Validation of a Model for Prediction of Host Damage by Two Nematode Species[1]

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Abstract: Plant roots were mechanically injured or subjected to nematode parasitism to test the model of host damage by two nematode species: $y = m' + (1-m')c'z_1^{P_{i1}}z_2^{P_{i2}}$ for $y \leq 1.0$ and $y = 1.0$ for $y > 1.0$, where $m' = m_1 + (m_2-m_1)(1-y_2)/[(1-y_1) + (1-y_2)]$ and $c' = (z_1^{-T_1} + z_2^{-T_2})/2$. Damage functions for greenhouse-grown radish plants (*cv.* Cherry Belle) mechanically injured with small or large steel needles were used to predict growth of plants injured by both needles. Growth predictions accounted for 94%, 87%, and 82% of mean treatment variation in plant height, stem weight, and root weight, respectively. Cowpea (*cv.* California Blackeye No. 5) damage functions, based on preplant population levels of *Meloidogyne incognita* and *M. javanica*, were used to predict seed yield of plants concomitantly infected with various levels of each species. Single species damage functions and population growth curves indicated significant host resistance to *M. incognita* and significantly lower virulence of that species compared to *M. javanica*. Model predictions accounted for 88% of mean seed yield variation in two-species treatments. In a separate experiment, mean top weights of 30-day-old cowpea plants, uniformly inoculated with 20,000 *M. javanica* eggs, increased with increasing levels of concomitantly inoculated *M. incognita* eggs. It is speculated that competitive interactions between *M. incognita* and *M. javanica* mitigated host damage by the more virulent species. *Key words:* root-knot nematode, interaction, population dynamics, Seinhorst model, modeling, damage function.

Journal of Nematology 15(2):227-234. 1983.

Systems involving plants infected by more than one nematode species are frequently studied (4,6,10,11,17), and mechanisms governing interactions in such systems were suggested by Jones (12) and Seinhorst (16). Duncan and Ferris (2) proposed a model of plant yield as influenced by two nematode species, based largely on Seinhorst's model, $y = m + (1-m)z^{P-T}$ for $P > T$ and $y = 1.0$ for $P \leq T$ (15). The model describes host damage as a multiplicative relationship between relative yields (infected plant yield/noninfected plant yield) predicted for the initial population density of each species and modified by interspecies competition. Advantages of the model are simplicity, since for each species only param-

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Received for publication 12 July 1982.

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eters from Seinhorst's equation are used, and the ability to predict host damage related to pairs of species using data from single-nematode species systems. The second point obviates the necessity of obtaining prior data from each host species-pair combination that may occur in the field. Results of three greenhouse experiments to test various aspects of the model $y = m' + (1-m')c'z_1^{P_{11}}z_2^{P_{12}}$ for $y \leq 1.0$ and $y = 1.0$ for $y > 1.0$, where $m' = m_1 + (m_2-m_1)(1-y_2)/[(1-y_1) + (1-y_2)]$ and $c' = (z_1^{-T_1} + z_2^{-T_2})/2$, are reported herein.

MATERIALS AND METHODS

1. *Multiplicative yield relationships:* A system uncomplicated by minimum yield effects of two species (m') was used to test the basic model assumption of multiplicative yield relationships. Because nematode-plant systems generally exhibit a minimum yield, radish (*cv.* Cherry Belle) root systems were mechanically damaged to simulate parasitism, and m' was considered to be 0.0. Plants were grown in 15-cm plastic tubes (4-cm d) filled to within 2 cm of the top with loamy sand (14). Wire screens were fitted in tube bottoms to prevent roots from growing beyond the containers. Tubes were sub-irrigated to provide uniform soil moisture by standing them on clay bricks in galvanized steel pans through which deionized water (1 cm deep) was circulated. Two seeds per tube were planted and thinned to one plant per tube. At weekly intervals, sub-irrigation was interrupted for 48 h while plants were fertilized with 5 ml Hoagland's solution (8).

