CHAPTER 16

Mathematical Approaches to the Assessment of Crop Damage

HOWARD FERRIS

Department of Nematology, University of California, Riverside, California

I. INTRODUCTION

Crop damage is seldom due to a single pest species in isolation. The damage or loss caused cannot be quantified without considering the pest in relation to its environment or to its interaction with other organisms. However, in attempting to develop mathematical models of losses in a total agroecosystem context, errors of measurement, identification, and conceptualization are often so great as to mask reality. On the other hand, models of individual pest species incorporating a minimum of input variables are most easily developed. This chapter will outline mathematical and modeling approaches which result in the understanding of complex agroecosystems at different levels of resolution. It will not attempt to summarize all available mathematical models. A recent summary by Jones and Kempton (1978) provides an excellent review. Rather, it will be

ISBN 0-12-782203-8

an attempt to interest the reader in the potential for quantitative approaches, even at extremely simplistic levels.

Crop damage is used herein to express loss of the crop due to injury by nematode pests, either alone or interacting with other pests and with the environment. The loss is expressed in terms of a decrease of quality or quantity of the harvestable yield. The loss may be expressed as actual loss or predicted loss with management implications. Essentially, there are two approaches to quantitatively describe the relationship between expected yield loss and numbers of pest organisms. In correlative models (Gold, 1977) or mathematical representations (Yarranton, 1971), the final outcome of the relationship is predicted from some measurement of the predictor, without any description or explanation of the internal operation of the biological processes. Explanatory models (Gold, 1977) or mathematical models (Yarranton, 1971), on the other hand, are a functional or mechanistic representation of the relationship which provides understanding and insight into the interaction between plant, pathogen, and the environment. Frequently, the improved understanding of the interaction provided by explanatory models is of more importance than their predictive ability.

Any model is a simplified representation or abstraction of a far more complex natural system. Complexity of the natural system is such that comprehension of the outcome of its multiple interactions in a holistic sense may defy intuitive capabilities. Abstraction of the system into a model that recognizes the essential components, the inputs, and the outputs relative to the objectives of the modeler allows experimentation and prediction of the behavior of the system when it is subjected to various levels of perturbation. The process of modeling, therefore, involves understanding and simplification. It is useful to consider the agroecosystem as a series of interacting subsystems as is done with total ecosystem models (Overton, 1975). Each subsystem can then be studied in isolation, provided that the coupling structures are identified and that the integrity of the subsystem can be maintained. This approach allows the development of hierarchical models of each subsystem at different levels of resolution. A plant model for example, may predict weight of plant parts relative to physiological time, whereas a nematode model might be at considerably higher resolution and incorporate age-specific population dynamics and damage characteristics of the population. It is recognized that models of a nematode subsystem of the agroecosystem represent only a component aspect of the total crop damage and management model. Assessment of potential crop damage is a basis for management decisions. The objective of crop management is to optimize the translation of solar energy to harvestable yield relative to environmental and economic cost. Biological

---

stress entities in the agroecosystem become
either by: (1) removing photosynthetic surfac
of photosynthesis by physiological disruptio
the translation of photosynthate into harves
disruption of the plant, (4) reducing the effi
competition for light, water, or nutrients, or
harvestable yield of the plant. Nematodes,
habit, fit into at least two of the above catego
some of the products of photosynthesis and
yield; and (2) they may cause physiological di
ing the efficiency of the photosynthetic proce
product into harvestable yield. Many organ
degree to which the destructive process occu
of all of the pests in all of their functional
Thus, the net effect of any one pest at any poi
only the state of plant development at that tin
other pest species and of the suitability of th

One objective of crop damage assessment
basis for pest management decisions. A fu
management is that disruptive management
used if and where necessary. The decision
constrained by environmental consideration
the relationship between the organisms pre
loss. Environmental monitoring may be invol
rence of conditions dictating the emergence
in the field, as with many insect pests, rathe
quantification of population levels. Manag
knowledge of the relationships involved may
farm, crop, regional, national, internation
should be some measure of the confidence
predictive capabilities of models used at eac
sion. Users of crop loss models include gro
decisions, pest control advisors for developin
management systems, and extension and ad

