

APPROACHES TO THE ASSESSMENT OF CROP
LOSSES DUE TO NEMATODES
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Abstract

Nematode damage to plants is related to the feeding habit, biology, and life style of the nematode, the relative favorability of its environment, and the host status of the plant. Biologically descriptive models of the relationship between plant growth and numbers of nematodes are available. They can be generalized for specific crop and environmental situations through a knowledge of the effect of these factors on model parameters. Further development of the models is necessary for effects of multiple pest interactions. Partitioning and assessment of crop losses due to nematodes generally involves nematode population density assessment, which may be the limiting factor in accuracy and reliability.

Feeding habits of plant-parasitic nematodes range from ectoparasitic browsing on cellular contents of root hairs, through endoparasitism in cortical tissues, to sedentary endoparasitism involving the formation of sophisticated feeding sites within the host tissues. Within this framework, nematodes damage plants through several behavioral modes relative to feeding habit and life style. Common to all is a withdrawal of cell content. The effect may be relatively minor in migratory ectoparasites, but substantial in sedentary endoparasites where physiological changes are induced so that feeding sites function essentially as transfer cells with expanded surface area and enhanced metabolic activity. Intercellular migration, accompanied by dissolution of middle lamellae, may result in spongy tissues and avenues for secondary infection. Intracellular penetration has similar effects and may result in cell death. Physiological changes induced in the host may alter priorities in the partitioning of photosynthetic products. Rather than providing photosynthates to expanding leaf and shoot biomass, or to fruit biomass depending upon the state of crop development, a large proportion may be channeled to the sink produced at the nematode feeding site. Hypertrophy and hyperplasia associated with complex feeding sites may result in disruption of vascular tissues and reduction of the ability of the plant to absorb water and nutrients (5, 16).

Assimilation by plants is a function of the active photosynthetic area and the level of physiological efficiency. Some nematode species have a major effect on reducing physiological efficiency, while others remove individual cell contents but induce little anatomical or physiological disruption. Both approaches have some survival advantages. The ectoparasites probably more closely approximate "k strategists," causing little damage to the plant but having a low rate of food intake per unit of energy expended and, consequently, reproducing and increasing rather slowly. Conversely, endoparasites are geared towards production, having high food intake rates, often at the cost of considerable plant damage, and exhibiting characteristics of "r strategists" (2,9).

In quantitatively describing the relationship between number of nematodes and plant growth, Seinhorst (14) drew upon the work of Nicholson and Bailey (13) in developing a biologically descriptive model (Table 1, Fig. 1). By this rationale the damage per nematode decreases as population density increases. If one nematode damages a proportion d of the root system, $1-d$ remains functional. Assuming that the nematodes attack the root system independently, a second nematode will, on the average, influence d of the already damaged proportion and d of the undamaged proportion leaving $(1-d)^2$ undamaged (Table 1). Extension of this logic indicates that P nematodes leave z^P , where $z = (1-d)$, of the root undamaged. It follows that the growth of the plant is related to the amount of root undamaged (14), so that the damage function (Table 1) describes the reduction of crop growth due to nematodes. At low population levels, however, there may be no measurable reduction in crop growth, either due to root systems which exceed plant requirements, or to the ability of the plant to compensate for damage. The population density at which damage becomes measurable is the tolerance limit (T) (14).

Similarly, there may be a point below which crop growth or yield is not reduced, regardless of nematode population density. This point is known as the minimum yield (m). For any given set of conditions, the tolerance limit and minimum yield may be zero. The damage function holds for population densities greater than the tolerance limit, and reduces crop growth over the range of relative yields from 1 to m (the minimum yield) (Fig. 1).

