

## Nematode-Degree Days, a Density-Time Model for Relating Epidemiology and Crop Losses in Perennials

J. W. NOLING<sup>1</sup> AND H. FERRIS<sup>2</sup>

**Abstract:** The impact of *Meloidogyne hapla* on alfalfa (*Medicago sativa*) yield was described by a multiple point damage model as a function of current plant status, cumulative pest stress, and crop history. Nematode-degree days (NDD<sub>e</sub>), calculated on a physiologic time scale as total area under the adult female population density curve, were used to express *M. hapla* parasitism as cumulative nematode dosage. NDD<sub>e</sub> increased exponentially over physiological time at rates relative to *M. hapla* initial population density of eggs and second-stage juveniles (Pi). Dosage accumulation rates, varying from 213 to 272 NDD<sub>e</sub> per degree day, did not differ ( $P = 0.05$ ) among six Pi levels. Cumulative yield reductions, increasing linearly with NDD<sub>e</sub> over time to 50% of the *M. hapla*-free controls, were well correlated for the six initial Pi levels ( $r^2 = 0.93$ ). Progressive reductions in alfalfa yields to 65% of the nematode-free controls, reflective of the prolonged exposure of the crop to *M. hapla*, were adequately described by NDD model estimates of either combined population densities of eggs and juveniles or adult females. Cumulative area under the combined eggs (e) and juvenile (J) population curve (NDD<sub>e+J</sub>) and NDD<sub>e</sub> were linearly related ( $r^2 = 0.97$ ).

**Key words:** root-knot nematode, damage function, multiple point model, crop loss assessment, alfalfa, *Medicago sativa*, *Meloidogyne hapla*.

Plant growth, yield response, and critical periods of plant sensitivity to nematodes have been described quantitatively by nematode damage functions (11,26,30). Critical point models, relating a parameter of plant performance to a single estimate of nematode population density, have been used extensively as nematode functions for annual crops (4). Attempts to relate perennial crop damage with nematode numbers at periodic intervals using critical point models (2,12,34) have generally failed in that they have not described the temporal nature or accounted for historical effects of the host-parasite interaction.

As with annual crops, a dose-response relationship for describing pest-induced damage in perennial crops is needed. The description of the relationship is more complex than with annual crops because of the protracted time horizons and cyclic growth processes associated with perennial crop productivity. In perennial crops, the relationship between nematode population density and yield can be influenced by

plant age (14,25,37), pest introduction and buildup of initially nondetectable populations (3), and seasonal variations of other biotic and abiotic factors (28).

Various methods have been used in plant pathological systems to describe stress development over time and to relate yield losses to stress severity. Cumulative aspects of plant stress have been demonstrated in plant pathology (5,7-10,16,17,29,33,36), entomology (1,15) and plant physiological studies (27). In each case, multiple point models, requiring periodic measurements of abiotic conditions or pest population density and plant growth, are used to quantify the sequential effects of plant stress over the phenological development of the plant.

A similar conceptual approach to considering the sequential effects of nematodes on perennial crops is proposed. Host response to nematode stress is described as a function of current plant status and cumulative pest stress as well as crop history. A yield-loss model linking the population dynamics of *M. hapla* with the long-term performance of a perennial alfalfa (*Medicago sativa* cv. Cuf 101) crop is presented. A field microplot experiment examined the effects of population development of seven initial inoculum densities of *M. hapla* on the growth, development, and yield of al-

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<sup>1</sup> Assistant Professor, Department of Entomology and Nematology, University of Florida Citrus Research and Education Center, Lake Alfred, FL 33850.

<sup>2</sup> Professor, Division of Nematology, University of California, Davis, CA 95616.

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falfa in terms of a cumulative pest dosage concept, nematode-degree days (NDD).

#### MATERIALS AND METHODS

*Yield-loss model:* A multiple point model (Fig. 1) was derived to describe the functional relationship between decreasing cumulative yield and *M. hapla* population density over time. Sequential yield responses in alfalfa, indicated by the vertical, sigmoidally-shaped planes, are described as functions of cumulative nematode stresses. In the model, preplant population density governs both rates and magnitude of the yield losses during the productive life of the alfalfa stand. The model assumes that population densities of *M. hapla* do not increase without limit but are damped by density-dependent factors and food supply constraints. As time progresses and nematode population densities increase, plants are weakened further by nematode stress. As a result, cumulative yield reductions increase through sequential harvests as indicated by the increasing height of each vertical crop loss plane over time.

Nematode-degree days, a stress unit index, are calculated as the product of each root-colonizing, *M. hapla* development stage density and the physiological degree-day units that each stage has been in contact with the alfalfa root, summed across all stages and time. Cumulative yield reductions are estimated by locating the point on the response surface corresponding to the X-Z intersection of the number of NDD to which the plant has been subjected and the current age of the plant in degree-day units. Damage is observable only after a threshold number of NDD. The tolerance limit is assumed to increase with plant age (31).