Another objective for crop damage assess
tion of damage caused by various pests at
organization, so that research objectives an
funded, and administered. The information
economists and resource planners for pestici
assessment, and by national and internationa
ing allocation and availability of food and
Even a casual familiarity with the state of th

stress entities in the agroecosystem become pests when they prevent this either by: (1) removing photosynthetic surface, (2) reducing the efficiency of photosynthesis by physiological disruption of the plant, (3) reducing the translation of photosynthate into harvestable yield by physiological disruption of the plant, (4) reducing the efficiency of photosynthesis by competition for light, water, or nutrients, or (5) by directly reducing the harvestable yield of the plant. Nematodes, depending on their feeding habit, fit into at least two of the above categories: (1) they remove at least some of the products of photosynthesis and divert potential harvestable yield; and (2) they may cause physiological disruption of the plant, reducing the efficiency of the photosynthetic process and the translation of its product into harvestable yield. Many organisms stress plants, and the degree to which the destructive process occurs is an integral of the levels of all of the pests in all of their functional modes at any point in time. Thus, the net effect of any one pest at any point in time is a function of not only the state of plant development at that time, but also of the level of all other pest species and of the suitability of the environmental conditions.

One objective of crop damage assessment and prediction is to form a basis for pest management decisions. A fundamental principle of pest management is that disruptive management techniques should only be used if and where necessary. The decision basis may be economic but constrained by environmental considerations; it requires knowledge of the relationship between the organisms present and the expected crop loss. Environmental monitoring may be involved to determine the occurrence of conditions dictating the emergence or arrival of pest organisms in the field, as with many insect pests, rather than by direct analysis and quantification of population levels. Management decisions based on knowledge of the relationships involved may be made at the plant, field, farm, crop, regional, national, international, or global levels. There should be some measure of the confidence which can be placed in the predictive capabilities of models used at each level of management decision. Users of crop loss models include growers for crop management decisions, pest control advisors for developing and justifying appropriate management systems, and extension and advisory services.

Another objective for crop damage assessments is to allow quantification of damage caused by various pests at various levels of structural organization, so that research objectives and priorities can be planned, funded, and administered. The information is also used by agricultural economists and resource planners for pesticide development and benefit assessment, and by national and international policy makers in determining allocation and availability of food and fiber throughout the world. Even a casual familiarity with the state of the art of crop loss assessment reveals the tremendous need for acceleration in research and conceptualization. Among specific needs are the development of crop loss assessment methodology, the development of models and survey systems for collating the crop loss information and measurements, and estimates of confidence intervals and reliability which can be placed on the data developed.

II. MATHEMATICAL MODELS FOR CROP DAMAGE ASSESSMENT

Models predicting final nematode densities from initial preplant nematode densities are generally based on modifications of the Verhulst logistic model (Jones and Kempton, 1978; Seinhorst, 1970). Models proposed for describing the relationship between numbers of nematodes and plant growth have been developed by Seinhorst (1965). They are elegant in concept, recognizing the decreasing influence per nematode as population densities increase. In general, the models pertain to annual crops and predict proportional yield loss in relation to preplant nematode populations. All these models are well described (Jones and Kempton, 1978; Seinhorst, 1970) and require no further documentation here.

One rationale for developing mathematical models is the simplification of the real world. Attention is focused on the components of the system that are critical as predictors of its output and, further, on the environmental parameters which affect the interactions among the components. Therefore, the model acts as a conceptual framework within which literature can be searched and current information assessed. It provides a summary of the state of knowledge of the system, and it allows the organization of available data and the determination of research needs by focusing on information gaps. A series of steps are prescribed in the development of the mathematical model. The regimentation involved in the procedure forces simplification and understanding of the system.