Plant-parasitic nematodes are relatively slow reproducing and nonmigratory so that, for annual crops, the population present in the soil prior to planting is a reasonable indicator of nematode stress on the crop as described by the Seinhorst model. A limitation of the model is not accounting for the effect of environmental fluxes on either the nematode or the plant system. In the irrigated agriculture of the southwestern United States, where soil moisture is maintained near an optimum, light is generally not impeded by cloud cover during the growing season, and cumulative temperature conditions are relatively constant among years, the model should hold for specific environments. Although seasonal differences may be minor, geographic variations do affect the relationship. Soil texture affects soil moisture and nutrient status, its environmental suitability for various nematode genera, and its suitability for plant growth. Geographic location may influence plant growth rates as well as rates of nematode metabolic activity. Consequently, it is necessary to define the parameters of the model for specific geographic locations and soil textural conditions. Since definition in every conceivable environmental situation is impossible, model generalization is useful (6,8). Thus, from a range of experiments conducted in different geographic areas, or with varying soil textures within a geographic area, there may be a relationship between the environmental condition and the observed tolerance limit (T), minimum yield (m), or z value of the damage function for a particular plant/nematode combination (Fig. 2). If such relationships were reliable, they would provide a rational generalization of the model to specific agricultural situations (Fig. 3).

Plant-parasitic nematodes seldom occur as monospecific populations in agroecosystems. Consequently, it is necessary to adapt any nematode crop loss models to account for multispecies interactions. Ferris (6,8) approached this problem by considering nematode equivalence, whereby damage functions are developed for a major pathogenic species and the pathogenicity of other species present is ranked in terms of this major species. The pathogenic equivalent index reflects an integral of the biology and mode of parasitism of a nematode. In this case, a single damage function is used and the total pathogenic equivalence of the nematode community is considered. A more satisfactory solution to the problem of multispecies interaction is the expansion of the Seinhorst explanatory model to predict the effects of two or more species (Table 2) (3,4). In this expansion, the differential damage level of the individual species is recognized, and the damage equation becomes a multiplicative function of the individual z values of each species raised to the power of the population level of that species. Some modification is necessary for the tolerance level and minimum yield concepts in the multispecies model. Essentially these become weighted averages of the values for the single species cases (4). Since the basic logic of this multiplicative model requires that the parameters of the single species models for each species be known, implementation of such approaches will be long-term projects. In the interim, the pathogenic equivalence approach (6) provides a biologically rational alternative.

A further requirement of multispecies models is that consideration be given to host status and environmental suitability for each interacting species. In the case of the pathogenic equivalent approach, the single species model is expanded to the appropriate set of environmental conditions (Figs 2 and 3). However, these conditions may not be equally suitable to the interacting species. Thus, a further weighting of the population count is necessary (6,8); for example, a textural preference index (10) (Fig. 4) for a particular species. Further, the pathogenic equivalence index is based solely on the biological capabilities of the nematode and not upon the host response to that nematode. Some cultivars and plant species may exhibit resistance, or even immunity, to particular nematode species and not to others. This can be incorporated in pathogenic equivalence models by

using a host status index. The pathogenic equivalence of the nematode community then becomes the sum of the number of nematodes of each individual species multiplied by its textural and environmental preference indices and by the appropriate host status index. Again, this is a biologically reasonable compromise solution in lieu of the absence of an analytical multi-species model for each crop and environmental situation.

In most experiments to determine nematode damage functions, other pests and stresses are eliminated from the system. In agricultural production systems, however, it is necessary to consider interactions with these pests. The majority of such interactions are perceived and integrated by the plant (7,8), although there are some direct relationships, such as vectoring. In considering the plant as the central subsystem of a crop ecosystem, many pests are primary consumers and can be categorized according to their effects on plant growth. Either they eliminate photosynthetic surface and thus reduce the energy supply into the plant, or they reduce the physiological efficiency of the plant which affects energy supply and its partitioning. Finally, the primary consumers may directly remove or destroy the harvestable yield of the crop (7,8). In most of these cases, the interaction can be considered multiplicative as with the multispecies nematode example (3,4), resulting in the concept of discounting coefficients (12) in multiple regression equations of crop loss. Another group of pests can be considered competitors, that is, weeds may be competing for water, nutrients, or light with the primary crop. In this case, the interaction coefficients may inflate the effect of the competitors, since primary consumers reduce crop growth and give an advantage to competitors.