The economic threshold for a specific management decision reduces to a single plane that slices horizontally through the crop loss surface parallel to the X-Z plane. Depending on Pi, a time-varying economic threshold exists as a function of host suitability and sensitivity.

*Data:* Alfalfa yields and *M. hapla* population densities (eggs, soil juveniles, and

root-parasitic stages) were assessed at seven consecutive harvest periods in microplots. Introduction of six Pi (4, 43, 217, 434, 1,085, 2,170 eggs and larvae/1,000 cm<sup>3</sup> soil) of *M. hapla* into the microplots on 6 January 1983 and the methodology employed in data collection were previously described (20,21). Cumulative yield was calculated by summing individual alfalfa yields for each microplot across time and cumulative yield loss was calculated by summing the difference between the average yield of the nematode-free controls and the observed yield in each of the *M. hapla*-infested microplots over time. A continuous record of soil temperature at 45 cm deep was used to calculate degree days from a basal development threshold of 10 C (20).

*Analysis:* Calculation of NDD based on the cumulative product of all root-parasitic stages and contact times, as initially proposed in the NDD model (Fig. 1), was not used in the damage analysis because of the inability to accurately determine the presence and (or) age distribution of the preadult stages of *M. hapla* in roots at high densities. Mature, egg laying females, which could be counted easily, were used as an integral of nematode stress (root contact) for all preadult, root-parasitic stages.

For the analysis, the mean number of mature females per gram of root for each Pi was plotted against degree days. Each sequential point on the population curve was linearly connected, and the area under the curve (AUC) was calculated by summing the areas of each trapezoid:  $\text{area} = 0.5 \cdot (H_1 + H_2) \cdot \text{base}$  (36). The heights of each trapezoid (H1, H2) are formed by the population densities of *M. hapla* females at each of two consecutive dates, whereas the base is the number of degree days elapsed between the two dates. The total area under the population curves represents the summation of NDD, and expresses cumulative nematode dosage. The relationship between NDD, (AUC) and cumulative yield reduction for each alfalfa harvest was then determined in a separate regression analysis for each initial inoculum level. Cu-

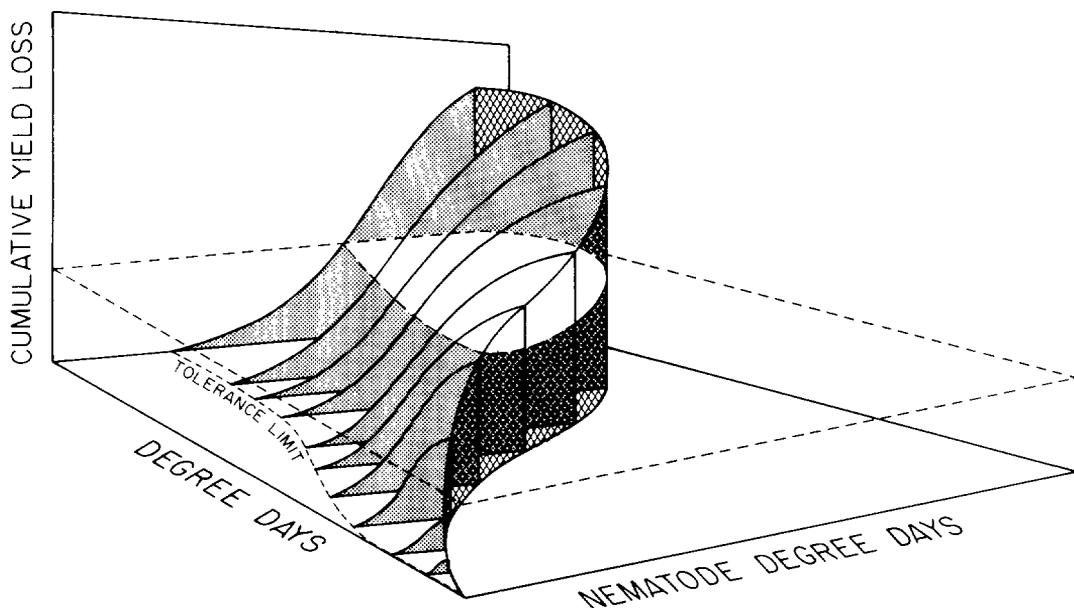


FIG. 1. Conceptual model of a nematode damage function for a perennial crop. Nematode-degree days is an index of cumulative nematode stress (area under nematode population curve), which increases with physiological time (degree days). The damage rate (slope of the surface) varies with time and cumulative nematode stress. The economic threshold is reached at any point in time and cumulative nematode stress at which its cumulative loss is equal to the cost of management.

cumulative area under the combined eggs and soil juvenile population curves ( $NDD_{e+j}$ ) was similarly calculated and used in a regression analysis as a predictor of  $NDD_e$  yield losses.

