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DYNAMIC ACTION THRESHOLDS FOR DISEASES INDUCED BY NEMATODES

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Pest management involves assessment of pest and crop biology at the population level and an understanding of the interaction of organisms at the molecular, cellular, tissue, plant, and population levels. These interactions frequently are sufficiently complex to require simplification through modeling to allow objective management decisions. The disciplinary orientation of pest scientists often results in development of sophisticated pest or disease models, but somewhat more limited plant models. The models are usually restricted to two biological factors (the crop and a pest or disease), and do not consider the many dynamic interactions of the total agroecosystem. A primary objective of practical agriculture is optimization of the transformation of solar energy into a harvestable yield. This objective is accomplished through crop management, one facet of which is the management of pests as appropriate. Any action taken to manage pests has repercussions throughout the system. A tremendous amount of reductionist research has been accomplished in all pest disciplines; however, optimization of yield will require a holistic approach to crop systems to explain and understand the interactions at the population level.

The implicit suggestion of additivity of estimates of individual pest losses in crops is not valid, as frequently discussed (11, 14, 16). One alternative is to use multiple regression techniques, resulting in discounting coefficients for interactions among different pests (18). More analytical solutions include synoptic approaches (22, 27). Because of the interest or expertise of the modeler, a conceptual error frequently confounded in models of crop losses by pest organisms is consideration of the pest as the focus of the

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system. The plant is the central feature of the system from an agricultural and production standpoint, and will always be present in this system even though individual pests may be absent.

THE GREAT INTEGRATOR: THE PLANT SYSTEM

It is useful to take a systems-analysis approach to the study of crop loss assessment and the interaction among the biotic and abiotic stress factors which lead to less-than-optimal crop production (9, 21). Stress factors affect crop yield in three general ways: (*a*) by decreasing photosynthetic surface, (*b*) by reducing the efficiency of photosynthesis by physiological disruption of the plant, (*c*) by reducing the amount of photosynthate incorporated into harvestable yield by physiological disruption of the plant, (*d*) by decreasing the efficiency of photosynthesis by competition for light, water, or nutrients, or (*e*) by directly reducing the quantity or quality of the harvestable yield (5). Not all of the interacting biological subsystems coupled with the crop system will be damaging at all times; the phenological state of both systems needs consideration. A leaf spot on senescing leaves may have little effect on fruit production. Although we speak of interactions among stresses in reducing growth, many of these interactions occur indirectly through effects on the plant. A simplistic model is to consider a crop as a supply-demand interaction (25). The plant is a vehicle for the translation of solar energy and nutrients into carbohydrate. It passes through a series of phenological stages during which its priorities for the disposition of the photosynthate change. The first priority for the use of photosynthate is for the maintenance and respiration of existing biomass. A second priority may be the production of reproductive structures, flowers and fruit, and a third priority may be the production of vegetative biomass. Priorities vary with the phenological state of the plant. A newly germinated seedling or perennial crop at bud break will have a high priority for the expansion of leaf area to allow the production of more photosynthate. After leaves have expanded to their genetically determined area, the priorities will change to flower and then fruit production. During flower production, the energy demand of the crop for expansion of leaf surface area or fruit production is relatively low. But photosynthesis continues and the photosynthate may be translocated into stems and roots. After maximum canopy size is achieved, leaf senescence commences, so that the rate of photosynthesis or the photosynthetic efficiency of the leaf decreases with time. These changing priorities during crop development dictate the nature of photosynthate supply and demand curves. When demand exceeds supply, as during fruit production, the plant experiences carbohydrate stress (28). Delaying the onset of carbohydrate

stress may increase fruit yield. Pests affect the supply and demand functions of the plant through four of the major activities described; they further influence yield by direct destruction of product (5).

MICROECONOMIC CONSIDERATIONS IN CROP MANAGEMENT

The economic threshold concept is a valid, if complex, criterion on which to base pest management decisions. In its simplest form, it could be considered as the pest organism population density or disease level at which the cost of controlling the pests is equal to the value of the damage done by those pests (3). A major problem with this definition is that control efficiency is seldom, if ever, absolute and there is an implicit assumption that the returns from the crop after the control procedure would be the same as in the absence of pests. A more workable definition for economic threshold is as follows: The disease or pest population level at which the additional profit realized from the control or management procedure is equal to the cost of that management procedure (2). This introduces a further complication, the need for quantification of control efficiency. The extent of control achieved relative to the cost or effort invested is a relatively unexplored area of pest management. The concept can be extended to optimization of pest management decisions. Optimization is achieved when sufficient management is applied so that the difference between the crop value at the new level of the pest and the cost of the management is at a maximum. The optimum level of management varies with the state of the crop system being managed, and with the density of the pest population being managed (3). Much research is needed to provide data bases for optimization in pest management.

