BASIC MODELING STRATEGIES FOR NEMATODE MANAGEMENT

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Models, in any sense of the word, are simplifications of larger, more complex systems, structures, or events. They promote understanding of the form and function of the system they represent. The model is a formal statement of hypothesis of system function or structure at a specified level of resolution. The hypothesis is usually developed as equations describing the processes and interactions within the system. Such formally stated hypotheses applied to agricultural pests are testable at the field level and can be reevaluated and refined based on field observations. Ultimately, they can be used as a rational basis for management decisions.

Several types of models are in use in integrated pest management. Critical point models predict crop yield, crop loss or pest densities from a single observation of the state of the system at a particular time. Multiple-point models also make such predictions, but are based on monitoring the state of the system at a series of times. Such models frequently fall into the category of analytical models since they consist of one or a group of equations for which a closed-form solution is possible. They are often correlative rather than explanatory since they cannot be sufficiently complex to describe biological phenomena realistically.

Simulation models, whose solution is determined by numerical integration techniques, are more complex. These models are generally mechanistically explanatory at a level of resolution compatible with the objectives of the modeling process. Other models of importance in integrated pest management fall into the category of management decision models. They may be extensions of analytical or simulation models. They might, for example, predict the relationship between the intensity of a monitoring or sampling process and the associated precision of the pest-population estimate.

Integrated pest management is, in practice, effective management of the crop and its associated community. The complexity of this process involves the understanding of how individual pest populations interact with the crop and with each other. Such understanding would allow prediction of repercussions throughout the system resulting from perturbation of one population or of one part of the system. The interaction among the individual populations is integrated essentially by the plant. The effects of this integration from a practical standpoint are reflected in yield and quality of the crop. A plant model is essential to the development of a multiple-pest mechanistic model. However, it may not be necessary for the simplistic analytical models, based on population assessment prior to planting, which are frequently used for nematode management.

TYPES OF MODELS

Descriptors of Spatial Distribution

Like many organisms, plant-parasitic nematodes generally exhibit an aggregated distribution pattern reflective of such aspects of their biology and ecology as feeding habits, food sources, and reproductive patterns (Fig. 1). Frequently, the distribution pattern is adequately described by the negative binomial model, a function of the current population mean and its index of dispersion (k) (5). Since the index of dispersion is a function of the mean and vari-