Alfalfa yield reduction at each harvest was expressed as a percentage of the average yield of the nematode-free controls and plotted against  $NDD_e$ . A natural growth function ( $y = a - ae^{-bx}$ ) was fitted to the data and used to describe the relationship between percent alfalfa yield reduction ( $y$ ) and cumulative  $NDD_e(x)$ . The maximum percent yield reduction ( $a$ ) for each  $P_i$  was estimated by averaging percent reduction in yield over the last five alfalfa harvests ( $DD > 4,007$ ). A natural log transformation was used to obtain estimates of the damage rate ( $b$ ) for each initial inoculum level. In a final comparison,  $NDD_e$  and  $NDD_{e+j}$  were used as independent variables and predictors of cumulative alfalfa yield in a Seinhorst regression model (30).

## RESULTS

Cumulative area under the female population curve,  $NDD_e$ , initially increased exponentially at rates relative to  $M. hapla$   $P_i$  (Fig. 2). Following an initial logarithmic growth phase and attainment of ceiling density,  $NDD_e$  increased linearly at constant rates. Dosage accumulation rates, varying from 213 to 272  $NDD_e/DD$ , did not differ ( $P = 0.05$ ) among  $P_i$  levels (inset, Fig. 2).

Cumulative yields increased through time at rates relative to  $P_i$ . Cumulative reductions in total yield, relative to the  $M. hapla$ -free controls, increased with time, generally increasing with increasing  $P_i$  (Fig. 3). By the end of the experiment, cumulative yield reductions were approaching 50% of the nematode-free controls at the lower  $P_i$  ( $\leq 434$  eggs and juveniles/1,000  $cm^3$  soil) and exceeded 50% at the two highest levels ( $> 434$ ).

Regression analyses of cumulative yield

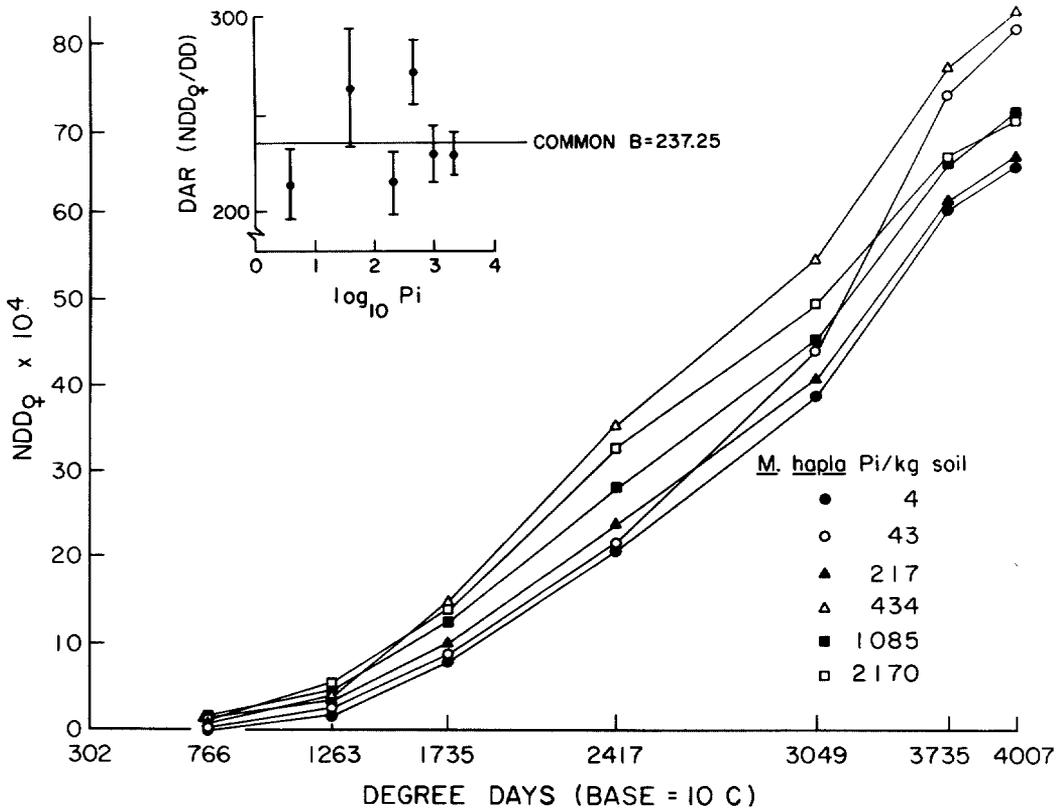


FIG. 2. Relationship between mean ( $n = 15$ ) cumulative area under curves of *Meloidogyne hapla* mature females per gram of alfalfa root (cv. Cuf 101) through physiological time for each of six initial inoculum densities (4, 43, 217, 434, 1,085, 2,170 eggs and juveniles/1,000  $\text{cm}^3$  soil). Each data point represents the mean of five replicates. Inset: Relationship between dosage accumulation rate ( $\text{NDD}_\text{♀}/\text{DD}$ ) and initial *M. hapla* inoculum density.  $b_c$  = common slope for entire data set.