The relationship between crop yield and the population density of plant-parasitic nematodes prior to planting can be described by linear regression models (1), or by Seinhorst's (19, 20) explanatory model (5). Consider the model developed by Seinhorst (19):

$$y = m + (1 - m)\, z^{(P - T)} \text{ for } P > T,$$

where y is the relative crop yield on a 0 – 1 scale, m is the minimum relative yield expected at high nematode stress, z is a reflection of the damage potential of the nematode, P is the population density, and T is the tolerance limit below which damage is not seen. The simplest case of the model is for $T = 0$ and $m = 0$; then $y = z^P$. If the nematode population can be reduced by a proportion ø from the level P to P_m at a management cost

C, the crop value V_a at the reduced population level $P_m = (1 - \phi)\ P$ is $V_a = Vz^{(1-\phi)\ P}$ where V is the potential crop value, and the increase in crop value (β) due to the management is $\beta = V\ (z^{(1-\phi)P} - z^{P})$. By definition, the economic threshold for this management approach is the population level at which cost of management equals increase in value: $C = V\ (z^{(1-\phi)P} - z^{P})$; solving the equation for P yields the economic threshold. Solving for the economic threshold is similar, but more cumbersome, for values of m and T greater than zero.

Optimization can be approached by determining the level of management at which the difference between cost and return is maximized (3, 10). Consider a hypothetical control efficiency function in which the control cost is exponentially related to the proportional population reductions:

$$C = e^{k\phi} - 1$$

or, since $\phi = (P - P_m)/P$, $C = e^{k(P - P_m)/P} - 1$, where k is a scaling constant which can be determined by substitution with a known pair of values for ϕ and C. The extent to which a population should be reduced to maximize returns (3) is determined by the intersection of the derivatives of the control cost function:

$$dC/dP_m = -(k/P)e^{k(P - P_m)/P}$$

and the nematode damage function:

$$dV_a/dP_m = V(1 - m)\ln z[z^{(P_m - T)}].$$

DYNAMIC NATURE OF THRESHOLDS

Biological stresses on the crop rarely occur throughout the history of a given crop and their appearance may not be predictable. The presence of some biological stresses may be known from the past history of a field or determined by biological monitoring before the crop is planted. A plant-parasitic nematode community in the soil constitutes such a predictable stress factor. However, prediction of the degree of stress should be holistic and include consideration of the functional effect of any environmental conditions. The biological damage function in Seinhorst's model (19) is described by three parameters: T, m, and z. The influence of the environment on these parameters determines the shape and position of the damage function on independent axis (nematode population density), and represents an integral of the many interactions within the system as a whole.

The predictive value of the model lies in the fact that most nematode-management decisions, such as chemical soil treatment, crop rotation sequence, and choice of variety, must be made before planting. The ability to base the decision on an estimate of the size of the nematode population prior to planting the crop is thus a distinct advantage. The crop yield may be influenced by subsequent immigration of another pest or disease population; however, the nematode damage relationship at least allows a rational preplant decision based on the existence and magnitude of the community. The interaction between nematode and plant growth is influenced by (*a*) the nature and age structure of the nematode community, (*b*) the effect of the physiographic and soil textural conditions, and (*c*) temperature conditions as influenced by location and planting date, on the various members of the nematode community (6, 17, 23, 24). The relationship is further a function of the crop type and variety and its susceptibility or tolerance to the individual populations of the nematode community. All these factors affect both the crop and nematode systems, and consequently their interactions.

