# Theory and Practice of the Cropping Systems Approach to Reducing Nematode Problems in the Tropics<sup>1</sup>

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Abstract: Plant-parasitic nematodes are major constraints to the productivity of tropical farming operations. Intensive land use and climatic conditions favorable to nematode development contribute to increased crop losses due to these pests. Many farmers in developing tropical countries have limited resources and management options. Cropping systems research is a relatively low-cost, low-input method of optimizing existing agricultural practices with respect to limiting losses due to plant-parasitic nematodes. Specific tropical farming practices are discussed along with problems they pose for research in quantitative nematology. Comprehensive, systematic research methods for delineating and using nematode—host relationships are described, and new ways of dealing with complex multicropping systems are suggested.

Key words: cropping system, tropical agriculture, nematode-host relationship, multicropping, intercropping.

The term "cropping systems" has been used to describe various concepts, and two extremes of generality have emerged for its use. In a more general sense, cropping systems have been confused with farming systems. Farming systems incorporate all aspects of farm operations, which in addition to cropping systems also include livestock management and cultural and economic studies. At the other extreme, however, cropping systems also have been used as synonyms for crop rotations, which are very specific elements of the farm operation. A workable definition for the term probably lies somewhere between these two extremes.

For the purpose of this paper, cropping systems research is defined to include quantitative analyses of the relationships among crops, pests, farming practices, and all management techniques deployed or deployable in the target system. In nematology, this area of research is further limited to consideration primarily of nematode-host relationships, although other

pests, economics, and sociology also must be considered in the systems analytic phase.

A comprehensive approach considers all available management techniques simultaneously; however, crop rotation is emphasized as a method of limiting losses due to plant-parasitic nematodes, especially within developing tropical countries. Crop rotation is one of the oldest and most effective means of limiting nematode losses (19). This technique requires few high-cost or high-technology inputs and is historically a part of many subsistence-level tropical farming operations. Optimizing existing crop sequences in a rotation should be a natural application for systems analytical techniques.

Although the study of tropical farming systems may emphasize crop rotation, other nematode-management options, such as nematicides, biological control agents, and crop resistance, must be evaluated if they are available. These alternatives, however, often are of limited use to tropical farmers. Nematicides are increasing in cost, and there are increased restrictions on their availability. Biological control agents are important emerging alternatives, but they have been of limited commercial effectiveness. The control afforded by currently available biocontrol agents is best used in conjunction with other cultural methods, such as crop rotation. Resistance is a preferred method of limiting losses due to plant-parasitic nematodes, but it is avail-

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able in only a few important crops and against certain nematode species. Even if new sources of resistance are eventually developed through emerging technologies, they will need to be deployed as new cultivars in a comprehensive cropping system. Appropriate deployment of any new source of resistance will be necessary to maintain its effectiveness.

All of these limitations emphasize the necessity of comprehensive on-site studies of existing tropical agricultural systems, so that improved crop sequencing and production practices can be developed. Optimization of existing practices is required to increase production efficiency immediately, and time must be allowed for the deployment and evaluation of new management technologies. Thus, this discussion of cropping systems research in tropical agriculture will focus on methods for analysis of quantitative nematode—host relationships, leading to optimization of existing management practices.

## TROPICAL FARMING PRACTICES

Unique systems of agriculture have evolved in the tropics for a number of climatic and cultural reasons. Each of these systems presents a different set of challenges for the design and implementation of research in quantitative nematology. Major divisions in tropical cropping practices are according to rainfall patterns, i.e., arid, semiarid, and humid tropics. The primary delineation of growing seasons in the tropics is the occurrence of a dry season, in contrast to delineation by a winter in temperate regions. The effects of a dry season on nematode population dynamics may be quite different from the effects of an overwintering period. Where a definite dry season does not occur, or where irrigation is available, crops may be grown continuously, resulting in another series of nematode dynamics.