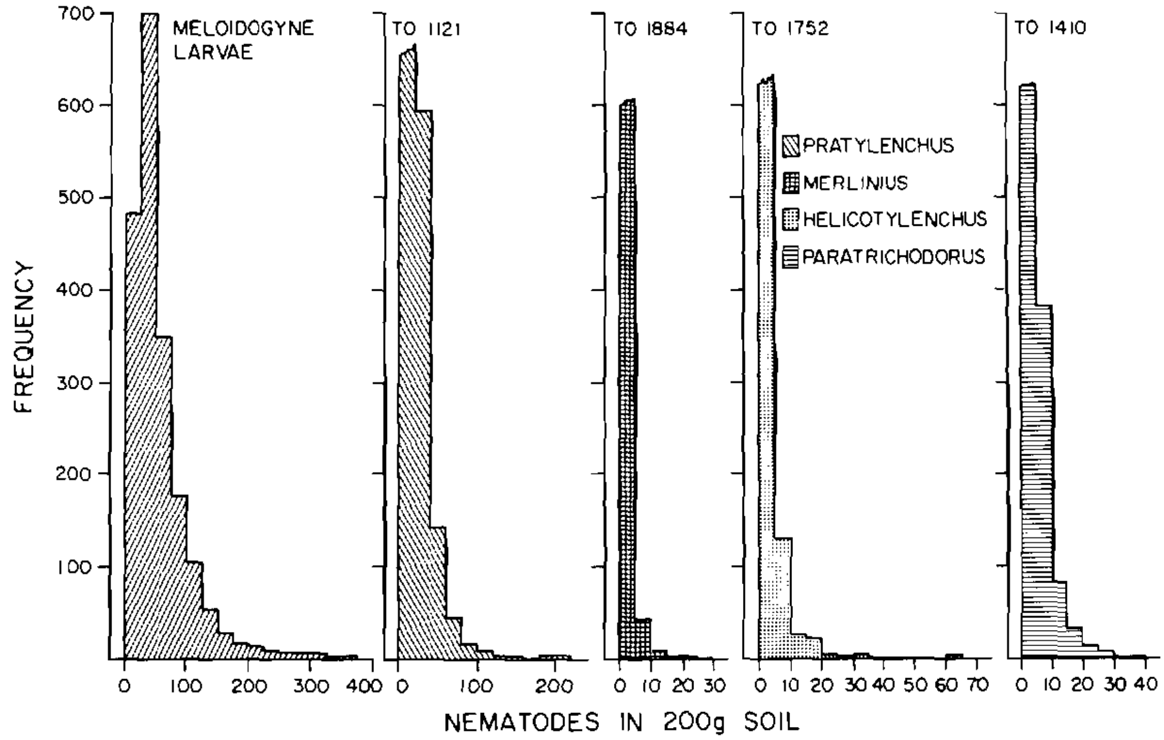

Fig. 1. Frequency distribution of nematode densities in soil samples from an alfalfa field. [from Goodell and Ferris (15)].

ance, it varies with time and population density. Means ($\bar{x}$) and variances (s^2) of sample counts can be empirically related by a power function such that $s^2 = a\bar{x}^b$, where b is an index of aggregation for the species (29,30). Assuming the stability of such indices, or knowledge of the environmental factors which influence their magnitude, it is possible to calculate the probability of obtaining a specific sample population estimate from a population of known mean and variance (5).

Knowledge of population mean and variance relationships allows generation of formulae indicating the number of samples (n) required to measure a population with a certain level of precision, given a specific population size and distributional condition (20,28). The general form of such relationships ($n = C^2(s^2/\bar{x}^2)$), where C is a probability constant provided by the standard normal deviate (Z or its t estimator) and the acceptable proportional deviation (d) from the true mean, such that $C = t/d$. The relationship can be used for determining required sampling intensity for crop management decisions of various costs (10), or the probable deviation associated with the population mean estimate given a specific sampling intensity (Fig. 2).

Spatial descriptors provide the basis for risk assessment associated with population monitoring activities and subsequent strategies in integrated pest management.

Phenology and Population Models

Both analytical and simulation forms of phenology and population models fall into this category. The systems are generally considered to be temperature driven, and the rate determining or limiting constraints include host presence, host quality, moisture availability and age-specific responses of the organisms.

Perhaps the simplest of these mechanistic models applicable to pest management are phenology models, which predict the timing of developmental events. Such events might include the appearance of various life stages of pest populations, or stages in the growth cycle of a crop relative to prevailing environmental conditions. Models at this level are useful for timing crop protection activities, or for the timing of monitoring and assessment efforts for the detection of pest species. If the expected age structure of the population is known relative to some starting point such as planting