Step 1. The limits of the universe to be considered in the model are defined. It may be an agricultural field and the pest communities limiting the production. Such a model would be extremely complex and involve a series of interacting subsystems. A simpler model would be a single plant and the plant parasitic nematode community parasitizing its root system. A danger of this simplification is that the resultant model may be misrepresentative in isolating one set of stresses on the growth of the plant and considering them apart from other interacting stresses in determining crop loss. Another simpler and less realistic situation is to consider the effect of parasitism of one nematode species on plant growth.

Step 2. The components of the system are defined. In the simplest case described, the components might consist of the nematode population system, the photosynthetic system of the plant, and the harvestable yield of the crop; even simpler components might be the numbers of nematodes and the amount of harvestable yield.

Step 3. The relationship between these components should be quantified. With nematodes on annual crops it is well documented that predictable relationships can be developed between harvestable yield and preplant nematode densities.

Step 4. The effect of environmental parameters on the defined relationship should be determined. This allows use of the model under a range of environmental conditions.

Step 5. Validation of the model is necessary before any quantification of crop loss due to nematodes is possible. One result of validation might be a realization that the original definition of the system was too narrow and that interaction with other organisms and other environmental conditions should be considered.

A. Critical Point Models

The classical models of Seinhorst relating expected plant growth to preplant nematode population levels fall into this category. These involve measurement of a nematode population at one point in time, usually before planting, and they predict losses based on knowledge of some damage function. Critical point models are frequently used in plant pathology (James, 1974). They allow prediction with a minimum of measurement and monitoring. The development of critical point models has certain advantages for nematodes over other pest groups. Nematodes are relatively slow-reproducing organisms compared to fungi or bacteria. They do not have winged stages which may result in crop invasion at unpredictable times. For annual crops, the critical population density is that which is present at the time of planting. This allows the development of predictive relationships between preplant population densities and crop growth. The existence of such relationships is fortunate, since most management alternatives, including varietal selection and soil fumigation, are preplant decisions. Since the nematode population is present at the time of planting, it is not necessary to consider the phenological state of the crop at the time of pest invasion, as might be the case with a foliar pathogen or an insect pest.

The basic damage function model of Seinhorst (1965) [$y = m + (1 - m)z^{(P-T)}$] has a strong foundation in biological theory. Oostenbrink

(1966) pointed out that the empirical relationship between log transformed nematode densities and final yield is mostly linear, with aberrations at either end of the population scale. Linearity occurs because the relative influence per nematode diminishes as nematode densities increase and as the amount of uninfected tissue available to each nematode decreases. Critical point relationships have been used in determination of economic threshold levels of nematode populations (Barker and Olthof, 1976; Ferris, 1978). The nature of both the empirical and theoretical critical point models is governed by three parameters; the tolerance level, the slope of the lines, and the minimum yield. These parameters are influenced by environmental and physiographic conditions. There is a need for researching the relationship between environmental conditons and the magnitude of the determinant parameters to allow interpolation and generalization of the critical point models to a range of conditions (Ferris, 1980).

Critical point models are usually developed for single nematode species, often in microplots. However, nematodes seldom occur in monospecific communities in agricultural soils. For practical implementation of critical point models, it is necessary to generalize for multispecific nematode communities. One approach to generalization is to conduct yield relationship experiments with a range of nematode communities at different density levels under each set of environmental conditions occurring in a particular physiographic region. A critical point model could be developed using multiple regression approaches for all the nematode species and environmental conditions. The time invested in development would be limiting and would considerably delay implementation of such models.

Another approach to generalizing critical point models for multispecific communities is to make use of available information on nematode feeding habits, biology, pathogenicity, and ecology. A "critical species" model is developed for crop damage relative to a nematode parasite of significant importance, and the pathogenicity of other nematode species is weighted relative to the critical species (Ferris, 1980). *Pratylenchus*, a migratory endoparasite of the root cortex, which does not set up specialized feeding sites or cause extensive physiological upset of the plant, might be ranked with a relative pathogenicity of 0.3 compared to *Meloidogyne*. An ectoparasitic nematode browsing on root hairs and epidermal cells might have a pathogenic equivalence of 0.05. This approach allows quantification of a nematode community in terms of its pathogenic equivalence relative to a critical species for which a damage function model has been developed. It is a similar concept to the cyst-nematode interspecific competition models (Jones and Kempton, 1978) and to Lotka-Volterra competition models, whereby interacting species are weighted relative to each other. It allows the use of a vast background resource of biological data to generalize damage function models. The notions are simplistic and ignore many potential interactions; however, the niches of most plant parasitic nematodes are somewhat different, so that direct interactions among them may be negligible. However, synergistic interactions in damage may occur, and these would probably be more readily explained in simulation models. There is some precedence in the weighting approach to damage functions from the work of Hijink (1964), who weighted *Rotylenchus* by a factor of 0.2 relative to the effect of *Meloidogyne hapla*.

