samples of large unit size is necessary to measure the population within 10% of the true mean.

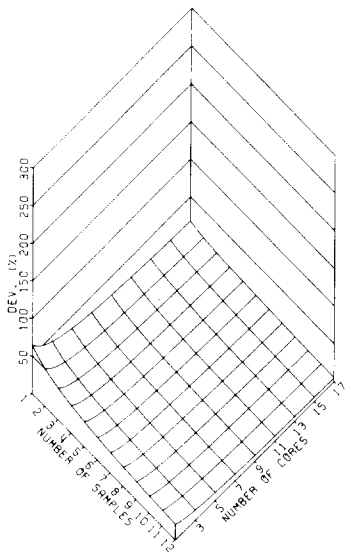

Fig. 7. Deviation of the sample population estimate from the true mean density with increasing number and size of samples. Data set for *Meloidogyne arenaria* in alfalfa. (After Goodell and Ferris, 1980, 1981.)

In an applied sense, we are not interested in measurement of the absolute population density, rather its assessment as an indicator of expected yield or dollar loss. If we wish to apply sufficient sampling intensity to the field to assess the population if it is at the economic threshold values, $\bar{x}$ in eqn. (i) can be considered the economic threshold (Ferris, 1978) for the particular management decision (Fig. 8). If sampling at this intensity reveals that the population is below this economic threshold level, it will have been measured with greater intensity than required, appropriate since we elect not to manage. If the population is above the threshold, we have measured it with less than required precision, but this is of little consequence since it invokes the decision to manage. In fact, we are interested in prediction of the expected crop loss with specified precision (Ferris, 1984).

Since the relationship between crop loss and nematode population density is such that the influence per nematode decreases at higher population densities (Seinhorst, 1965; Oostenbrink, 1966) it is appropriate to consider the relationship between unit change in the crop value and the relative change in the nematode population. A management option costing 20% of the expected crop value would only be applied if the population density of the nematode was greater than the economic threshold density. To make

the decision, it is appropriate to ensure that the crop loss estimate is within a known range (damage interval) of the economic decision value, that is, the break even point between crop loss and cost of management option. Projecting such a damage interval onto the nematode damage function, the projected d-value in the intensity/precision relationship is somewhat greater than the proportion represented by the damage interval (Fig. 8). In Fig. 8, a damage interval of 10% projects a d-value about the economic threshold population of approximately 60%, i.e., $d = 0.6$. Then $(1/d)^2 = 2.8$, a large difference from the 100-fold effect of applying the 10% decision to the population estimate. Population assessment for management decisions is, in this light, a more palatable process (Ferris, 1984).

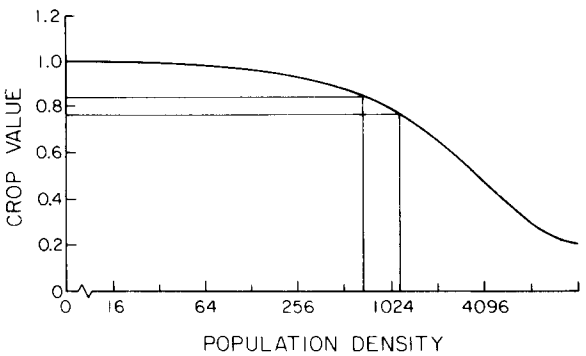

Fig. 8. Determining sampling intensity as a function of management cost and cost value. Projection of an acceptable damage-interval estimate onto the damage function to determine the required precision of the population estimate (Ferris, 1984).

Basing sampling intensity on management cost dictates that sampling intensity varies with the cost of the management option, since each management option will result in a different economic decision value and corresponding economic threshold level. The d-value for nematode population assessment becomes smaller with increased management costs and with increased precision requirements of the damage interval. The impact of a 10% precision requirement for the damage interval reflects a range from less than 1 to about 8 in component contribution to sampling intensity dependent upon the management cost and the form of the damage function (Fig. 9).