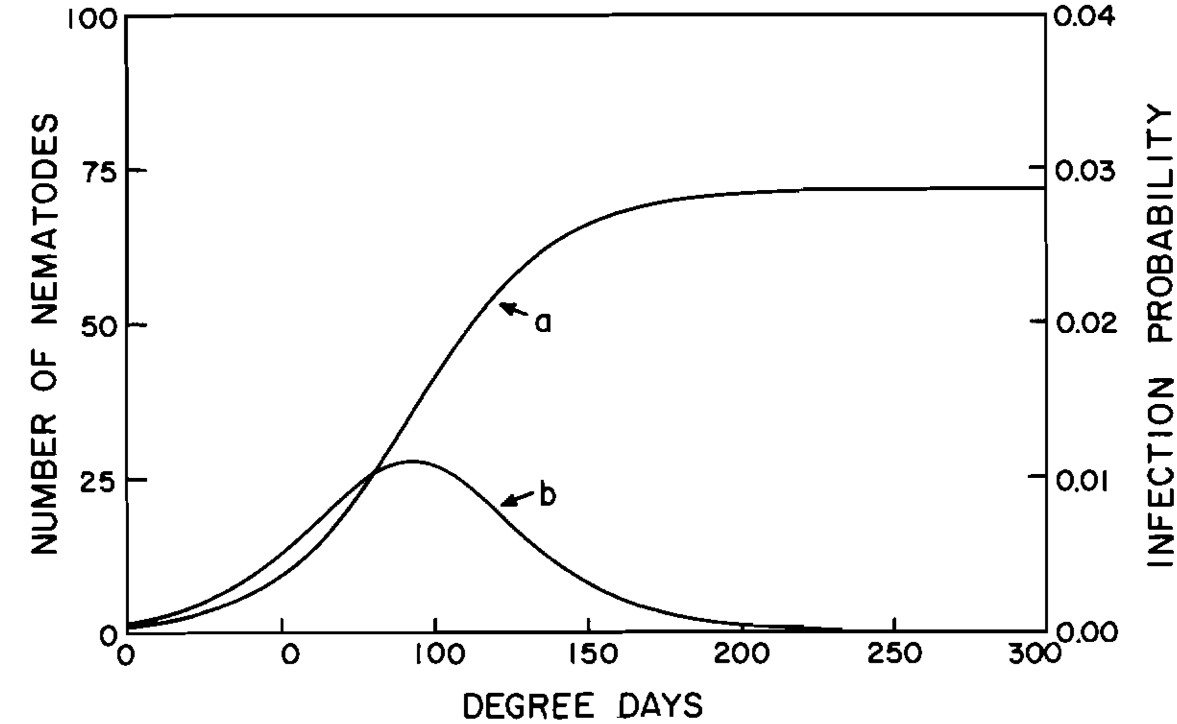

Fig. 3. Cumulative number of nematodes (a) and probability of penetration (b) in the vascular region of grape roots cv. 'French Colombard' relative to length of exposure (DD_{10}) to a single age cohort of *Meloidogyne arenaria* juveniles. [from Ferris et al., (13)].

stage juvenile is able to penetrate different varieties of grape roots, the variance associated with this penetration period, and the probability that penetration will occur have been determined (13). Similarly, the host dependence of the developmental period and its variance (12), and the variability in the fecundity period and rate of egg production/female (14) have been calculated. Survivorship values for each developmental stage have been determined (Table 1). The development of simulation models of this form requires an interactive plant-host model, the appropriate coupling structures for the effects of the nematode on the host supply/demand system (33), and the effects of the physiological stress level on the nematode biology (14) (Fig. 4 & 5).

Yield Loss Models

Damage-function predictions from population densities are critical to management decisions (6,18,34,35). Such models may be of the typical analytical form, either critical or multiple point (2,4,19,27), or they may be simulation models (1,6,7,24). Simulation models generally require a plant model in tandem with the pest models in predicting crop growth or yield loss. They are at a greater level of complexity than the analytical models and tend to have greater variability in their predictiveness. They have the advantage, however, of allowing multiple pest linkages in a biologically rational manner rather than relying on multiple regression approaches only valid for the existing data set.

Utilization of yield loss models forms the basis for economic threshold determinations. The economic threshold for nematodes can be defined as that population of nematodes which will reduce crop value by an amount equivalent to the cost of controlling or managing the nematode population. At another level of resolution, it is that level to which the population must be reduced to maximize the difference between crop value and management costs (8). These determinations usually involve critical-point analytical models; however, similar application can be made of simulation models. Forward predictions in time are necessary, involving projections of expected crop value and projections of regional weather conditions. The threshold determinations provide a rational basis for management decision.

Table 1. Stage-specific development, fecundity, and survivorship data for *Meloidogyne arenaria* on three grape varieties (from 11,12,13,14).