Another consideration in the generalization of multispecific interactions is the relative environmental suitability for each of the species present. To approach this problem, Ferris and Duncan (1980) used a textural preference index, where nematode populations in critical point models would be weighted not only on the basis of their pathogenic ability, but also on the basis of the suitability of the soil texture to their movement, survival, and infectivity. Many of these data are available in the literature. This is approaching the concept of the limiting factor being a determinant in the level of interaction and is similar to use of Liebig's Law of the Minimum by Waggoner *et al.* (1980). It has many of the problems they recognized; the foundation is not wholly logical, and use may be limited by ability to estimate the parameters involved. Again, multiplicative interactions among pest organisms are not considered with this approach. Part of a validation process of any models developed would be to determine the need for consideration of the nature of interaction.

B. Multiple Point Models

Another model type used in plant pathology is the multiple point model (James, 1974). This type involves repeated measurement of the disease progress to predict losses. Such models have not been explored thoroughly in nematology. They may have potential for use with perennial crops but are unlikely to be useful with annual crops.

In perennial crops, yield during a current year is frequently influenced by the amount of stored products accumulated during a previous year, which would be affected by previous levels of nematode stress. Consideration of nematode populations at a point in time in successive years might allow prediction of yield losses.

The cost involved in sampling to determine population development at various points during the growing season would probably become limiting in the use of these models in annual crops. Further, the lack of available management techniques during the growing season would negate their usefulness.

C. Simulation Models

Rather than predicting crop damage based on a population density at a single point in time or at a series of points in time, simulation models mimic the biology of the interaction of pest, plant, and environment at their prevailing levels at any point in time. Such models are real time explanatory models that are descriptive of both pest and plant biology. They deal with the actual conditions influencing the interaction rather than assuming average seasonal conditions affecting the relationship. Simulation models, when initially implemented, require frequent biological monitoring for confirmation. As confidence is gained in the model, monitoring can become less frequent (Tummala and Haynes, 1977).

Simulation models deal with relative rates of growth of pest and plant populations. In poikilothermic systems, the metabolic rate is proportional to the temperature to which the system is exposed. Between definable upper and lower limits, the cumulative development is proportional to the cumulative heat to which the system is exposed. Measurements of cumulative heat above a basal threshold (heat units) can be expressed in terms of degree days or degree hours. Such measurement of physiological time has been used with many biological systems and allows prediction of the phenological state of the system after exposure to a specified temperature regime, assuming that other environmental conditions are not limiting.

In damage assessment modeling, it is useful to consider the plant as a supply/demand system (Wang *et al.*, 1977). The energy supply of the plant is a function of the rate of photosynthesis and the amount of photosynthetic surface at any point in time. The energy fixed is transformed into various plant parts according to a genetically determined sequence of growth priorities. Initial growth priority may be the expansion of the photosynthetic surface by development of leaves, stems, and the supporting root system. After a genetically predetermined accumulation of heat units, the growth priorities may change to the production of flowers, and ultimately the production of fruit. As leaf surface increases during the initial growth of the plant, the net photosynthesis increases proportionally. A herbivorous pest feeding on the leaf of the plant reduces net photosynthesis by reducing photosynthetic area. A parasite feeding on the plant root has a direct effect of removing the products of photosynthesis from the root. A sophisticated vascular parasite, such as

Meloidogyne, also reduces photosynthetic efficiency by disrupting the transpiration and translocation streams. The effect early in the growth of the plant, when priorities are for vegetative production, is to reduce the rate of increase of photosynthetic surface and hence, the rate of plant growth. As plant growth priorities change to flower and fruit production, the energy supply to these plant priorities is reduced because of the smaller photosynthetic area and the less efficient photosynthetic process. If the plant has a predetermined number of flower or fruit initials, the result is a reduction of fruit size. Simulations of the system will reveal the partitioning of energy and the effect of the nematodes on the growth and, ultimately, the yield of the plant.