Two treatment series were established: one to determine Seinhorst parameter values for each damage agent and the other to test the two species model. Five days after planting, 200 plant root systems were randomly stabbed in a continuous series from 1 to 100 times with one of two different size steel needles. Each needle was 10 cm long, but diameters were 0.15 and 0.3 cm to simulate attack by agents with different damage potential. Roots were stabbed by randomly piercing the soil in the tubes at a slight angle toward the center and to a depth of 10 cm. Individual root systems were treated with identical numbers of stabs on four occasions at 3-day intervals so that total stabs ranged from 4 to 400. The second series of treatments consisted of root systems stabbed variously with both needles (Table 1) to simulate multispecies infections. All treatments were completely randomized and grown at daily average temperatures of 24 ± 3 C in a 4.8-m² area in a greenhouse. Two-needle treatments

Table 1. Observed* and predicted effects of number of stabs to radish roots with different diameter needles on plant height and dry stem and root weight.

Number small stabs	Number large stabs	Relative plant height		Relative stem weight		Relative Root weight	
		Obs.	Pred.	Obs.	Pred.	Obs.	Pred.
20	20	0.98	0.96	0.95	0.98	0.91	0.93
	40	0.92	0.93	0.95	0.95	0.84	0.86
	60	0.87	0.89	0.95	0.93	0.73	0.80
	80	0.89	0.86	0.86	0.90	0.72	0.75
	120	0.77	0.80	0.83	0.86	0.60	0.64
60	20	0.96	0.93	0.91	0.96	0.85	0.88
	40	0.89	0.90	0.93	0.93	0.76	0.82
	60	0.91	0.87	0.90	0.91	0.75	0.76
	80	0.83	0.84	0.89	0.88	0.71	0.71
	120	0.81	0.78	0.82	0.84	0.63	0.61
120	20	0.89	0.89	0.92	0.93	0.77	0.82
	40	0.85	0.86	0.89	0.90	0.66	0.76
	60	0.81	0.83	0.87	0.88	0.59	0.71
	80	0.79	0.80	0.88	0.86	0.57	0.66
	120	0.72	0.75	0.82	0.81	0.55	0.57
200	200	0.58	0.61	0.71	0.71	0.40	0.39

*Treatment data are means of 10 replications.

were replicated 10 times; single needle treatments were not replicated. Plant heights were measured 22 days after planting, plants were harvested 5 days later, and stem and root dry weights determined. Height and weight data from each treatment series (large or small needle) were used to determine best fit values for parameters of the Seinhorst model (3) These values were then used in the two-species model to predict mean relative yields in treatments probed with both needles.

2. *Competition-yield effects I:* A similar study was conducted to test whether the minimum yield term of the two-species model adequately approximates interspecific competitive effects on yield. Tubes described in experiment 1 were inoculated in a geometric progression (0, 10, 20 . . . 20480) with various P_i levels of eggs of either *Meloidogyne javanica* (Treub 1885) Chitwood 1949 or *M. incognita* (Kofoid and White 1919) Chitwood 1949. The abbreviation P_i is used in this paper to represent initial population as defined by Seinhorst (15). The subscript, i, represents "initial" as opposed to "mid-season" (m) or "final" (f); it does not refer to the general case of the parameter as commonly used in mathematical literature. Because of wide acceptance of the term by nematologists, P_i should be double subscripted when it is necessary to distinguish between initial populations of more than one species, such as P_{i1}, P_{i2}, $P_{i\ M.\ incognita}$.