Additionally, unique land-use patterns in the tropics will significantly alter the methods for analysis of nematode-host relationships. Several categories of land-use patterns in the tropics already have re-

ceived extensive study by agronomists, crop scientists, and economists (18,21,27). Analysis of the nematode components of these farming practices would be a productive extension of existing information. Derivation of quantitative host-parasite relationships in tropical systems is complicated by various unique spatial and temporal patterns of planting crops. Common planting patterns include intercropping, in which two or more crops are planted at the same time in regular geometric patterns; relay cropping, in which a second crop is planted between the rows of a previous crop before the first crop is harvested; and mixed cropping, in which various crops are planted in an area with little regard for time of planting or spatial pattern. Mixed cropping usually occurs in more primitive areas of shifting cultivation, but there are variations of all three systems and indistinct boundaries among the definitions. Perennial and annual crops may be combined in any of the cropping patterns.

Shifting cultivation: A shifting cultivation pattern begins with slash and burn clearing, followed by varying periods of cultivation and long-term reversion (forest regeneration). During reversion, the farming community typically moves to a new location. Shifting cultivation patterns are widespread in the tropics and may account for 45% of the arable land use (27). Quantitative studies of nematode communities in these patterns would be useful for determining the optimum lengths of cropping versus reversion periods, as well as for determining the best cropping sequences within the cultivation period. Novel approaches to determining nematode-host relationships will be required, since crops are seldom planted in rows and mixed cropping is common. Shifting cultivation may have a negative impact on populations of plant-parasitic nematodes (20); however, improved systems of mixed cropping and sequences of crops for limiting increases in populations of plant-parasitic nematodes would improve production during the crop phase and could shorten the required reversion period.

Reversion cultivation: A second tropical pattern, reversion systems, is closely related to shifting cultivation. In this pattern, the land is cleared and cropped for 3-10 years and then left idle for a similar period of time. The length of cropping and idle periods and the crops grown in the systems vary widely in different agricultural areas. The primary difference between this pattern and shifting cultivation is that the farming communities are landholders with relatively large holdings consisting of smaller segments which are continuously rotated in and out of production. There is more opportunity to implement improved cropping systems in this pattern, since the farmers are geographically stable and more interested in the long-term productivity of the land. Keeping population densities of plant-parasitic nematodes below economic thresholds would be important to the landholding community. Quantitative studies would again focus on optimizing the lengths of cropping and idle periods and on choosing appropriate crop sequences during the production phase. Determination of nematode-host relationships in these systems is greatly complicated by the common practice of spatial intercropping, often including annual and perennial crops interplanted in the same system.

Intensive rainfed systems: Intensive rainfed cropping systems are similar to their temperate counterparts in many ways. Farming occurs primarily on clearly defined individual landholdings, and cropping is continuous to the extent that seasons and rainfall will allow. Within this pattern are landholders of distinct economic strata, including a large group of subsistence-level farmers, usually with less than 2 ha of arable land, and a smaller group of capital-intensive farmers with large land holdings.

The large-scale farmers operate in the same manner as their temperate climate counterparts, except for the delineation of seasons by dry periods and a greater possibility of year-round crop production. There is also a greater reliance on perennial crops, such as bananas, cacao, coffee, etc., as high cash-value crops. The dry sea-

son delineation may pose special problems and opportunities for quantitative studies in nematode population dynamics, since nematodes may survive in anhydrobiotic stages. The reliance on perennial crops makes determination of crop yield-nematode density relationships more involved. Large-scale farmers usually have more resources and management options available to them, such as nematicides and resistant cultivars, and may be reluctant to consider rotating to less valuable crops. All of these factors may make these intensive rainfed tropical systems less attractive targets for cropping systems analysis, and the possible rewards are limited at this time. However, as fewer management options remain available to these growers, particularly through the reduced availability of effective nematicides, there will be increased interest in optimizing production through a comprehensive analytical approach.