Plants and nematodes are subjected to other environmental inputs besides temperature. Many environmental inputs, i.e., soil moisture, oxygen, and texture, are themselves interrelated. Multiple regression approaches would be useful to quantify the influence of these interacting factors on the growth rates of plants and nematodes relative to physiological time. However, frequently data are insufficient to develop such models. A useful approach here is the accumulation of *effective* heat units, whereby heat units are accumulated maximally at ambient conditions when other environmental conditions are within their optimal range. As other environmental conditions become suboptimal for development, the rate of development decreases. Heat units can be accumulated at a reduced rate by multiplying the accumulation function by a factor of less than one. The effect of each environmental factor can be weighted on a zero to one scale relative to the optimum conditions for that factor. As the factors become limiting to the rate of development, their effect is reduced below unity. This approach allows partitioning of each of the individual influences. It is rather simplistic and has a tendency to ignore potential interactions among the effects. However, it does allow implementation and model development from available data.

More data are necessary to construct and use simulation models than are needed for critical and multiple point models. Plant and pest biology must be known to develop the explanatory framework of the system. Much required information on growth and development of the organism and plant relative to environmental conditions can be extracted from the literature once this framework is established. It is a useful way of organizing available research information. The plant should be considered as the primary subsystem of the total system being modeled, since it is the producer in the system and the source of energy. A source of weather data and environmental input, on either a real time or historical basis, is needed to drive simulation models. Operating in a real time mode, in attempting to predict damage, requires the use of a historical data set to predict probable environmental conditions from the current time until the end of the growing season.

A major problem in real time simulation with available weather data is that ambient conditions of temperature and moisture may not be the microclimate perceived by the plant or the pest. The microenvironment for a pest shaded under a plant leaf is very different from ambient conditions. Similarly, conditions for a nematode 6 in. below the soil surface differ from ambient atmospheric conditions. Soil texture, irrigation status, phenological growth stage, and plant shading effects are all important. There is a real need for on-site measurements of microclimate and for models which predict microclimate from ambient conditions relative to growth status of the plant and physical environmental parameters. Fortunately, low-cost electronic environmental monitoring systems are becoming increasingly available.

A critical portion of simulation models is the coupling between subsystems to allow determination of crop damage relative to varying pest densities attacking the plant over time, and to varying rates of plant growth. Both plant and pest subsystems are dynamic, and the state and nature of the interaction varies constantly. The modeling rationale is that the rate of photosynthesis is proportional to the efficiency of the root system, which is related to the proportion of the root system not damaged by vascular disruption. Assuming that each root-knot nematode requires at least one syncytium as a feeding site, and that the inefficiency of the root system is related to the relative density of syncytia, it should be possible to determine the number of syncytia per unit root size when the root is nonfunctional. Then, the level of root effectiveness at any point in time would be related to the density of syncytia, as predicted from the size and age structure of the nematode population and the size of the root system. Since the number of syncytia per nematode probably increases at lower nematode densities, the nature of this relationship requires determination. It may be necessary to weight the population according to its age structure in developing the relationship. Root size at any time is a function of plant growth rate and growth priorities. Nematode population density and structure is a function of reproduction rate and environmental conditions. Both subsystems are affected by the coupling interaction, which itself is dynamic and would be continually evaluated in a simulation model. At some levels of interaction, a critical state may be reached which triggers changes in the biology of the nematode, for example, increased production of males.