reductions with  $\text{NDD}_\text{♀}$  for each harvest strongly support the proposed  $\text{NDD}$  yield-loss model (Table 1). As  $\text{NDD}_\text{♀}$  increased, cumulative yield losses increased linearly as indicated by the increasing height of each response plane from one harvest to the next (Fig. 4). The rates of cumulative yield reductions per  $\text{NDD}_\text{♀}$ ,  $b$ , generally increased with  $P_i$  (Table 1). The range of regression coefficients of determination, 0.97–0.98, indicates that almost all of the variation in cumulative yield loss for each *M. hapla* population curve is explained by the  $\text{NDD}$  yield-loss model. For the entire set, cumulative yield reduction and area under the curve for the six  $P_i$  levels were well correlated, explaining 93% of the variation. Evaluations across *M. hapla* treatments, however,

indicated in some cases that large  $\text{NDD}_\text{♀}$  values were associated with relatively lower cumulative yield losses. This is evident when the surfaces of harvest-specific response planes are examined. The width of each response plane represents the range of mean  $\text{NDD}_\text{♀}$  values observed at a specific harvest date. The disproportionality of  $\text{NDD}_\text{♀}$  to cumulative yield reduction is represented by the "ridge" effect produced on the top surface of each plane for degree days  $> 1,735$  (Fig. 4).

Percentage alfalfa yield reductions at each harvest generally increased at a decreasing rate over time as cumulative  $\text{NDD}_\text{♀}$  increased (Fig. 5). In contrast to final cumulative yield reductions of 50%, yield reductions for individual harvests increased

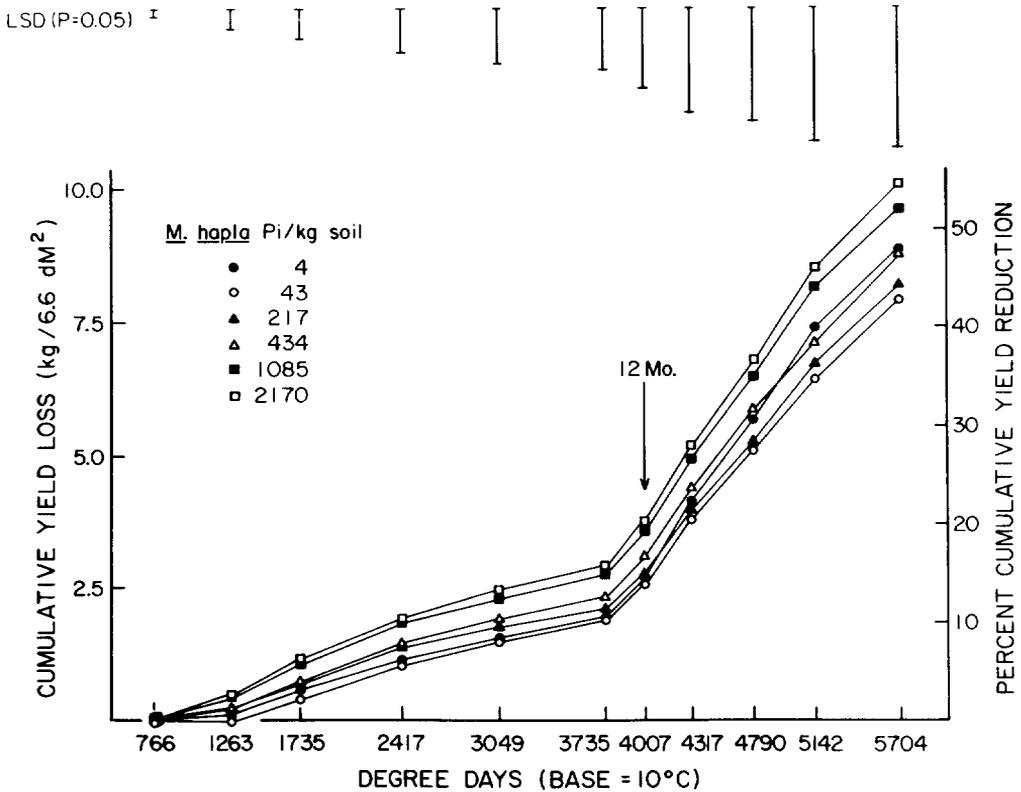


FIG. 3. Influence of *Meloidogyne hapla* on cumulative yield loss of alfalfa (cv. Cuf 101) through time for each of six initial inoculum densities (4, 43, 217, 434, 1,085, 2,170 eggs and juveniles/1,000 cm<sup>3</sup> soil).