Subsistence rainfed systems: Subsistence rainfed agriculture is perhaps the most promising target for increasing production through cropping systems analysis. Relatively large numbers of farmers depend on these systems, and a large number of annual crops typically are grown, since the farmer is growing everything included in the family's diet. Available management options are quite limited, and monetary inputs are low. This production type is ideal for optimization through analytical methods, especially when the natural crop diversity is considered. Crop rotations usually have evolved over many years, and much can be learned from a careful study of existing subsistence systems. The small size of landholdings and intensive cultivation of vegetable crops suggests the occurrence of severe nematode infestations, although there have been few studies of plant-parasitic nematodes in tropical subsistence-level farming operations (7,26). A comprehensive monograph has been published on nematode problems on cassava (13), an important crop to many subsistence tropical farmers. This review can serve as a good starting point for further research in these cropping systems.

Determining quantitative nematodehost relationships in subsistence systems is complicated by the complex spatial and temporal arrangements of crops during the long growing seasons. Interplanting, including relay cropping, is common, and many crops are not planted in rows or other orderly patterns. Planting patterns usually follow topography and the natural distribution of soil micro-sites within the arable area. Topographic complications are common, with crops and management practices changing rapidly over small distances as altitude increases.

Results of cropping systems analyses from tropical subsistence-level farms will probably be of very limited, local use. Local scientists and crop protection specialists must identify important nematode pests for each area. Experiments should be repeated with diverse crop combinations and in different topographical-climatic settings. All of these factors, however, underscore the need for an efficient, standardized approach to the implementation of cropping systems research in nematology and in other plant protection disciplines. As the laborious task of collecting data beings, researchers must collect their data by systematic, standardized methods to ensure their usefulness in future studies as the crop-pest database is expanded. Accurate quantitative models will be useful to scientists in other regions and may be extendable to modeling efforts in larger commercial farming systems.

Intensive irrigated systems: Irrigated farming systems, especially those built around rice production, constitute the most intensive and high-yielding cropping operations in the tropics (25). Temperatures are suitable for plant growth year round, and crops are produced continuously, with some areas producing 6–8 crops per year. Irrigated farming may include intensive vegetable production, usually for export to winter markets in temperate areas, various high-cash crops such as sugarcane and pineapples, or intensive grain-based production of food for local consumption.

Wetland rice usually is considered an ir-

rigated crop. Although the primary source of irrigation water may be rainfall, the water still is managed artificially by channels, terraces, and dikes. The cropping systems are centered on rice production as the most important food source in many tropical areas. The number of rice crops per year ranges from one to three in various regions, depending on temperatures and rainfall, and other crops are usually grown with the rice through interplanting, relay cropping, and sequential rotations. Extremely intensive rice-based systems of up to eight crops per year (including interplanted vegetables) are common in southern Taiwan and Southeast Asia.

These will be challenging systems for research in quantitative nematology. Periodic flooding of the wetland rice induces unique shifts in the nematode communities (23) but also should be useful in limiting populations of some plant-parasitic nematodes. The interplanting and relay planting of vegetables will provide further challenges in the manipulation of nematode communities. Increasing food production, however, even by slight increments, is a necessity in the Asian rice-based systems, and growers should be responsive to any recommendations which may increase yields. With land so intensively cropped, plant-parasitic nematodes can increase to levels that become limiting factors in production. The complexity and diversity of crops and planting patterns offer much opportunity for further optimization through systems analysis, after problems in determining multiple-species quantitative hostparasite relationships in mixed plantings are overcome.

### CROPPING SYSTEMS RESEARCH

In order to simulate, optimize, and make predictions about systems of crops, pests, and management techniques, mathematical models must be derived for essential relationships in the system. As indicated in the discussion of tropical cropping practices, there will be many unique and interesting challenges in the formulation and derivation of these models. The results of

optimization and predictions will be no better than the mathematical models on which they are based, and the models will be no better than the data used to derive them. Sound approaches to experimental design, data collection, and analysis are needed to make progress in understanding the enormous complexities of tropical systems. Also, some degree of uniformity in approaches will facilitate sharing of information and results among different regions with similar problems. A proposed delineation of methods for use in cropping systems research in nematology (15) has been published and distributed by the Crop Nematode Research and Control Project, a USAID-funded project administered at North Carolina State University. One of the goals of that project was to encourage and implement cropping systems research among nematologists in developing tropical countries, and distribution of the guide was a part of that effort.