The coupling system may be different for an ectoparasite such as *Tylenchorhynchus*. If the uptake of water and nutrients requires a living epidermal region, the proportion of the root influenced by the nematode would be the relative surface area damaged in the region of moisture and nutrient uptake, presumably, the root hair region of the plant. There is considerable work needed in this area for realistic quantification; however, conceptualization of the system in quantitative terms is an important initial step.

Multiple species interactions again could be handled by multiple regression, where the effect of all combinations of all levels of a nematode community on the plant has been analyzed at all stages of phenological growth of the plant. Obviously, this would be extremely difficult, and many of the objections raised earlier would apply. Again, the pathogenic equivalent system is probably applicable, where the available root system for plant growth becomes a function of the damage caused by each nematode group.

Simulation models are useful for research and analysis of crop damage through the partitioning of energy flow. They are also useful for prediction in the pest management decision process. A simulation model may be the most logical way of abstracting and conceptualizing the system in an analysis of the crop damage due to nematodes and other biological and environmental stresses in perennial crops. The numbers of computations involved in real time simulation models require the use of a computer. The advent of high-speed, low-cost computers has made the use of simulation models a more practical reality. The flexibility of computer and simulation languages allows the modeler certain advantages not available in classical, analytical approaches, such as critical point models. One advantage of programming languages is the "IF . . . THEN . . ." statement. Any function can be allowed to operate in the model as long as a certain set of conditions exist. Once that set of conditions no longer exists, as determined by input data or prediction, then another function pertains. This allows the use of a series of simple functions which are biologically descriptive and easy to comprehend, rather than a complex analytical model.

D. Synoptic Approaches

Stynes *et al.* (1979) assessed crop loss of wheat in South Australia by reducing a complex data set into natural subsets by multivariate statistical procedures. The data included many measurements of soil chemical and physical properties, pathogen and pest levels, and environmental conditions. Initial procedures are to determine which of the parameters measured are appropriate in the yield-loss analysis. An advantage of the approach is that it requires and promotes consideration of all the factors likely to influence crop yield or crop loss. Predictive regression models are based on those variables deemed relevant by the initial analyses. As mentioned earlier, a real danger in the study of crop damage from a disciplinary standpoint is that factors outside of the discipline are not considered. This results in inflated estimates of crop losses by additive consideration of losses from individual pests. Consequently, interaction and discounting effects of damage overlap are ignored.

The synoptic approach represents a classical mutivariate statistical version of the systems analysis approach to an agroecosystem. All significant components of the system are considered. The complexity of the system is reduced through principal components analysis and determination of those parameters which provide greatest explanation of the observations. In a systems analysis approach, the parameters and state variables considered important in determination of the output variables to be monitored would be selected intuitively. Generally, they would be in greater number and in greater detail than necessary and would be reduced by trial simulations of the system. Sensitivity analysis determines which state and input levels affect the system when they change. The multivariate statistical approach (Stynes *et al.*, 1979) would be a rational and logical way of choosing the components for an agroecosystem model for a systems analysis and simulation approach to the assessment of crop damage.

III. PARAMETER MEASUREMENT AND ESTIMATION

Predictions of yield loss based on the assessment of nematode populations are limited by the reliability of the soil samples representing the field population. Problems in reliably estimating nematode population densities are well documented. They relate to variation in the macro- and microdistribution of nematodes as a function of their edaphic and environmental requirements, and of their biological requirements in terms of feeding habits and reproduction pattern. Plant parasitic nematodes are primarily distributed according to the root system of their host, but their distribution and density varies with soil texture, previous cropping history, soil moisture-holding capacity, drainage and cultural patterns, and plant spacing. The vertical distribution of nematodes varies with food availability, root distribution pattern, and cultural and tillage procedures. Nematodes aggregate around specific feeding sites, such as root tips, and around areas of egg deposition, particularly in those species which are sedentary and deposit eggs in masses.

The most reliable method of determining potential nematode stress on a crop would be to extract and count the nematodes from all of the soil in a field. A more practical reduction is to represent the field by a series of soil samples. Since the processing of soil samples is expensive, it is customary for each sample to consist of several individual cores of soil taken from an area of supposed distribution uniformity. As number of soil samples and constituent cores are increased, a point is reached at which there is no further improvement in reduction of variation among samples. This point of diminishing returns may represent the optimum sample and core number for that field and is a function of the nematode distribution in that field. There are cost/benefit considerations in this optimization, particularly with regard to the estimation of nematode densities for predictive and pest management purposes.