A problem arises in attempting to model the relationship between expected crop yield and nematode population densities in perennial crops. The growth of the crop during the current year reflects not only an integral of the biological and environmental stresses currently upon the crop, but also the historical stresses (7). Since these may vary from plant to plant in the orchard, plantation, or forest stand, yields may be extremely variable and relationships unreliable. Considering the simplistic crop model, during periods of the year when photosynthesis is occurring rapidly and demand of the crop is relatively low, the excess of supply over demand may be channeled into roots or stems. This material may not be structurally incorporated into the plant but may instead form food reserves to be remobilized during subsequent periods of high demand, such as fruit production. Similarly, after harvest of fruits, the demand of metabolic maintenance of the harvested biomass is removed, and if the leaves are not totally senesced, supply again exceeds demand. At the same time there is a mobilization and downward translocation of the remaining metabolites in the leaves before they are shed. This material is stored in the roots and stems and becomes a supply of energy and substance for the early vegetative growth of the subsequent season, before canopy expansion is great enough to supply the needs of the plant.

Current growth is a function of the energy reserve from the previous year's growth and the current stress of supply over demand. Embodied in this concept are the size and vigor of the plant as affected by past history. Nematode parasitism of the root system will be reflected in the current growth in that it is likely to decrease physiological efficiency of the translation of solar energy into carbohydrates. However, parasitism of storage

roots may have less effect on physiological efficiency than parasitism of feeder roots involved in uptake of water and nutrients if the nematodes disrupt translocation. Nematodes that merely withdraw cell contents may be more detrimental when parasitizing storage tissues. A critical predictive model incorporating threshold concepts may involve the energy flow through the crop system during the previous year. The importance of a plant model is evident.

Damage functions are usually developed for the relationship between a single nematode population and a plant (19, 20). This relationship is influenced by soil texture and physiographic region (1, 4, 5, 17, 24), and when measured over a range of conditions, parameters of the damage function for specific field conditions may be estimated by interpolation (4, 5). Such interpolations are fairly intuitive; however, they do not account for the multispecific nature of nematode communities, or for differing environmental influences on the members of these communities. The pathogenicity of individual species of plant-parasitic nematodes is a function of their mode of parasitism, favorability of the environmental conditions to the nematode and the plant, and the tolerance or resistance of the plant cultivar. It may be possible to generalize species-specific nematode damage functions by weighting numbers of nematodes of different species in a community relative to their pathogenic equivalence to the species for which the damage function was developed (4, 5). These estimates of pathogenic equivalence are refined by further weighting relative to the favorability of environmental conditions to the individual species (5, 6). All the above factors determine characteristics of the nematode community that warrant consideration in economic threshold decisions. The dynamic nature of such thresholds is evident, both within and between localities. The models developed by the weighting methods described may be lacking in interaction terms and coefficients; nevertheless, they do describe the biology reasonably well. An alternative would be the use of multiple regression and synoptic approaches (22, 27), which might result in both correlative and explanatory models but which would delay implementation of threshold estimates by requiring considerable experimentation.

Considerable data are available on the efficiency of nematode control relative to environmental conditions (15, 26). Empirical tests are made to determine the amount of control achieved with different amounts of pesticides. Frequently, however, recommendations for field use of pesticides are based on maximum control, without regard to the cost. Embodied in these experiments, however, is the information for developing control-efficiency curves relative to the amount of control applied. As the cost of management alternatives increases, management-cost curves become of greater signifi-

cance. Information exists on the decline rate of plant-parasitic nematode populations on nonhosts or under unfavorable conditions—either natural or induced (17). It allows prediction of the cost of reducing nematode populations to various levels under different environmental conditions—an important component of the economic threshold consideration as defined.

ASSESSMENT OF PEST POPULATION AND CROP LOSS

The use of economic threshold concepts assumes that the amount of loss induced by a given pest population can be quantified. This involves knowledge or estimation of a reference yield which is obtainable in a given field in the absence of pests. Zadoks (28) and Zadoks & Schein (29) discussed the problem of reference yield and defined several alternatives. The "theoretical yield" represents the genetic potential of the crop but is probably unattainable with the constraints of current technology. Below this is an "attainable yield" which could be achieved in the absence of biotic and abiotic stresses. The "actual yield" will be obtained with the current level of pest stress, and the "economic yield" could be obtained under the current level of pest stress if current pest management strategy is applied. This recognizes that control efficiency is not absolute. Attainable yield encompasses attributes of the grower's expertise, as well as the physical characteristics of the field. Consequently, the grower's experience is probably the most useful basis for estimating attainable yield. A less satisfactory alternative is to use an average yield for unstressed crops in the same geographic location.