Methods for cropping systems research are built on the efforts of many researchers in quantitative nematology. Considerable work already has been reported on the determination and formulation of nematode damage functions (1,5,22), reproductive curves (10), and in crop rotation development (7,8,12). Further studies have shown the utility of small-plot methods in determining nematode-host relationships (2,9,12). Nematode spatial patterns in infested fields have been described by various mathematical approaches (6,14). Recent research has provided new insights on how to determine the effects of multiple infestations (more than one nematode species on a single host) (3,24) and how to derive multiple-point damage functions for describing long-term nematode effects on perennial crops (17).

All of these areas of research provide tools necessary for a tropical cropping systems research program, but the methods must be assembled into an appropriate and orderly approach to delineating system components. Most important are the nematode-host relationships, including damage functions and nematode repro-

ductive curves. The use of nematicides, resistant cultivars, and biological control agents all can be expressed through their effects on these fundamental relationships. The mathematical functions also serve as a basis for modeling crop sequences. Derivation of damage functions and reproductive curves that accurately represent the situation in farming operations can be done using small-plot methods in naturally infested fields.

The emphasis on understanding the mechanics underlying crop performance and nematode population dynamics within each growing cycle separates cropping systems research from traditional crop rotation work. In traditional approaches, specific crop sequences were selected and planted in replicated designs, extending over as many growing seasons as were required to study the selected crop rotations. Data collection was oriented toward determining the final results of each rotation in terms of target-crop yields, changes in nematode population levels, or other final-state indicator variables. These methods constituted a black-box approach to understanding the internal dynamics of the system and were useful primarily for selecting a recommended rotation from those tested.

In contrast, the cropping systems approach implements a research design for determining mathematical relationships which in turn represent system components. These components then are assembled into simulations of crop sequences and management practices. Functions representing individual crop-nematode relationships can be assembled in different arrangements to simulate any possible cropping sequence or combination of management practices. By understanding system relationships, researchers are not limited to post hoc evaluations of management sequences which were implemented individually in trial plots.

There is a price to pay, however, in the increased data collection necessary to estimate parameters of the required functions for all crops and nematodes in a complex farming operation. Additional

problems in experimental design arise where attempts are made to include other pests in the systems analyses. Work can be minimized, however, by using efficient research-plot designs in naturally infested fields, using grower-managed fields where possible, and taking full advantage of certain aspects of the spatial ecology of plant-parasitic nematodes.

Field-plot research: Plots arranged in rectangular grids in naturally infested commercial fields can be used to collect data necessary for estimation of the parameters in mathematical representations of nematode-host functions. Deploying a grid system of relatively small plots (20-30 m<sup>2</sup>) takes advantage of the naturally clustered horizontal spatial pattern of plant-parasitic nematodes (6,14). Large differences in nematode densities among plots within the grid are typical because of the natural variation in counts. This large range in counts allows the determination of density-dependent effects on crop yield and nematode reproduction. The use of small plots in naturally infested fields will minimize the resources required from developing country institutions for implementing this research, although follow-up and auxiliary experiments in the greenhouse and microplots would be useful.

After the establishment of field plots, all that is necessary in a relatively simple datacollection scheme is assessment of nematode densities at planting and at harvest and measurements of yields in each plot. Yields then are expressed as a function of nematode densities with an appropriate mathematical model, and final nematode densities are expressed as a function of initial densities. Elaborations on this design can include assessment of midseason nematode counts, or counts at regular intervals for perennial crops, which then are used to estimate functions representing time or degree-day dependent reproduction. Soil parameters may also be measured in the plots and then used to estimate the effects of edaphic characteristics on nematodehost relationships (16).