Nematode-free treatments, each received a 5-ml micro-organism suspension obtained as filtrate from nematode inocula passed twice through a 26-μm sieve. A second series of treatments combined various numbers of eggs of both nematode species (Table 2). Eggs were obtained (9) from cultures maintained on greenhouse tomatoes. They were inoculated into soil columns by slowly pipetting 5 ml of appropriate dilutions along the side of a 10-cm-deep hole from bottom to top. Three days following inoculation, one cowpea (*Vigna sinensis* (L) Engl. *cv.* Blackeye No. 5) seed per tube was planted; only those which emerged within 5 days were used in the experiment. Plants were grown under the same conditions as experiment 1 until it was determined that cowpeas did not respond well to Hoagland's nutrient solution. At that time sub-irrigation was discontinued and surface-applied, slow-release fertilizer was combined with daily overhead irrigation. The host cultivar was chosen because it is relatively resistant to damage by *M. incognita* while being susceptible to *M. javanica.* Consequently, the assumption of identical niche requirements implicit in this competition model (2) was fulfilled using species which produce different levels of effects. All treatments were replicated 10 times and arranged in completely randomized blocks in a greenhouse. Eighty-one days after sowing, seeds were harvested and dry weights determined. Soil was carefully washed from plant root systems and eggs were extracted and counted. Seed weight averages from single-species inoculations were used to obtain values for Seinhorst model parameters (3) for each species. Mean relative seeds yields in the multispecies treatments were predicted using these values in the two-species model.

3. *Competition-yield effects II:* Results of experiment 2 suggested the need to further test the possibility that host damage caused by nematodes of one species might be mitigated by competition with a less virulent species. Tubes of loamy sand as previously described were infested with 20,000 eggs of *M. javanica,* either alone or in combination with 1,000, 5,000, 10,000, 20,000, or 40,000 eggs of *M. incognita.* Nematode-free treatments received equivalent aliquots of micro-organism suspension as in experiment 2 and all treatments were repli-

Table 2. Observed* and predicted relative bean weights at various P_i of *Meloidogyne javanica* and *M. incognita.*

Initial population		Relative yield	
M. javanica	*M. incognita*	Obs.	Pred.
40	40	1.00	0.96
160	160	0.86	0.85
320	640	0.77	0.77
640	640	0.71	0.73
1280	640	0.70	0.71
2560	640	0.68	0.69
1280	320	0.71	0.71
1280	1280	0.77	0.70
1280	2560	0.67	0.70
20000	20000	0.73	0.68

*Treatment data are means of 10 replications.

cated 10 times. Cowpeas were planted and grown without sub-irrigation as in experiment 2. The first true leaves were removed from all plants early in the experiment because of heavy, random thrips (*Thysanoptera sp.*) damage. Subsequent thrips activity was controlled with dimethoate. Plant dry weights were obtained 30 days after planting. Several seeds which failed to germinate or produced stunted plants were marked during the first week following emergence and discarded from subsequent analysis.

RESULTS

Multiplicative-yield effects: Regression of plant heights (which were incorrectly reported as plant weights [2]) against number of stabs for treatments involving individual needles produced Seinhorst model statistics of $z = .9982$, $m = 0.0$, $T = 11$ for the large needle and $z = 9993$, $m = 0.0$, $T = 7$ for the small needle. Stem and root dry weights resulted in respective parameter values of $z = .9987, .9964$, $T = 10, 7$, $m = 0.0$ for the large needle treatment series and $z = .9995, .9988$, $T = 20, 10$, and $m = 0.0$ for the small needle. Both needles in two-needle treatments had significant effect on plant growth as measured by analysis of variance ($P = 0.01$). Relative yields predicted from estimated parameter values in the two-species model accounted for 94%, 87%, and 82% of variation in height, stem weight, and root weight, respectively, between treatments stabbed with both needles (Table 1). An additive plant damage model, $y = 1 - [(1-y_1) + (1-y_2) \ldots + (1-y_n)]$, as suggested by several workers (1,7,17), accounted for 78% and 75% of variation between stem and root weights in two-needle treatments. Analysis of variance indicated significant improvement of multiplicative model root and stem weight prediction compared to those of the additive model ($P = 0.05$).