	Nematode life stage						
	Egg	Infective J_2		Parasititic J_3/J_4		Adult	
Variety	$\bar{x}^a$	$\bar{x}^b$	p^c	$\bar{x}^d$	p^e	$\bar{x}^f$	E^g
French Colombard	176 ± 7.5	115 ± 58	0.36	532 ± 102	1.0	580 ± 70	0.81 ± 0.07
Carignane	176 ± 7.5	113 ± 56	0.22	532 ± 90	1.0	660 ± 60	0.98 ± 0.02
Thompson Seedless	176 ± 7.5	73 ± 36	0.11	655 ± 104	1.0	550 ± 60	0.53 ± 0.03

[a] Mean and standard error of egg development period (DD_{10}).
[b] Mean and standard error of probable penetration period (DD_{10}).
[c] Proportional survivorship of penetration under unstressed conditions.
[d] Mean and standard error of development to maturity (DD_{10}).
[e] Proportional survivorship of development period under unstressed conditions.
[f] Mean and standard error of egg production period (DD_{10}).
[g] Mean and standard error of egg production/female/DD_{10}.

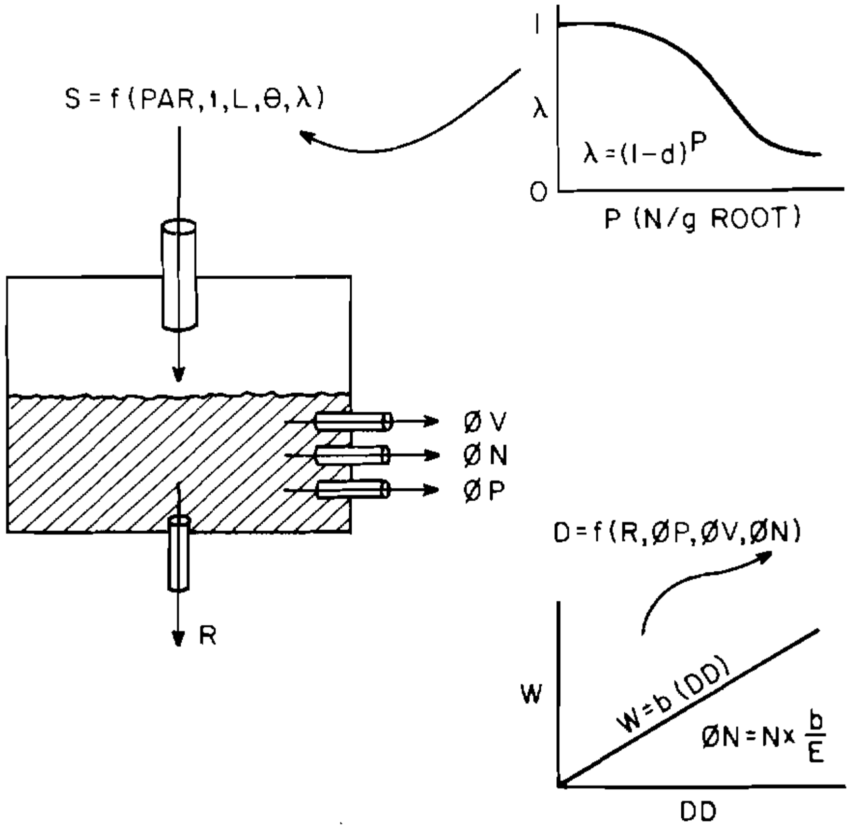

Fig. 4. Coupling structures between plant and nematode based on a metabolic pool concept of plant growth. Supply is a function of PAR, temperature, leaf area, photosynthetic efficiency of current leaf age structure, and physiological efficiency as influenced by current nematode population density. Demand is a function of maintenance respiration and the cost of new tissue formation (vegetative or propagative) including growth, respiration, and nematode demand, as a function of nematode growth rate [adapted from Wang et al. (33) and Ferris et al. (14)].