Field applicable nematode damage functions are appropriately developed in microplots, field plots, and whole field trials. Theoretical models can be tested and validated in greenhouse experiments, but for advisory purposes or crop loss assessments, they must be parameterized under field conditions. In parameterizing a nematode damage function, it is necessary to have a series of plots representing many initial nematode population levels. Such levels may be generated by soil manipulation, partial soil treatments or appropriate rotation patterns. In each case, there is a danger of incorporating another variable into the experiment through the manipulative procedure. Further, a balance must be struck between the number of plots required and the minimum size acceptable for yield measurements on the particular crop. A further consideration, if only nematode losses are to be considered, is the necessity for hand labor or continuous monitoring to eliminate other pests and stresses from the environment. In whole-field trials, some other pests may have to be accepted, but the field can be delimited into subareas with the recognition that nematode populations are seldom uniformly distributed. By randomly locating a series of plots across a field, there is a high probability that a large range of initial population densities will be encountered. Problems associated with this type of experiment include locating of the plots at harvest time, development of a harvesting strategy compatible with the growers requirements, and practical equipment considerations.

Implicit in the assessment of crop losses due to nematodes is the measurement of the nematode population or community. Nematode populations characteristically exhibit a clumped distribution (1,11). In developing nematode damage functions through small plots, it is necessary to base the initial population estimate on at least two separate samples of 12 cores of soil each. The philosophy behind the use of small plots is to reduce the within-plot variability, both in plant growth and nematode population distribution. This raises the question of the validity of extrapolating from models developed in such plots to describe the whole field situations where variability is much greater. Even though a field may be stratified to reduce variability, variances encountered are greater than in small plot studies. However, because of the aggregated distribution of nematodes and the nature of the nematode damage function, sampling systems tend to overestimate damage due to the nematodes and, hence, result in conservative recommendations for population management (15). A major consideration in the measurement of nematode populations is the efficiency and reliability of the extraction system used for removing nematodes from soil samples. Such systems vary in efficiency relative to the size and type of nematode present in the soil, the soil textural char-

acteristics, sample size, and the time of sampling relative to the life stage and activity level of the nematode. It is essential that nematode extraction processes be tested for efficiency, and that nematode count data be adjusted to an absolute scale, to allow comparison between damage functions developed in different locations and with different extraction systems.

In summary, there are many factors which influence the damage to crops by nematodes. These include environmental conditions, soil texture, host variety and structure of the plant-parasitic nematode community. They also include the influence and interaction of other pests and stresses in the environment as integrated by the crop. Partitioning of that portion of crop loss due to nematodes requires the development of biologically explanatory models parameterized under a series of realistic environmental conditions and interpolated appropriately to specific locations. It further involves the accurate measurement and assessment of nematode population levels and community structures, including consideration of the associated variability. Pest-specific crop loss data are useful at various levels for decision processes. On the farm, they should form a basis for pest management decisions and cropping practices. At higher levels, they are indicators of necessary research and funding priorities and of potential need for regional redistribution of resources.

References

1. Barker, K. R., and C. L. Campbell. 1981. Sampling nematode populations. In B. M. Zuckerman and R. A. Rohde (eds) *Plant Parasitic Nematodes*, Vol. III. Academic Press, New York. 508 pp.
2. Cody, M. L. 1966. A general theory of clutch size. *Evolution* 20:174-184.
3. Duncan, L. W., and H. Ferris. 1981. Preliminary considerations of a model of multiple nematode species-plant growth relationships. *J. Nematol.* 13:435 (abstr.).
4. Duncan, L. W., and H. Ferris. 1982. Interactions between phytophagous nematodes. In D. W. Freckman (ed) *Nematodes in Soil Ecosystems*. Univ. Tex. Press (in press)
5. Endo, B. Y. 1975. Pathogenesis of nematode-infected plants. *Ann. Rev. Phytopathol.* 13:213-238.
6. Ferris, H. 1980. Nematology status and prospects: practical implementation of quantitative approaches to Nematology. *J. Nematol.* 12:164-170.
7. Ferris, H. 1981. Dynamic action thresholds for diseases induced by nematodes. *Ann. Rev. Phytopathol.* 19:427-436.
8. Ferris, H. 1981. Mathematical approaches to the assessment of crop damage. In B. M. Zuckerman and R. A. Rohde (eds) *Plant Parasitic Nematology*, Vol. III. Academic Press, New York. 508 pp.
9. Ferris, H. 1982. Nematodes as primary consumers. In D. W. Freckman (ed) *Nematodes in Soil Ecosystems*. Univ. Tex. Press (in press).
10. Ferris, H., and L. W. Duncan. 1980. Consideration of edaphic factors in quantifying nematode stress on plant growth. *J. Nematol.* 12:220 (abstr.).
11. Goodell, P. B., and H. Ferris. 1980. Plant parasitic nematode distributions in an alfalfa field. *J. Nematol.* 12:136-141.
12. MacKenzie, D. L., and E. King. 1981. Developing realistic crop loss models for plant disease. *Proc. Stakman Crop Loss Symposium. Misc. Publ. 7, Minn. Agric. Exp. Sta., Univ. Minn. Press.*
13. Nicholson, A. J. 1933. The balance of animal populations. *J. Anim. Ecol.* 2:132-178.
14. Seinhorst, J. W. 1965. The relationship between nematode density and damage to plants. *Nematologica* 11:137-154.
15. Seinhorst, J. W. 1973. The relation between nematode distribution in a field and loss in yield at different average nematode densities. *Nematologica* 19:421-473.