Competition-yield effects I: Regression of mean treatment relative yields against P_i (3) in the single-species treatment series produced the following Seinhorst parameter values: *M. javanica,* $z = .999$, $m = .62$, $T = 10$ (range $y = 0.54$–0.99); *M. incognita,* $z = .994$, $m = .86$, $T = 20$ (range $y = 0.83$–1.07). The Seinhorst model accounted for 66% and 82% of between-treatment variation in the *M. incognita* and *M. javanica* series, respectively. Analysis of variance showed significant effect by each species on bean yield in two species treatments ($P = 0.01$). Use of these parameter values in the multi-species model accounted for 88% of the variation in yield between multi-species treatments (Fig. 1 and Table 2).

The superior host status of Blackeye No. 5 for *M. javanica* when compared to *M. incognita* is evidenced by final egg densities (Fig. 2). *M. javanica* egg production at low initial population densities was nearly 25 times that of *M. incognita* after 81 days.

Competition-yield effects II: Addition of *M. incognita* eggs to treatments of 20,000 *M. javanica* eggs resulted in higher yields in direct proportion to *M. incognita* levels (Fig. 3). Linear regression of mean treatment dry weights against ln $(P_i + 1)$ *M.*

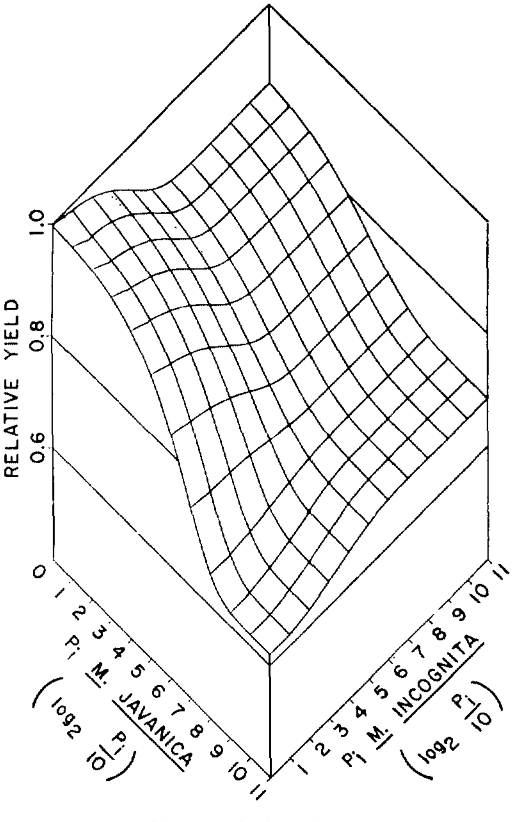

Fig. 1. Predicted relationship between relative dry bean yield of *Vigna sinensis* and P_i of *Meloidogyne javanica* and *M. incognita.*

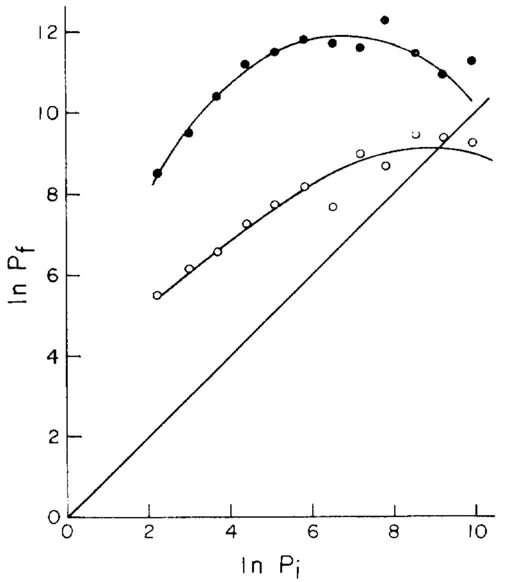

Fig. 2. Egg production on 81-day-old *Vigna sinensis* by *Meloidogyne javanica* (●) and *M. incognita* (o).