A further extrapolation of this approach is consideration of risk. Confidence intervals can be drawn around the damage function with a known probability level. Similarly, the t_α in the intensity/decision relationship dictates the probability level associated with the sampling precision. Since the two probabilities are independent, the probability level associated with the damage interval estimate is a product of both of them. If each has a probability level of 0.8, the probability associated with the damage interval estimate is 0.64. If the user is risk-averse, a higher probability on the damage interval may be required. This could be achieved by selecting a t_α value

with greater probability, which would increase the required sampling intensity. Further, if the required damage interval was reduced to zero, that is absolute precision of the damage estimate, this would dictate a population assessment with absolute precision, i.e., $d = 0$, and consequently, from eqn. (i), an infinite sampling intensity (Fig. 8) (Ferris, 1984).

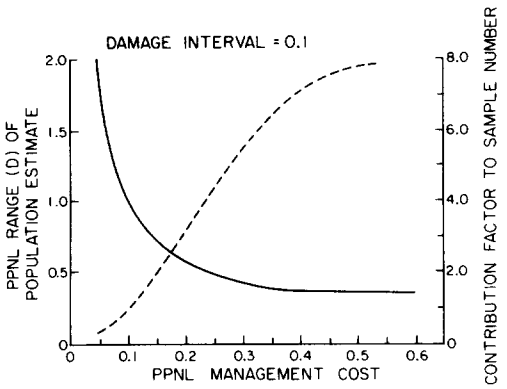

Fig. 9. Influence of management cost on required precision of population estimate if a 10% precision in the damage estimate is required. Dashed line represents component contribution to sampling intensity imposed by the increase in management cost.

Management strategies

Consider now the rationale of nematode management strategies based on critical point models. Assume the management strategy under consideration is rotation to an alternate crop of lesser value which is not damaged by the nematode population (Fig. 10). If the population density in the field is at level $P1$ (Fig. 10), the optimal short-term management decision is to grow the alternate crop. If during the period that the alternate crop is grown, the population in the absence of a host will be reduced to level $P2$, the optimal decision the second year is again to grow the alternate crop. After the third year the optimal decision is to grow the primary crop. This optimization approach may be short-sighted because reversion to the primary crop then provides a food source to the nematode population and may allow it to increase to high levels, exacerbating the problem for subsequent years. A solution yielding higher profits over the whole cropping sequence might have been to grow the alternate crop for two more years, reducing the nematode population to very low levels, before reverting to the primary crop (Ferris, 1978; Ferris, 1981; Duncan and Ferris, 1983).

Multiple crop sequence decisions require not only critical point models of the damage function, but also critical point models of seasonal multiplica-

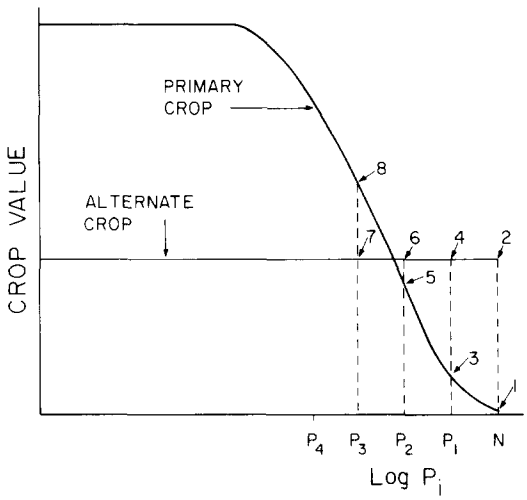

Fig. 10. The relationship between crop value and nematode density for a susceptible and resistant crop, as a basis for crop rotation decisions. Points on the population axis indicate expected population decline with time (Ferris, 1978).

tion rates of nematodes (Duncan and Ferris, 1983; Fig. 11). Data from several years of experiments with tomatoes at the University of California South Coast Field Station in Orange County, California indicate an expected density-dependent relationship between seasonal multiplication rate and initial population density. The maximum multiplication rate is seen at low initial density. At higher population density an equilibrium point may be reached at which the final and initial nematode populations are equal. When seasonal nematode multiplication rates are plotted against the log of the initial population level, a strong negative exponential relationship is revealed. I elect to express the maximum multiplication rate for all nematode densities below the tolerance level, that is the population level of nematodes at which damage to the crop is first measurable, and at which resources must become limiting to the nematode population as well as to the plant.