Implementation of grids of plots and

analyses of nematode-host relationships should be done in replicated designs across fields for each crop and nematode species included in the system. This research is labor intensive, but it does not require high technology equipment or resources from institutions within developing countries. Costs are further restrained by doing the research in growers' fields. In developing tropical countries, labor is often the most available resource to scientific researchers. Technical assistance in the data analysis phases may be required, but this can come after the field phase, and expertise in statistics often is available locally.

Derivation of models, simulations: Because of the long growing seasons in the tropics, mathematical models required for systems optimization can be derived in a relatively short time for a large number of crops. Studies should be done over more than one growing season to assess the effects of climatic variation, but the systems approach will not take as long as studies where each rotation or management sequence has to be implemented in the field and conclusions cannot be made until the last rotation is terminated. Although the initial data collection phase of cropping systems research may entail more effort and more tedious sampling than traditional crop rotation studies, the resulting models will provide rapid evaluations of promising crop sequences and other management practices. The systems analyses will add to our understanding of crop-nematode interactions and indicate areas for further research. Models that can be built upon and expanded to other pests are essential for long-term studies of complex tropical agricultural systems.

The final phase of a cropping systems analysis consists of assembling the models for yield relationships and nematode population dynamics for all crops and nematodes in the system into a simulation model. This model then can be used to assess the effects of sequences of crops and the impact of various management options. At this step, economics, sociology, and cultural factors can be brought into the anal-

ysis. Weighted averages of commodity prices can be used to translate yield information into income and profitability studies. Economic thresholds can be calculated where data on the costs of various management practices are available. Crops can be weighted in importance according to their cultural desirability and local marketability. All of this information then can be assembled into decision models and used to derive optimal cropping sequences.

Results of the cropping systems analyses, in the form of recommended cropping practices for specific nematode infestations, will have to be validated in followup field studies. Variability in the data will typically be high, and very broad confidence intervals must be applied to the recommendations. Grouping recommendations into general hazard categories and letting farmers choose desirable sequences may be a more realistic approach. Regardless of the problems in precision and accuracy, however, the recommended management sequences will be based on the best data available, as opposed to best guesses, and can be refined with additional experience.

Quantitative host-parasite relationships in multiple cropping systems: Research designs for delineating nematode-host relationships in multiple cropping systems, as are common in the tropics, require unique methods. Techniques have been proposed for deriving nematode damage functions for concomitant infestations of more than one nematode species (3,24) and for nematode dynamics on perennial crops (17), but no methods have been proposed for delineating effects of mixed populations of nematodes in mixed plantings of host crops.

Although formidable, the task of separating nematode-crop dynamics in multiple cropping is not impossible. Approaches need to be developed which combine information from the mixed plantings with information from simpler research designs based on single crop-nematode relationships. Key elements in partitioning nematode density-based crop-loss models among several susceptible crops will be the relative

volumes of soil occupied by host root zones and the preferential feeding behavior among the nematode species. Relative hazard indices can be developed for each crop and nematode species and for each crop and nematode combination to be considered by using greenhouse or microplot studies (4). This information then can be used to formulate models that explain net outputs in the multiple plantings, based on relative nematode densities.

A multiple crop-multiple nematode species damage function could be formulated as:

$$Y = a_1 F_1(n_1, n_2, n_3, \dots, n_n) + I_1(F_2, n_1, n_2, n_3, \dots, n_n) + a_2 F_2(n_1, n_2, n_3, \dots, n_n) + I_2(F_1, n_1, n_2, n_3, \dots, n_n).$$
(1)

Where Y represents the total yield output of the intercrop system,  $F_1$  and  $F_2$  are nematode damage functions of the two crops, relating yields of each crop to variables representing all plant-parasitic nematodes  $n_1, \ldots, n_n$  in the cropping area,  $a_1$  and  $a_2$  are scale factors representing the proportion of total area planted to each crop  $(a_1 + a_2 = 1)$ , and  $I_1$  and  $I_2$  are functions representing the intercrop component of productivity for each crop, in terms of the performance of the other crop,  $F_1$  or  $F_2$ , and nematode densities,  $n_1, \ldots, n_n$ .