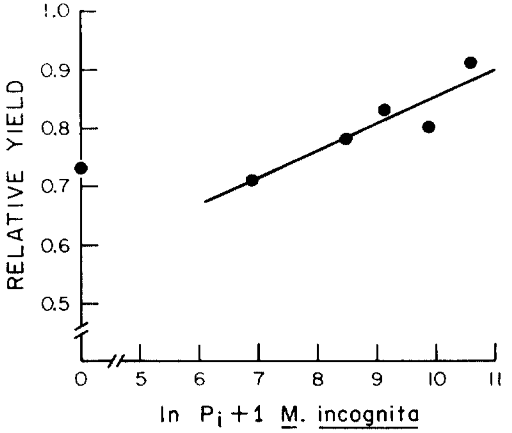

Fig. 3. Effect of increasing *Meloidogyne incognita* inoculum on relative dry stem weights of *Vigna sinensis* inoculated with 20,000 *Meloidogyne javanica* eggs.

incognita accounted for 84% of treatment variation (P = 0.01). Linear regression of individual plant dry weights against the independent variable was significant at the 5% level. A threshold population level of 1,000-5,000 *M. incognita* eggs per tube was required under present conditions before effects on plant growth were detected.

DISCUSSION

Differences between observed relative yields and those predicted by multiplicative yield models of multiple species host damage (i.e., $y = y_1 \times y_2 \ldots \times y_n$) may be partly caused by minimum yield effects (2). Although the highest treatments (400 stabs) in experiment 1 failed to result in 0.0 yield, it is assumed that such a level exists. Close agreement between predicted and observed relative yields in experiment 1 supports the model assumption of multiplicative yield relationships in the case of species that damage identical host tissues (Table 1). Species that damage different tissues may also cause such an effect through functional interactions between host tissues (2). Although two-needle treatments did not exhibit the widest possible range of host damage, they demonstrated significant differences between predictions of the multiplicative yield model and an additive damage model frequently cited.

Damage to root tissue in experiment 1 was not proportional to stem weight reduction and may reflect excess root production as well as a shift in allocation of resources from roots to shoots in response to pathogenesis. The observation may be due largely to experimental method, however, as uniform availability of water and nutrients precludes the necessity of an extensive root system. Also, damage was unnaturally severe from needles which frequently sliced secondary roots from the root system, so that establishment of final root-shoot biomass relationships may not have occurred in the relatively short period between final treatment and experiment termination.

Lack of replication in each single-needle treatment series resulted in low coefficients of determination (r^2 range = 0.12–0.33) for the Seinhorst model compared to those for model predictions of the replicated double-needle treatments (r^2 range = 0.82–0.94). Model ability to predict individual plant growth was measured in unreplicated single-needle treatments, whereas mean data from replicated double-needle treatments provided a measure of model fit to growth of plant populations, masking innate growth differences between individuals. Since knowledge of treatment effects on plant population is of primary concern for applied purposes, it may be preferable to increase replication of fewer treatments to obtain meaningful measures of model accuracy.

Incorporation of the interaction term m′ in the multiplicative yield model significantly improved predictions in experiment 2. The effect was partly caused by holding yield at or above minimum yield of the most virulent species, *M. javanica.* In addition, interspecific competition reduces the amount of host damage caused by either species from that which would occur at the same respective P_i levels in the absence of competitors. In the case of species of different virulence, the resulting damage will be less than that predicted by multiplicative yield effects, although plant damage may be greater than would occur at the same respective P_i levels of single-species infestations (Fig. 1). When P_i levels of a virulent species are sufficient to result in minimum yield, competition for feeding sites or host nutrients by less virulent individuals may so limit the virulent species or its offspring that yield is maintained above the minimum. One treatment in experiment 2 had appropriate P_i of each species to indicate whether this might occur. Minimum yield caused by *M. javanica* in experiment 2 was estimated as 0.62 and occurred when P_i levels exceeded 5,280 eggs/tube. When P_i of both species was 20,000 eggs/tube, yield predicted by the proposed model was 6% greater than 0.62, close to the observed value of 0.71. This observation was supported in experiment 3 by increased growth of plants proportional to *M. incognita* P_i levels, despite high, uniform populations of *M. javanica* in all treatments. Such direct evidence of competition-mitigated damage at the extreme end of the damage curve (Fig. 1) emphasizes a fundamental basis for considering competition in the damage relationship.