Seinhorst (1973) investigated the problem of representing a nonuniformly distributed nematode population for use in predictive models, by basing it on a soil sampling process measuring the average population in a field. He calculated that yield loss is overestimated when the average population is greater than twice the tolerance limit for that crop. The more the distribution of nematodes differs from random, the greater the overestimation. The distribution of nematodes in a field is usually log normal or negative binomial (Goodell and Ferris, 1980). The overestimation of yield losses can be minimized by suitable stratification of the field, so that each stratum represents an area of uniform population density of the parasitic species of interest. Physical and cultural differences are an obvious basis for stratification. There is a danger of allowing one sample to represent too great an area of an apparently uniform field because of naturally occuring variations in the population distribution. The Society of Nematologists (1978) suggests that one sample of 20 cores be used to represent no more than 5 acres in which there is no obvious basis for stratification. From a practical sense, the overestimation of losses by averaging populations densities when nematodes are not randomly distributed results in conservative recommendations based on preplant population assessments.

It is often desirable to assess or predict crop losses for areas larger than a single field. In such cases it is necessary to have data on nematode densities and distribution on a regional basis. In areas where nematode advisory programs have been conducted by public institutions for many years, a wealth of quantitative information is available on nematodes.

Such information includes sampling sites, cropping histories, soil texture, and nematode population densities. If yield-loss prediction models were available, such data would allow assessment of losses, either predicted or historical, on a regional basis, according to the actual distribution of the nematode parasites of each crop.

It is a practical impossibility to measure the response of each variety of a crop to each of its nematode parasites under every set of environmental conditions. Levels of horizontal resistance and tolerance will, however, dictate the expected quantitative response of individual varieties to the same nematode density. An approach to the problem is to determine the damage function relative to a range of nematode population densities for one common variety of the crop, and to rank all other useful varieties in terms of their relative intolerance by greenhouse and field measurements of growth under nematode stress (Ferris, 1980). The intolerance can be expressed on a zero to one basis relative to the least tolerant variety and used in weighting the damage function for specific cultivars.

It may be possible to evaluate environmental suitability of the physiographic region and edaphic conditions based on literature currently available on nematode biology and ecology. The use of textural preference indices (Ferris and Duncan, 1980) involves transforming the effect of the soil texture on nematode multiplication to a zero to one scale, in which one represents the maximum multiplication detected in a set of experimental data. Soil texture is arbitrarily quantified and a tripartite model fitted to the data with an optimal range of soil texture and a region of declining favorability on either side. For any nematode species, any portion of this tripartite model may be inoperative. Nematode counts from soil samples can be weighted for use in predictive models.

Similar information can be gathered on temperature requirements of nematodes and used to express a regional preference or physiographic preference index for each nematode species. Depending on the location of the nematode community and the crop to be grown, it may be possible to weight the populations in that community according to their physiographic and textural preference indices, pathogenicity relative to a major pathogen of the region, and the relative intolerance of the host variety to be grown. This allows development of a weighted nematode stress total which is on the same relative basis as the population series for which the nematode damage function was determined (Ferris, 1980). It allows prediction of potential yield losses for the proposed crop which can be used for management purposes, and which are customized to the physiographic region, nature of the nematode community, the edaphic conditions, and crop variety.

IV. MODEL VALIDATION AND PREDICTION

A problem with validating any model used to predict plant growth relative to a nematode population is that crop yield in a field without nematode stress will vary, even in the same region, due to microclimate differences and grower expertise. Seinhorst (1965) approached this problem using a relative yield measurement with yield loss represented as proportional decrease from the maximum yield for that field. A further generalization is the concept of minimum yield below which no further reduction will be seen even at high nematode densities (Seinhorst, 1965).