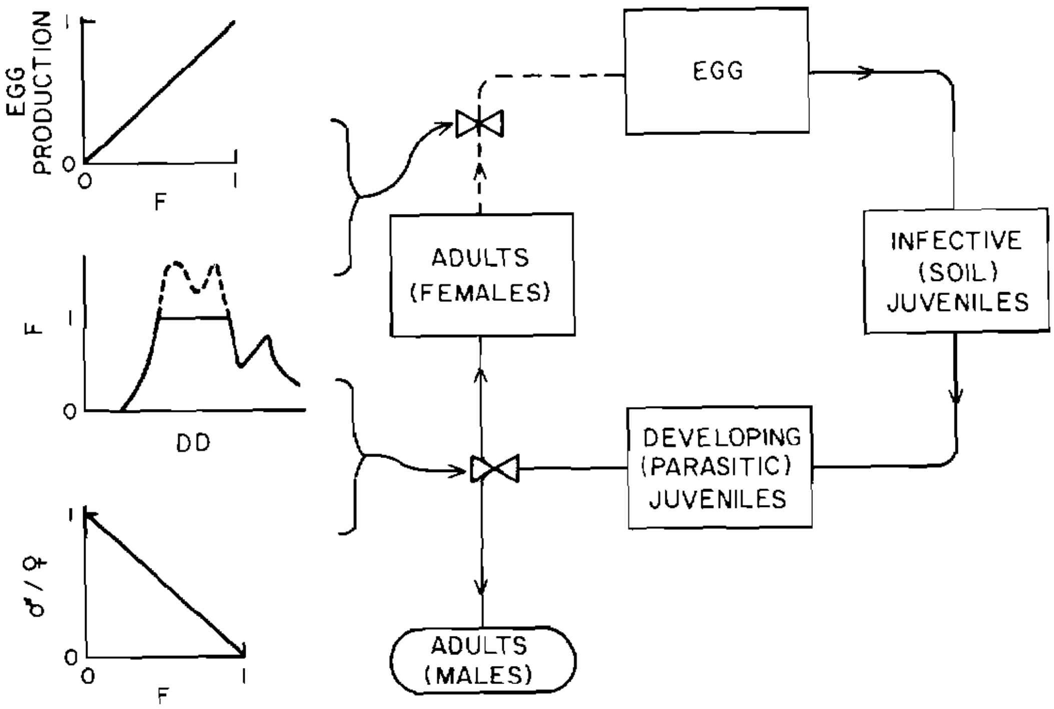

Fig. 5. Coupling structures between plant and nematode. Effect of plant physiological stress (*F*) as influenced by phenology, metabolite demand priorities and physiological stress on nematode population development (sex ratio and egg production rate). [from Ferris et al., (14)].

Management Optimization Models

Models of this type represent the next level of organization. Their accuracy and predictive reliability is constrained by the resolution and error in lower level models on which they are based. They provide a framework for optimization of the management process. Among the simplest forms are management models predicting control efficacy for a particular management approach based upon environmental conditions. Thus, the expected efficacy of a fumigant nematicide is influenced by the soil texture and pore spaces, and soil moisture and temperature, resulting in predictability in the amount of nematicide required to obtain an acceptable level of control (21,22,23). A higher level of organization is to superimpose the control-cost model on the nematode-damage function so that the amount of control to be invested, in order to reduce the nematode population to a point at which the difference between the crop value and cost of control is a maximum, can be determined. This method is an optimization approach to the economic threshold, in fact, the true economic threshold (8,17), but one difficult to achieve with available information due to lack of data on control cost functions (Fig. 6). Similar control-cost functions can be developed for crop-rotation programs where the cost of reducing the nematode population to specified levels is predictable relative to the reduced value obtained by the nonhost crop (3,8,26).