Many techniques have been discussed and documented for crop loss assessment and for measurement of the influence of pest organisms on crop losses (12). There is an increasing awareness and consideration of the interaction among pests, and the need to deal with such interactions quantitatively. Synoptic approaches involving principal components analysis and multivariate statistics are useful (22, 27). The systems approach previously discussed, with consideration of the plant or crop as the integrator, addresses the same problem.

If assessment of amount of disease or pest population density and amount of crop damage is a necessary basis for pest management decisions, then the cost of such measurement must be included as part of the management cost. It may be that the assessment necessary for the use of economic thresholds is prohibitively expensive. It is, of course, unrealistic to determine pest or pathogen populations in the field by counting and measuring every plant and pest in the field. A compromise is achieved through sampling. There

is a great need for information on the relative precision of sampling procedures and of their cost efficiency (8). Inability to adequately measure the amount of disease or pest population density may be a limiting factor in using crop and disease loss estimates as a basis for pest management.

THE MANAGEMENT DECISION PROCESS

There is great potential for application of computerized systems for manipulating data files and storing information in the development and use of dynamic action thresholds for diseases induced by nematodes (4). A tremendous amount of information is already available on the susceptibility or tolerance of various cultivars of crops to different nematode species. All this information can be digitized for ready access through computer terminals. Data gaps in the information can be estimated at full tolerance or full resistance, dependent upon the general trend within that crop species. Similarly, there is considerable information available on environmental influences on various nematode species; these data can be used for weighting their population count for use in damage-function models. This information can also be digitized for ready access. A further body of information exists on the efficiency and cost of various management strategies and tactics.

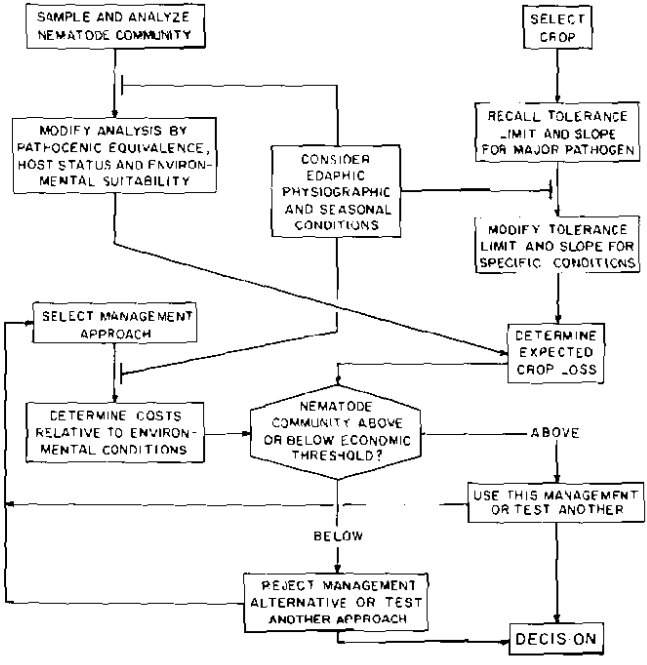

Figure 1 Flow chart of the decision process in nematode pest management [From Ferris (4)].

Again, gaps in existing data will point the way to new research from which more reasonable estimates can be made. A summary flow chart of an algorithm for making nematode-management decisions based upon these factors (Figure 1) demonstrates how computers may be programmed to interrogate and prompt the user into consideration of all relevant questions fundamental to making a decision.

One extension of the rationale is the possibility for studying the effect of crop rotation programs on nematode communities. This involves some knowledge of the reproductive potential of the nematode populations relative to the environmental suitability and crop host status. There are probably considerable accumulations of data in this area resulting from initial and final population measurements in various experiments. Another aspect of rotational studies is the decline of the population between crops relative to time and environmental conditions. This information on survival in the absence of host crops is necessary for predicting population mortality and therefore analyzing preplant population densities of the nematodes. Since it is impossible to standardize sampling dates, sample data require adjustment to predict the population at the time of planting (13).

Quantification of the underlying concepts of the development and use of dynamic action thresholds for nematode diseases of plants stimulates new research questions in some fundamental areas of nematode population ecology. The regimentation of the decision process models dictates the research objectives. It also allows reevaluation and extraction of new information from a considerable amount of available and published data.

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