 $F_1$  and  $F_2$  can be any nematode damage function which accurately represents the observed relationship in experimental data. Curves for individual crops can be derived by traditional microplot or small field-plot research. In the simplest situation, where only one parasitic species is present, the Seinhorst formula (22) can be used. Where there are many nematode species in the systems, more elaborate models relating crop yield to multiple infestations will be needed. Yields should be expressed in common production-oriented units across crops, such as kg/ha, food calories/ha, or monetary units, so that the summation to total yield Y will be meaningful.

The actual number of nematodes included in the damage function for each crop will depend on the host range of each nematode species. Obviously, nematode species will be excluded from models for nonhost crops, but a more complicated situation arises from preferential feeding behavior among nematodes presented with more than one host. In a spatial intercropping, parasitic species may feed preferentially on one of the crops, all but excluding the less desirable host. In this situation, the estimates of nematode densities, n<sub>1</sub>, used in F<sub>1</sub> and F<sub>2</sub>, can be scaled by a series of constants b<sub>ii</sub>, where b<sub>i1</sub> represents the proportion of nematode ni preferentially attacking the host represented by F1, and b10 represents the proportion remaining on host  $F_2$  ( $b_{i1} + b_{i2} = 1$ ). Estimates of these proportions can be obtained in greenhouse or microplot experiments.

The intercropping productivity functions, I<sub>1</sub> and I<sub>2</sub>, represent the differences between yields of the crops grown separately and the yields of the intercrop. Usually, if two compatible crops are planted together, there is more total yield than if an equivalent area were planted in each of the crops. Increases are as much as 60% in some combinations (27). Intercropping systems have evolved in the tropics empirically, as a method of allowing more intensive use of land and water resources. Additional yields are the result of compensation among the crops and more efficient utilization of solar energy and other resources through noncompetitive spatial arrangements of specific crop combinations. These systems have been slow to evolve in more developed systems of agriculture because they are not well suited to mechanized cultivation and harvesting.

The interplanting function for each crop,  $I_1$  and  $I_2$ , is expressed in terms of the performance of the other crop,  $F_1$  or  $F_2$ , and nematode densities,  $n_1, \ldots, n_n$ , in recognition that the yield of one crop depends to some extent on the performance of the other crop, and both yields and the ability to compensate depend on the severity of nematode infestations. Experimental derivation of the intercrop functions should be done in field-plot studies, where all components of the crops and nematodes can

be observed simultaneously. Appropriate mathematical models for these functions will include multiplicative (interaction) and simple additive terms.

Studies of nematode population dynamics in intercropping systems may be even more complicated than studies of yieldloss relationships. In fact, the most workable approach may be to analyze beginning and final state variables, where input (Pi) and output (Pf) are measured for each crop combination and nematode species in the system. The dynamics subsequently can be described by an empirically determined mathematical model. This approach is less than desirable, since it adds little to our understanding of the within-system dynamics, but it will serve to move the research forward. Even in this simple approach, however, simultaneous analyses of the dynamics of all species are required. Reproduction of one species impairs to some extent the availability of resources for the reproduction of other parasitic species, due to competition for feeding sites and plant energy. The dynamics of each species must be followed carefully, even for species unimportant to the current crops, to allow analysis of the impact of those species on the performance of future crops, which will have different susceptibilities.