16. Wallace, H. R. 1973. Nematode Ecology and Plant Disease. Edward Arnold, New York. 228 pp.

Table 1. The relationship between number of nematodes and proportion undamaged root tissue (after Seinhorst (14))

Number nematodes	Proportion root damaged	Proportion root not damaged
1	d	$(1-d) z = z$
2	$d+d(1-d)$	$(1-d) z^2$
3	$d+d(1-d)+d(1-d)^2$	$(1-d)^3$
P		$(1-d)^P = z^P$

Table 2. The relationship between number of nematodes of two species and proportion undamaged root tissue (from Duncan and Ferris (4))

Number nematodes	Species A	Species B	Proportion root damaged	Proportion root not damaged
1		0	a	$(1-a)^2$
2		0	$a+a(1-a)$	$(1-a)^2$
2	1	1	$a+a(1-a)+b(1-a)^2$	$(1-a)^2(1-b)$
2	2	2	$a+a(1-a)+b(1-a)^2 + b((1-a)^2(1-b))$	$(1-a)^2(1-b)^2$
P_a		P_b		$(z_a)^{P_a} (z_b)^{P_b}$

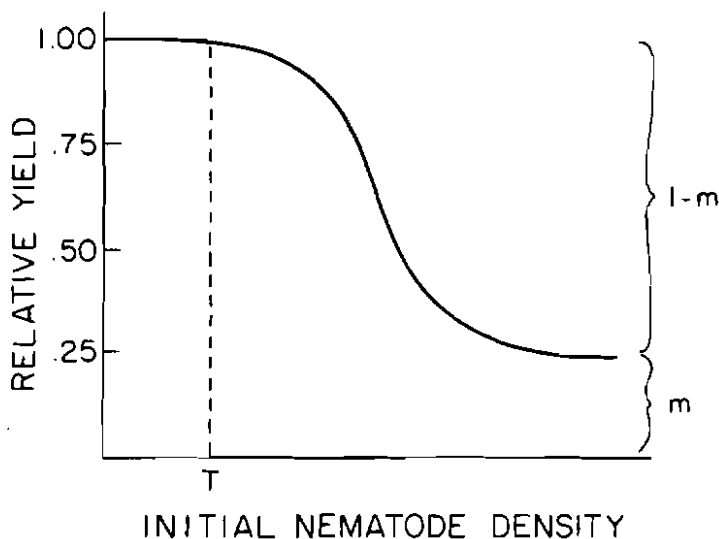


Fig. 1. The relationship between relative plant growth and number of nematodes; y = relative yield, m = minimum yield, T = tolerance limit, z is a constant reflecting nematode damage, P is the initial population density (after Seinhorst (14)).