The data in experiment 3 (Fig. 3) indicate that a threshold P_i of *M. incognita* is required before measurable increases in plant growth occur. The proposed model reflects this threshold as a function of the P_i of *M. javanica* in the system. Presumably, if half the number of *M. javanica* eggs per tube had been used in experiment 3, minimum yield would have resulted, but fewer eggs of *M. incognita* may have been required to maintain yield above this level.

An important threshold may also exist at low P_i levels of both species. If it is assumed that competition is mediated through the plant (reduced feeding sites or nutrients) rather than directly such as through allelopathy, then for a given species, intraspecific competition is similar to interspecific competition. A threshold level of plant damage must occur before a reduction in development or reproduction rates will be observed. For a given species this level of host damage or competition threshold can be caused independently or in concert with a second species. All that is required are sufficient initial numbers of one or both species. Host damage below this threshold can be estimated by the relationship, $y = [m_1 + (1-m_1)z_1^{P_{i1}-T'}][m_2 + (1-m_2)z_2^{P_{i2}-T'}]$, where $T' = \log (z_1^{T_1}/2 + z_2^{T_2}/2)/(\log z_1 + \log z_2)$, (2). Competition thresholds may be of small consequence for economic management decisions, however, since the competition coefficient (m′) did not influence predictions in the present experiment until considerable host damage had occurred, presumably at damage levels above competition thresholds for either species. For example, setting an arbitrary competition threshold for both species in experiment 2 as low as 81% maximum yield resulted in predictions which were nearly identical to those reported and which explained no additional yield variation.

Variations of the multi-species model that do not incorporate a competition term were less valid predictors of results from experiment 2. For instance, the multiplicative model $y = [m_1 + (1-m_1)z_1^{P_{i1}-T'}][m_2 + (1-m_2)z_2^{P_{i2}-T'}]$, where yield was held at or above 0.62 (i.e., minimum yield of the most virulent species, *M. javanica*), accounted for 56% of variation between seed weight data compared to 88% by the proposed model. A model of additive plant damage explained none of the seed weight variation in experiment 2. When predictions were held at or above 0.62, the additive model accounted for 51% of seed weight variation. Damage overestimates occurred, since the model reflects neither competition nor overlapping damage by individual parasites predicted by the Nicholson model (13,15).

The proposed model is descriptive only in the broadest sense. It reflects the integrated effects of several nematode generations without regard for variable host-parasite relationships through time (16). Competitive interactions are not distinguished based on type of competition, competition thresholds are ignored, and competitive fitness is assumed only to be a function of virulence. Thus, in some respects, the model is of the familiar black-box variety. Models designed for applied use, however, must be balanced between complexity (sometimes accuracy) and manageability. Iterative models of host damage caused by successive generations of parasites could provide more accurate simulation of host-parasite relations if the influences of host phenology on these relationships are known. Interspecific competitive effects on population development could be incorporated in the form of logistic models of population growth (18), given appropriate values for a number of additional parameters. Applied forecasting is unlikely to require models of such complexity due to error levels in population sampling as well as prediction error due to environmental variation. However, such models would be useful to validate performance of less complex equations, which would be more suitable for agricultural forecasting.

Variation between pea yields in field plots naturally infested with three nematode species has been predicted using multiple regression damage coefficients for log numbers of each species (5). Regression models are useful when suitable levels of each species of interest are present in test fields. Parameter values for the present model can be generated in similar fashion by taking partial derivatives (3). An additional advantage of descriptive models, however, is an ability to predict interactions based on hypothetical relationships between system components. The proposed model predicted results of multiple species interactions without historical data from multiple species systems required by regression models. This approach may be useful as models increase in complexity due to inclusion of more components of natural systems as independent variables.

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