A system of linked equations can be used for simultaneous analysis of the population dynamics of multiple infestations of plantparasitic nematodes. Each equation in such a linked system represents changes in the population of a single species, in terms of the initial population densities and dynamics of the other species:

$$\begin{split} dN_1 &= R_1(P_{N1i}, \, dN_2, \, dN_3, \, \dots, \, dN_n) \\ dN_2 &= R_2(P_{N2i}, \, dN_1, \, dN_3, \, \dots, \, dN_n) \\ dN_3 &= R_3(P_{N3i}, \, dN_1, \, dN_2, \, \dots, \, dN_n) \\ &\cdot \\ &\cdot \\ dN_n &= R_n(P_{Nni}, \, dN_1, \, dN_2, \, \dots, \, dN_{n-1}) \end{split}$$

Where  $dN_1$ ,  $dN_2$ , . . . ,  $dN_n$  represent the changes in population densities of nematode species  $N_1, N_2, \ldots, N_n$  under the intercropping,  $R_1, R_2, \ldots, R_n$  represent nematode population dynamic functions, expressed in terms of initial population densities  $P_{N1i}$ ,  $P_{N2i}$ , ...,  $P_{Nni}$  of the particular species, and population changes of all other species  $dN_1$ ,  $dN_2$ , ...,  $dN_n$  in the system. Extended time series functions can be used to represent dynamics in perennial crops, or in annual crops over a number of growing seasons. Species that do not infest any of the currently planted hosts can be excluded from the models and represented by a simple function showing the decrease under a nonhost.

Although interactions among population changes of the various nematode species can be tracked by these systems of equations, it will be much more difficult to separate the components of reproduction occurring on individual crops in the spatially mixed plantings. First, the spatial arrangement of the roots will have to be considered. If the root zones of crops planted in alternate rows remain separated for most of the season, then we may be able to consider the intercropping as two spatially separate systems, with little interaction. In this case, however, placement of future rows of crops will have to be studied carefully to take advantage of the different levels of infestation remaining in alternate rows.

If the root zones of the interplanted crops are mixed, then many types of interactions are possible. The entire area could be considered as planted in a single crop that has a proportional combination of the host ranges and reproductive potentials of the two crops. The constants of proportionality should represent relative volumes of soil occupied by the individual root systems, which could be determined experimentally. These proportions then can be applied to the linked systems of equations representing multiple-species population dynamics on each host crop.

Other factors, such as preferential nematode feeding behavior where both crops are hosts, can cause further complications. Separating these effects will be tedious and will require elaborate experimental designs. Many of these factors, however, will not have experimentally measurable effects on the population dynamics of the system because of the tremendous variability inherent in nematode assays. For the purposes of cropping systems analysis, all that will be required is a reasonable prediction of residual densities of plant-parasitic nematodes representing a risk to future crops.

### Conclusions

Crop losses due to plant-parasitic nematodes in tropical agricultural systems could be reduced by improved deployment of crop rotations and other existing management practices. Optimizing these agricultural practices would not require any hightechnology, high-cost inputs and could be accomplished in a relatively short time. A comprehensive approach to the analysis of cropping systems, incorporating previously published analytical methods and new techniques, can be used to provide the information necessary to begin simulation modeling and optimization. Scientists and crop protection specialists in tropical countries already have begun the task of identifying important nematode pests, and some have begun evaluating crop rotations. These scientists have the capabilities and facilities to continue in the delineation of nematode-host relationships as part of a cropping systems research design. Coordination, communication, and assistance in the implementation of standardized research methods are necessary to promote information sharing and to avoid duplication of efforts. Considerable research will be required to increase our understanding of nematode dynamics in the many complex cropping patterns found in the Tropics.

#### LITERATURE CITED

- 1. Barker, K. R., and T. H. A. Olthof. 1976. Relationships between nematode population densities and crop responses. Annual Review of Phytopathology 14:327–353.
- 2. Cooke, D. A., and I. J. Thomason. 1978. The relationship between population density of *Heterodera schachtii* Schmidt, soil temperature, and the yield of sugar beet. Journal of Nematology 11:124–128.
- 3. Duncan, L. W., and H. Ferris. 1983. Validation of a model for prediction of host damage by two

nematode species. Journal of Nematology 15:227-234.