over time to an asymptotic, maximum level of 70% during the final harvests. Initially, alfalfa yield reductions were negative, a result of the general yield stimulation that occurred in the presence of *M. hapla* at the first harvest. A natural log linearization of the percentage yield reduction curves showed that the damage rate for individual harvest yields did not differ among Pi (inset, Fig. 5). A strong linear relationship, explaining 97% of the variation, described the relationship between cumulative area under the combined eggs and juvenile population curves (NDD<sub>e+j</sub>) and NDD<sub>s</sub> (Fig. 6).

DISCUSSION

The impact of *M. hapla* on alfalfa yields begins in the seedling stage, with damage expressed throughout the crop growth period as a difference in the number and size of plants (20). There is a progressive reduction of yields, from an initial stimula-

tion to losses exceeding 70%. This progressive reduction in yield reflects the effects of prolonged exposure of the crop to *M. hapla* and demonstrates the need for studying the impact of nematode disease over the productive life of the crop. Similar host-parasite relationships with other perennial crops have been observed in re-

TABLE 1. Regression analysis of cumulative yield loss and area under the female population curve (NDD<sub>s</sub>) over degree days for each of six initial inoculum densities (Pi) of *Meloidogyne hapla*.

<i>M. hapla</i> Pi (per 1,000 cm <sup>3</sup> soil)	Damage rate (b) × 10 <sup>-9</sup>	b ± SE × 10 <sup>-5</sup>	r <sup>2</sup> × 10 <sup>-4</sup>
4	790,800	6	9,686
43	834,871	6	9,781
217	812,082	6	9,766
434	874,982	5	9,829
1,085	971,475	6	9,789
2,170	1,005,321	6	9,799
$\bar{x}$ (Pi[1-6])	894,109	4	9,274

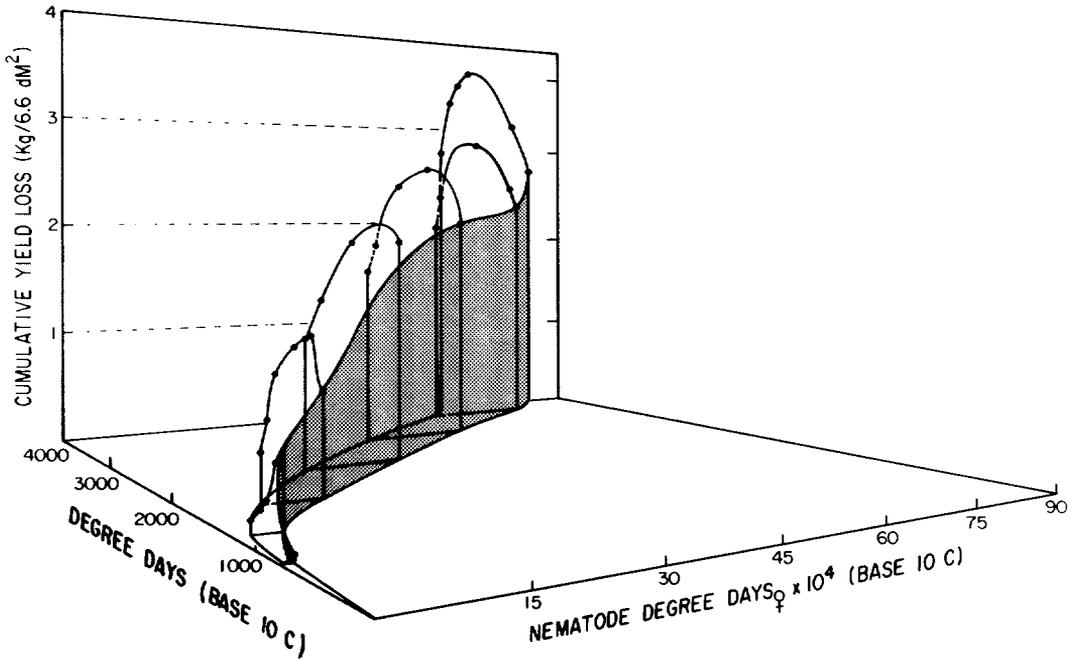


FIG. 4. Response surface relationship between mean cumulative yield loss of alfalfa (cv. Cuf 101) and mean cumulative *Meloidogyne hapla* plant stress, measured as nematode-degree days (NDD<sub>s</sub>), through physiological time. Each data point represents the mean of five replications.

response to nematode attack (22,35). In citrus, reductions in plant growth closely paralleled nematode population density increase, with losses increasing with time (23,24,32). Bird (6) showed that growth of peach at the end of the first year still reflected Pi of *Pratylenchus penetrans*, but by the end of the second year, all Pi had equivalent effects. Although *P. penetrans* populations were not assessed over time, it was suggested that this may be an indication that the nematode populations reached ceiling density by the end of the second growing season.