Measurements of actual crop yield relative to nematode communities assessed prior to planting and weighted relative to edaphic and physiographic conditions can be used for validations of the conceptual models. This validation may result in a perception that the simplistic approaches suggested are inadequate and reveal a need for further consideration of the interaction among the determinant factors. A convenient tool for handling the problem of multiple-species nematode communities, differential host ranges, and varying environmental and edaphic requirements, is to use an interactive scenario on a minicomputer. Information would be input for the actual conditons of a field for which the prediction is being made. Hence, the damage prediction is customized according to the nematode community, environmental conditions, crop type, and grower expertise. Management decisions are based upon the best current information of nematode biology, ecology, and expected damage (Ferris, 1980).

V. PERSPECTIVE

Implementation of quantitative approaches involves real problems. The cost-effectiveness and reliability of nematode population assessment are poor. Since any use of predictive models in a management mode is based on population assessment, reliability becomes critical. There is a tremendous need for development of basic damage functions for key nematode species and crops as a basis for predicting yield losses from preplant densities. Simulation models require systems approaches to nematode biological problems and the availability of suitable plant models with which pest models can be interfaced.

We are entering the stage in pest management technology of synthesizing information achieved through reductionist approaches to disciplinary research, and of using the management tools developed in the disciplines to achieve the expressed goals of optimizing crop production relative to economic and environmental costs. Technologically, such synthesis may require systems approaches and the ability to manipulate data files to use simulation and predictive models on a real time or rapid-feedback basis. The technology is available, but key portions of the quantitative coupling of subsystems are lacking. However, as the conceptual framework evolves, the research questions that should be answered to allow rational management decisions based on best estimates of crop loss become apparent. This is an exciting period in quantitative nematology. The tools and many of the parts are available, and the objectives can be defined. It remains only to decide how the pieces fit together.

REFERENCES

Barker, K. R. and Olthof, T. H. A. (1976). *Annu. Rev. Phytopathol.* **14**, 327–353.

Ferris, H. and Duncan, L. W. (1980). *J. Nematol.* **12**, 220.

Ferris, H. (1978). *J. Nematol.* **10**, 341–350.

Ferris, H. (1980). *J. Nematol.* **12**, 164–170.

Gold, H. J. (1977). "Mathematical Modeling of Biological Systems" Wiley, New York.

Goodell, P., and Ferris, H. (1980). *J. Nematol.* **12**, 136–141.

Hijink, M. J. (1964). *Meded. Landbouwhogesch. Gent.* **29**, 818–822.

James, W. C. (1974). *Annu. Rev. Phytopathol.* 12, 27–48.

Jones, F. G. W., and Kempton, R. A. (1978). *In* "Plant Nematology" (J. F. Southey, ed.), pp. 333–361. HM Stationery Office, London.

Oostenbrink, M. (1966). *Meded. Landbouwhogesch. Wageningen* **66**, 1–46.

Overton, W.S. (1975). *In* "Systems Analysis and Simulation in Ecology" (B. C. Patten, ed.), Vol. III, pp. 117–138. Academic Press, New York.

Seinhorst, J. W. (1965). *Nematologica* **11**, 137–154.

Seinhorst, J. W. (1970). *Annu. Rev. Phytopathol.* **8**, 131–156.

Seinhorst, J. W. (1973). *Nematologica* **19**, 421–427.

Society of Nematologists (1978). *In* "Methods for Evaluating Plant Fungicides, Nematicides, and Bactericides." Amer. Phytopath. Soc., St. Paul, Minnesota.

Stynes, B.A., Wallace, H. R., and Veitch, L. G. (1979). *Aust. J. Soil Res.* **17**, 217–225.

Tummala, R. L., and Haynes, D. L. (1977). *Environ. Entomol.* **6**, 339–349.

Waggoner, P. E., Norvell, W. A., and Royle, D. J. (1980). *Phytopathology* **70**, 59–64.

Wang, Y., Gutierrez, A. P., Oster, G., and Daxl, R. (1977). *Can. Entomol.* **109**, 1359–1374.

Yarranton, G. A. (1971). *J. Ecol.* 59, 221–224.