- 4. Ferris, H. 1980. Nematology—status and prospects: Practical implementation of quantitative approaches to nematology. Journal of Nematology 12: 164–170.
- 5. Ferris, H. 1981. Mathematical approaches to the assessment of crop damage. Pp. 405–420 in B. M. Zuckerman and R. A. Rohde, eds. Plant parasitic nematodes, vol. 3. New York: Academic Press.
- 6. Francl, L. J. 1986. Spatial analysis of *Heterodera* glycines populations in field plots. Journal of Nematology 18:183–189.
- 7. Hutton, D. G., P. L. Coates-Beckford, and S. A. E. Eason-Heath. 1983. Management of *Meloidogyne incognita* populations by crop rotation in a small-scale field trial and nematode pathogenic effects on selected cultivars (Jamaica). Nematropica 13:153–163.
- 8. Johnson, A. W., C. C. Dowler, and E. W. Hauser. 1975. Crop rotation and herbicide effects on population densities of plant-parasitic nematodes. Journal of Nematology 7:158–168.
- 9. Jones, F. G. W. 1956. Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. II. Microplot and field plot results. Annals of Applied Biology 44:25–56.
- 10. Jones, F. G. W., and R. A. Kempton. 1978. Population dynamics, population models, and integrated control. Pp. 333–361 in J. F. Southey, ed. Plant nematology. London: Her Majesty's Stationery Office.
- 11. Kinloch, R. A. 1983. Influence of maize rotations on the yield of soybean grown in *Meloidogyne incognita* infested soil. Journal of Nematology 15:398–405.
- 12. Kinloch, R. A. 1986. Soybean and maize cropping models for the management of *Meloidogyne incognita* in the coastal plain. Journal of Nematology 18: 451–458.
- 13. McSorley, R., S. K. O'Hair, and J. L. Parrado. 1983. Nematodes of cassava, *Manihot esculenta* Crantz. Nematropica 13:261–287.
  - 14. Noe, J. P., and C. L. Campbell. 1985. Spatial

- pattern analysis of plant-parasitic nematodes. Journal of Nematology 17:86–93.
- 15. Noe, J. P. 1986. Cropping systems analysis for limiting losses due to plant-parasitic nematodes: Guide to research methodology. Raleigh: North Carolina State University Graphics.
- 16. Noe, J. P., and J. L. Imbriani. 1986. Yieldloss relationships and population dynamics of *Hoplolaimus columbus* on cotton, as modified by edaphic parameters. Journal of Nematology 18:624 (Abstr.).
- 17. Noling, J. W., and H. Ferris. 1987. Nematode-degree days, a density-time model for relating epidemiology and crop losses in perennials. Journal of Nematology 19:108-118.
- 18. Norman, M. J. T. 1979. Annual cropping systems in the tropics. Gainesville: University Presses of Florida.
- 19. Nusbaum, C. J., and H. Ferris. 1973. The role of cropping systems in nematode population management. Annual Review of Phytopathology 11:423–440.
- 20. Ogbuji, R. O. 1979. Shifting cultivation discourages nematodes. World Crops 31:113-114.
- 21. Ruthenberg, H. 1980. Farming systems in the tropics. Oxford: Clarendon Press.
- 22. Seinhorst, J. W. 1965. The relation between nematode density and damage to plants. Nematologica 11:137–154.
- 23. Trivedi, P. C., and K. R. Barker. 1986. Management of nematodes by cultural practices. Nematropica 16:213-236.
- 24. Wallace, H. R. 1983. Interactions between nematodes and other factors on plants. Journal of Nematology 15:221–227.
- 25. Ward, W. B. 1985. Science and rice in Indonesia. Boston: Oelgeschlager, Gunn & Hain.
- 26. Wilson, G. F., and F. E. Caveness. 1980. The effects of rotation crops on the survival of root-knot, root-lesion, and spiral nematodes. Nematropica 10: 56-61.
- 27. Wrigley, G. 1981. Tropical agriculture. London: Longman.