In this study, increasing the number of nematodes (NDD<sub>s</sub>) that contact the alfalfa root system results in an increasing reduction in cumulative yield. Due to the rapid population increase to ceiling density, final cumulative yield reductions did not differ ( $P = 0.05$ ), although yield differences were generally reflective of Pi.

Initial inoculum levels or population densities at each harvest were not adequate predictors of plant growth. An improvement in the predictive ability of the Sein-

horst model (30) occurs when cumulative *M. hapla* population densities are regressed with yield or cumulative yield for specific harvest dates. Inclusion of cumulative parameter values into the Seinhorst model was an attempt to recognize, at least partially, the dependence of alfalfa yields to a history of plant stress. Even then the Seinhorst model did not adequately describe the damage relationship. Once all Pi converged to a ceiling density, any curve, all of which had low  $r^2$  values, could be fit to the two separate groups of data points formed by the nematode-free control, forming one cluster of points, and the *M. hapla*-infested microplots forming the other. Considering the initial stimulatory effects of *M. hapla* on alfalfa yield, interpretation of damage function parameters based on single assessments of population density may also contribute to erroneous expectations of yield loss. A more appropriate use of the Seinhorst model for describing yield losses in perennial crops would be to relate changes in relative yield to NDD (Fig. 7).

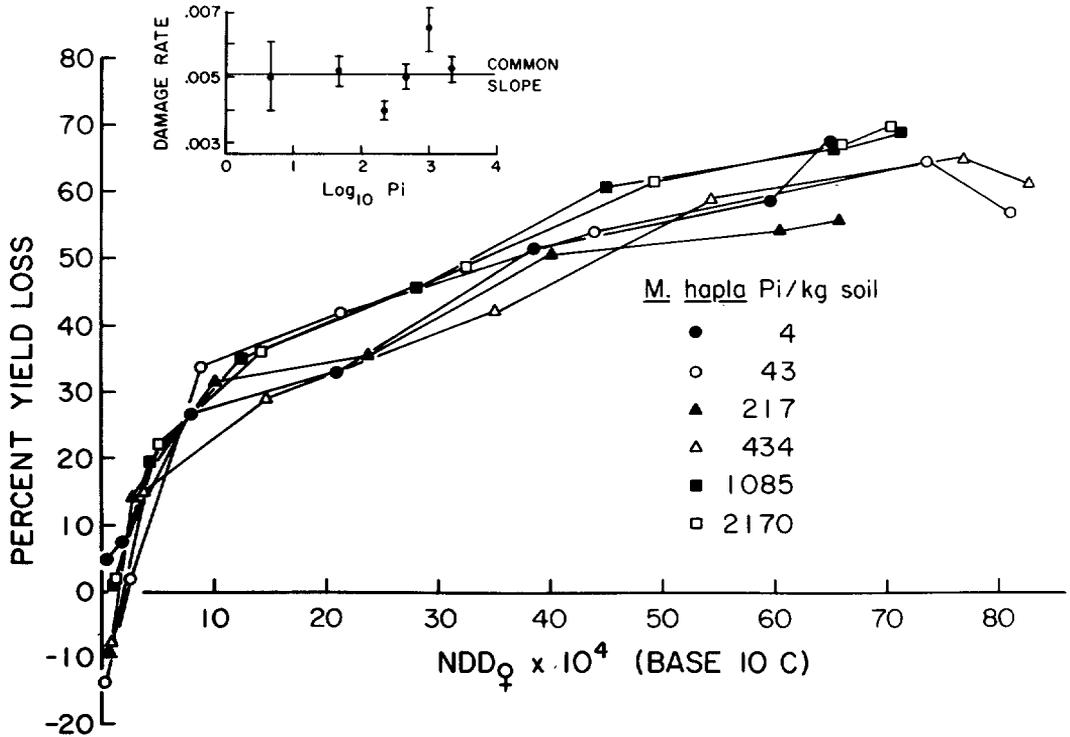


FIG. 5. Relationship between percentage suppression in alfalfa yield (cv. Cuf 101) at each of seven alfalfa harvests and cumulative area under population curve of *Meloidogyne hapla* mature females per gram of root for each of six initial inoculum densities. Negative suppressions indicate a yield stimulation. Inset: Relationship between damage rate (% yield suppression/ $NDD_0$ ) and initial *M. hapla* inoculum density.  $b_c$  = common slope for entire data set.