Management and optimization models can be considered in the short and in the long term. In the short term, the returns for single growing seasons may be optimized by reduction of the nematode population to a specific level, but the problem may be exacerbated for subsequent crops (2,3,8). However, data generated for analytical models of population increase during a single growing season on a given host crop (2,3) allow prediction from a preplant population estimate of the expected crop value (or crop loss) and the expected final nematode population. Further, data on nematode overwintering survival (2,16,32) allow prediction of the expected nematode-population densities at the start of the following cropping season. These relationships allow prediction of expected crop yield or value on a series of possible subsequent crops. Calculations of this type generate the possibility of optimizing cropping sequences for nematode management over multiple years (3). Such approaches are particularly appropriate with plant-parasitic nema-

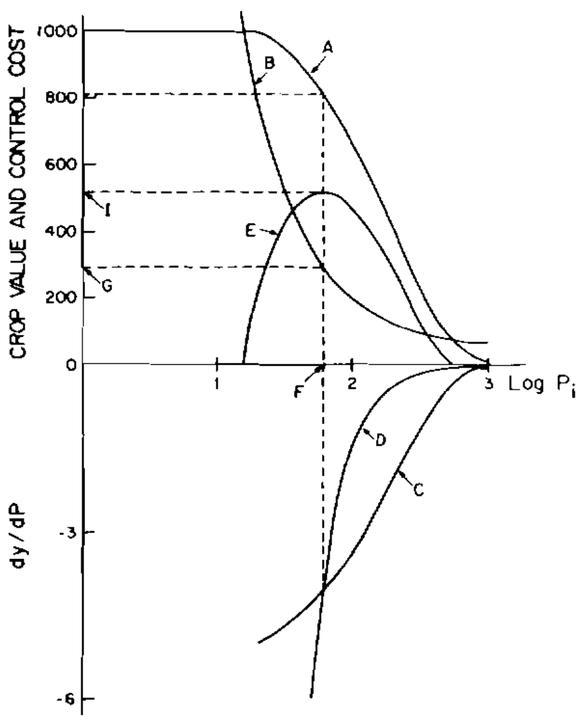

Fig. 6. Determination of the economic threshold by maximizing the difference (curve E) between the nematode damage function (curve A) and the control cost function (curve B). The economic threshold is the population level at which the derivatives of the damage function (curve C) and the control-cost function (curve D) interact. [from Ferris (8)].

todes, and perhaps with other soilborne pathogens, because of relatively slow reproductive and dispersal rates and yield loss predictability from simple analytical models.

The selection of a cropping sequence, of course, involves some forecasting of crop values over a series of years and an expectation that average weather conditions will prevail. However, the commencement of a particular cropping sequence does not lock the user into that program should conditions change over the period for which the predictions were made. The optimal solution may involve reassessment of the system through biological or economic monitoring at the beginning of each growing season and selection of the most profitable route from that point forward. Linear programming techniques are adaptable to this approach.

SUMMARY AND CONCLUSIONS

The status of modeling as a basis for integrated pest management strategies for nematodes is conceptually well advanced. The structures of models of nematode distribution, population phenology and development and those for yield loss due to nematodes have been developed and tested in various crops. Primarily these have been analytical models, simple to develop and generally useful. Attempts at simulation models have been useful in the investigation of nematode and plant systems in demanding clear hypothesis statements and in delineating efficient research approaches. They have not yet been implemented in pest management programs.

Current studies on the required intensity of nematode-population assessment relative to crop value and to the cost of the anticipated management approach (10) indicate that the basic approach of measuring a nematode population at the beginning of a growing season to determine the required management is viable. The resolution required is crop and nematode specific as well as management-cost specific. Further, since the expected damage per nematode decreases with increased nematode densities (3,4,9,19,27), and since fairly large increases in nematode density are required to achieve proportionally much lower increases in crop loss, the required precision of population assessment for management decisions may not be cost-prohibitive (10). With root-knot nematodes, where the population density can frequently be estimated by a gall rating from the previous crop, the use of modeling strategies for prediction in integrated pest management for nematodes is especially promising. The basic utility of simulation models is in hypothesis statement and testing and in the definition of priorities. Critical-point analytical models of crop loss, nematode increase, and overwintering survivorship that have rational and understandable parameters can be developed readily and are easily implemented. The biology, motility and reproductive patterns of nematodes make them an attractive biological system for the implementation of quantitative strategies.

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