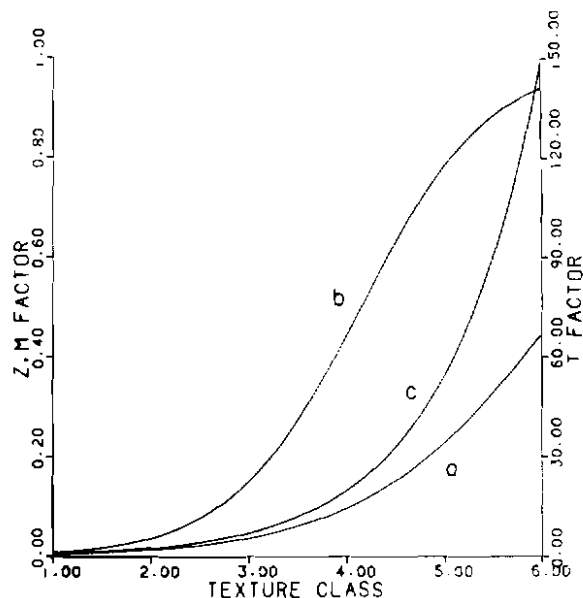


Fig. 2. Hypothetical relationship between soil characteristics and parameters of the nematode damage function $y = m+(1-m)z^{P-T}$; (a) a weighting factor ($f_1(\phi)$) where ϕ is the texture class for the z value such that $z_\phi = z_1 + (1-z_1)(f_1(\phi))$; (b) a weighting factor ($f_2(\phi)$) for the m value such that $m_\phi = m_1+(1-m_1)(f_2(\phi))$; (c) a weighting factor ($f_3(\phi)$) for the T value such that $T_\phi = T_1(f_3\phi)$.

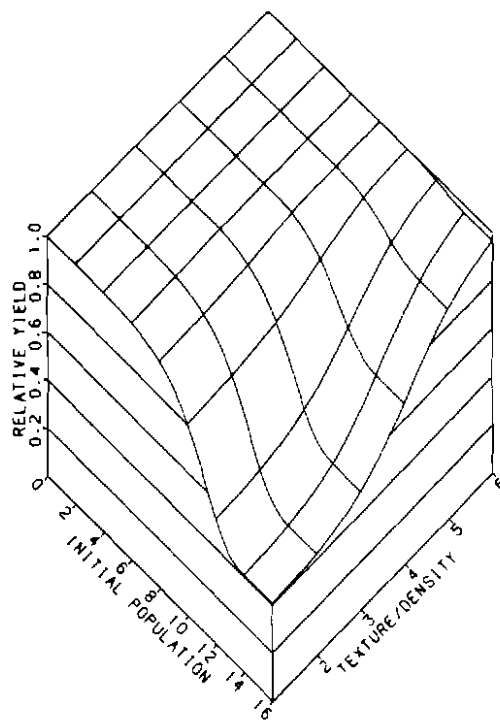


Fig. 3. Potential effects of weighting factors based on soil texture characteristics for z , m and T parameters of the nematode damage function on the nature of the function across textural classes.

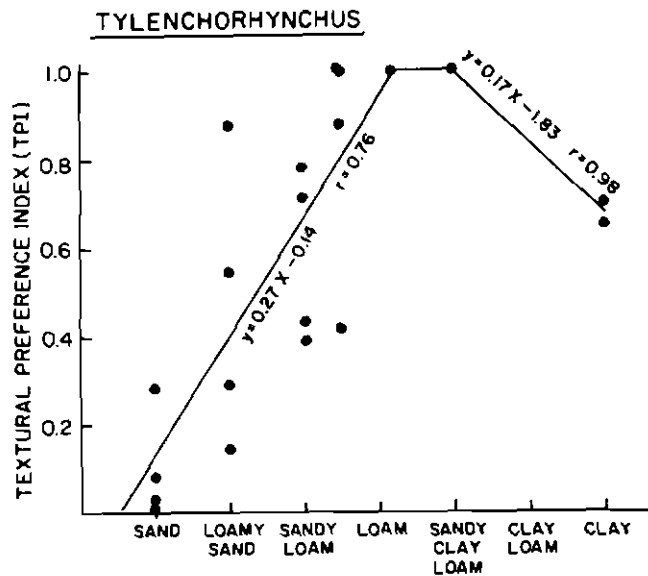


Fig. 4. Textural preference index for the nematode genus *Tylenchorhynchus* as a weighting factor for the potential influence of the nematodes in different soil textural situations (after Ferris and Duncan (10)).