When nematode stresses to the developing seedling are extensive, the ultimate size attained by the plant is limited and further nematode population growth is constrained. The result is greater cumulative yield loss with fewer  $NDD_0$ , relative to other *M. hapla* populations which were not growth limited. This deviation from simple linear proportionality has been documented for other disease loss systems (33). For nematological systems, it is expressed in the form of the nematode damage function where damage per nematode decreases to a minimum asymptotic level as  $P_i$  increases (30). A logical modification of the yield-loss model would incorporate a ridge effect to compensate for the disproportionality in the damage relationship. Plant sensitivities, apparently higher during stand establishment, may need heavier

weighting in relation to time when describing yield losses (18).

The fact that all populations of *M. hapla* in this study converged on a ceiling density was an interesting outcome from an ecological and population biology perspective. However, this outcome prevented a full test of the validity of the proposed response surface and of the dynamic nature of the tolerance level. This is illustrated in the response surface in that the only areas in which yield loss information is available are in close proximity to ceiling densities. Research in alfalfa resistance and plant age effects (14) suggests that yield reductions may decrease as the alfalfa plant ages, due to increased resistance to penetration and development of subsequent generations of nematodes.

The damage rate (b) expresses the in-

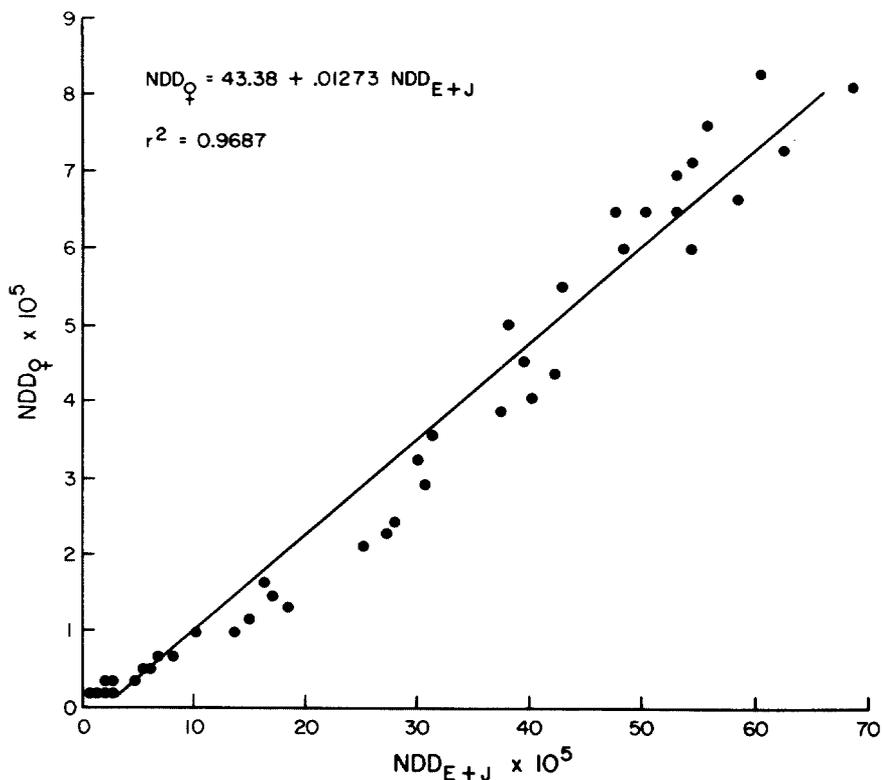


FIG. 6. Relationship between cumulative area under *Meloidogyne hapla* adult female population curve ( $NDD_{\text{♀}}$ ) and area under combined eggs and juvenile population curve ( $NDD_{E+J}$ ). Each data point represents mean of five replications.

stantaneous rate of change in cumulative yield or percentage yield reduction to each unit increase in  $NDD_{\text{♀}}$ . The shape of the percentage yield reduction curves indicates that the maximum growth potential of an alfalfa plant is about 30% of the yield of the nematode-free controls. It is not known if a minimum yield level of 30% is a seasonally modified, temperature-dependent phenomenon. Minimum yield may cycle, increasing during the winter and spring in nondormant alfalfa and decreasing during the summer and fall as a result of differential growth rates of plant and nematode.

A major emphasis of this study was to develop a data base with which to test a model relating nematode stress and yield reductions in a perennial crop. This study demonstrates that cumulative yield losses from *M. hapla* can be measured from  $NDD_{\text{♀}}$

dosage levels, calculated as area under the population curves. The numerous observations that were made over time provided more complete information about the biology of the nematode and its interaction with the host plant than is currently available. The high  $r^2$  values obtained for the NDD analysis indicate that the generalized model may have sufficient predictive power for practical use in agriculture.