Critical point models of nematode multiplication exhibit crop- and regionally-specific parameters in preliminary testing. They allow projection of the expected consequences of a management decision on the nematode population (Duncan and Ferris, 1983; Ferris, 1985). Information is also necessary on the overwintering survivorship of the nematode population to determine a pre-plant population density for the subsequent crop, and to allow projections of profits through time (Fig. 12). Surprisingly, the relationship between initial population density and overwintering survivorship is also a negative exponential function (Duncan and Ferris, 1983; Ferris, 1985). In this case, the initial population density is regarded as that population in the soil at the start of the overwintering period. The final population density is the population level at the end of overwintering period, or the

pre-plant density for the subsequent crop. The maximum overwintering survivorship at low initial population densities was 0.2.

There are several possible explanations for the density dependence of survivorship. One is that since the nematodes are surviving with an energy component derived from the parent, the population at high density was produced under high competitive stress, and perhaps has reduced energy reserves. Another possibility is a greater prevalence of parasites and predators at high population densities and consequently greater mortality due to these biological antagonists. We tested this theory by examining overwintering survivorship rates in locations where nematodes had been recently introduced for experimental purposes. In these locations maximum survivorship rates were about 0.4, perhaps supporting the biological antagonism theory, and suggesting strategies for considering the efficacy of biological control of nematodes over longer periods than single cropping seasons. In another location, several cultural events occurred during winter months due to the preparation for an early spring crop. Overwinter survivorship was reduced, presumably pointing to the benefits of cultural or mechanical control of nematode populations.

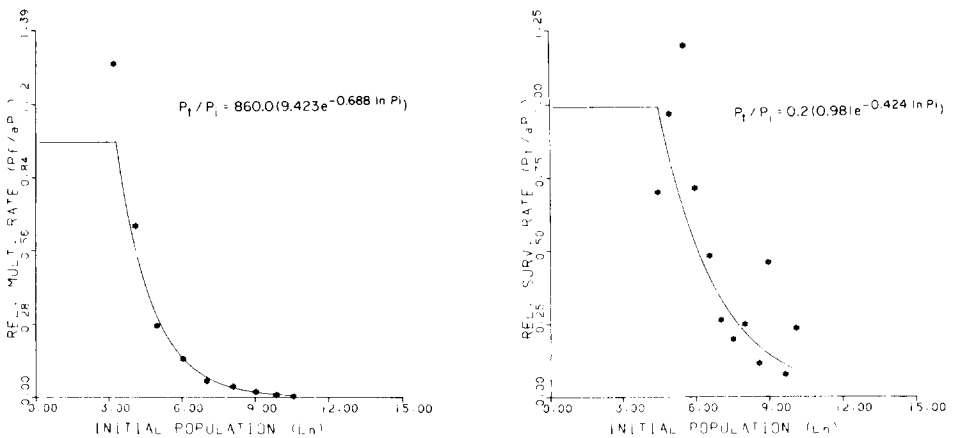

Fig. 11. Relative multiplication rate of *Meloidogyne incognita* in relation to P_i, according to the model: $Pf/Pi = ace^{-b\ln Pi}$. Values for *Meloidogyne incognita* on tomatoes: $a = 860$, $c = 9.4$, $b = 0.688$.

Fig. 12. Overwinter survivorship of *Meloidogyne incognita* in relation to autumn population densities, acoording to the model: $P_f/P_i = ce^{-b\ln Pi}$ constrained by a max value of 0.15 where $c = 0.98$ and $b = 0.424$. Tulare Co., California. In this case, P_i is the population density at the start of the overwintering period, and P_f density at the end.

CONCLUSIONS

The stage is now set for use of critical point models to project expected crop yields and value associated nematode populations through several

growing seasons. Nematodes may be one of the pest groups where multi-season cropping sequence optimization is most readily achieved. The information involved in these critical point models for rational nematode management decisions is readily deliverable through computer networks or through floppy disks on microcomputers. We are on the verge of being able to use current information delivery technology in agriculture to allow a basis for rational management decisions relative to nematode pests in crop production systems.

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