The very nature of the multiple point model requires that numerous observations be made to describe the functional relationship between nematode stress and plant growth over time. To apply the NDD yield-loss model in established perennials would have similar information requirements. First, some reference nematode-free condition is needed to provide a benchmark for the calculation of yield losses. From a practical standpoint, reference

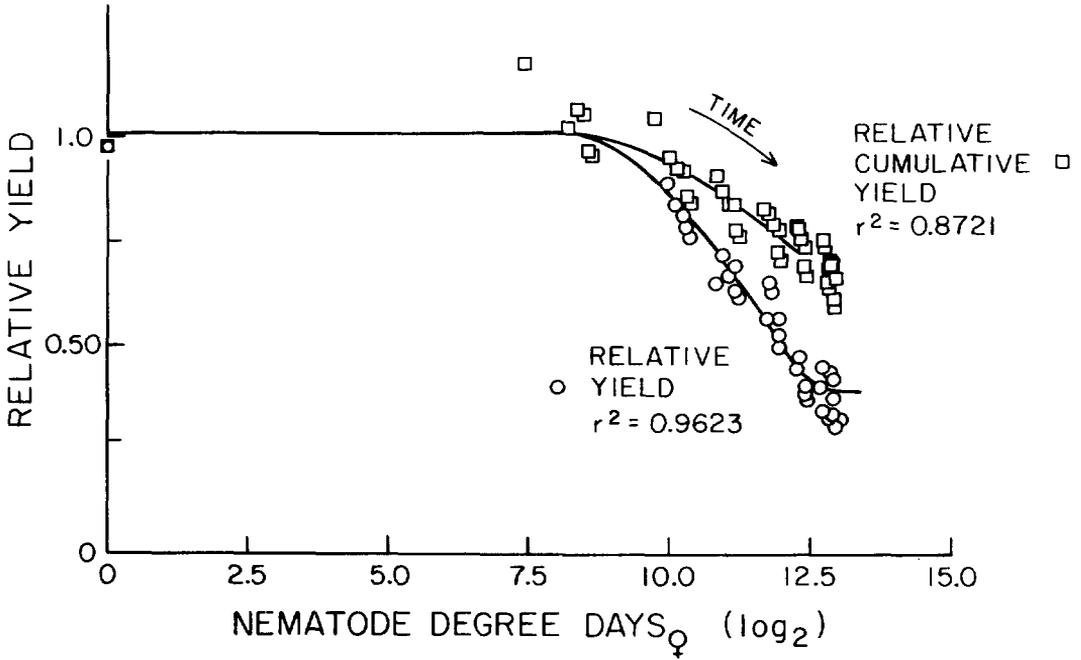


FIG. 7. Relationship between relative yield and relative cumulative yield and nematode-degree days (NDD<sub>e</sub>). The general influence of time is indicated.

yields may be based on grower experience and expectations of crop performance. At the same time the influence of other yield reducing factors and crop management practices needs to be estimated to adjust crop yields accordingly. Second, observations of yield and nematode population growth at and between two consecutive harvest dates are required. From this information, a current fix on the damage rate can be estimated and used to project future losses. The process is repeated and damage rate estimates updated based on additional sampling and yield loss information. As the number of yield loss and nematode population observations increases, so then does the precision of the loss estimate.

Density determinations for root and soil populations of *M. hapla* were conveniently scheduled at ca. 500 degree day intervals. The timing of population assessments, although somewhat fortuitous, closely approximated average generation time of the nematode and harvest scheduling. In other crops, the timing of population assessments must relate to the temporal aspects

of population change from an understanding of the biology and phenology of the nematode-crop interaction. The strong linear relationship between  $NDD_{e+J}$  and  $NDD_e$  suggests that  $NDD_{e+J}$  may be a useful, cost-efficient predictor of alfalfa yield losses. The biological significance of the slope value (0.012373) indicates the non-equivalence of  $NDD_{e+J}$  and  $NDD_e$  units, but also represents the low probability of survival to adults occurring in egg and juvenile populations of *M. hapla*. The cost involved in sampling to determine population development at various points during the growth of the crop, as required by multiple point models, may also limit the use of these models in low-value annual or perennial crops. In these cases, simulation techniques may be useful for prediction of population growth processes, estimates of area under the population curves, selection of appropriate cultivars or rotation crops, and projection of crop plow down dates. Further, the absence of available postplant management options during the growing season for perennial crops such as alfalfa may dis-

count their practical utility. The utility of the model may not be in its real time descriptive ability, but in its predictive abilities in the formulation of long-term optimization of crop management strategies based on nematode dosage accumulation and dose-response functions for crops and cultivars with different levels of resistance and tolerance to nematodes. In addition, the model points out that Pi below detection thresholds (four eggs and juveniles/1,000 cm<sup>3</sup> soil) can build to ceiling densities rapidly and inflict serious losses in crop yields. Support for preplant attempts to eradicate nematodes may therefore be justified for some perennial crops. The need for development of postplant control strategies and an epidemiological management decision information base to determine when it is appropriate to employ these models is also underscored (13,19,36).

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