# Modification of a Computer Simulation Model for a Plant-Nematode System

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*Abstract:* New data on egg development and death rates, and refinements of logic concerning interaction of the nematode and host, were incorporated into a simulation model of a *Meloidogyne arenaria* and grapevine system. Simulations of field data improved but other areas of weakness in the model were discovered. Two peaks in the egg population curve suggested that the nematode was able to complete two life cycles before host dormancy and declining temperatures limited physiological activity. *Key Words: Meloidogyne arenaria,* population dynamics, nematode-host interaction.

The development of a computer simulator (MELSIM) of a nematode-plant system (2, 3) has assisted in directing research efforts (4, 6). Experimentation with the simulator has exposed errors which required refinements in the logic of the model. The result is that the simulator must be updated periodically. It is hoped that the simulators predictive ability will improve as knowledge of the system is gained. This paper reports the effects of incorporating data on egg development and death rates (4) into the model, and of some logic refinements in the relationship of numbers of nematodes to plant damage and the influence of the physiological status of the host. Trial simulations are compared with field data (5).

*Egg development and death rates:* Experiments on *Meloidogyne arenaria* egg development relative to temperature (4) indicated the need for two regression models, one to describe the development and hatch rate of 74% of the egg population and the other to describe the slower hatch of the remainder. The simulator was modified to partition each cohort of newly deposited eggs into two developmental/hatch groups. Eggs developed according to a temperature-dependent rate (proportion of development completed per h):

$$D = (23.5\,T - 235)(10^{-5})$$

Seventy-four percent of the eggs hatched at maturity while the remainder hatched at a rate (egg hatch/egg/h):

$$H = (3T - 30.5)(10^{-5})$$

Studies of the effects of temperature on egg death rate (4) were used to formulate models based on temperature and length of exposure. Death rates (deaths/egg/h) during the first week of exposure to sub-optimal temperature were described by:

$$R = (459.5 - 38.5T + 0.9T^2)(10^{-5})$$

and during subsequent exposures by:

$$R = (10855.9 - 606.2T + 14.7T^2 + 20.3L^2 - 1.9TL^2 + 0.04T^2L^2)(10^{-7})$$

where T = temperature and L = length of exposure in days.

Since temperature experiences of each daily cohort of eggs will vary, the deaths of each age group of eggs are determined individually. The data base for the models was developed at constant temperatures (4), and the simulations involve fluctuating temperature. It could be argued, therefore, that the temperature-death rate models are somewhat misused in the simulator since the age of an egg is not a measure of time

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of exposure to constant temperature. However, temperature fluctuations in soil are buffered, and changes are gradual. Consequently, use of these models is more reasonable than in an aerial system, where time-temperature interactions might be greater.

*Relationship between nematode densities and plant damage:* Seinhorst (13) developed models relating plant damage to numbers of nematodes based on Nicholson's (11) competition curve. The essential point of these models is that as the number of nematodes per unit weight of root increases, the damage to plant growth caused by each nematode decreases. The relationship between log nematode density and plant growth approaches linearity beyond the tolerance limit of the plant, supporting empirical observations (12). The diminishing effect of increased densities was not considered in the original simulation model (2), but its logic is recognized and has been included.

Seinhorst (13) elaborated upon the basic model in consideration of continued plant growth and replacement of affected parts. This elaboration is unnecessary for the simulation model since the number of nematodes and amount of root tissue are continually updated. The validity of the underlying assumptions of Seinhorst's (13) damage model has been questioned on the basis that attraction of larvae to infected root tips would negate the criterion of independent larval activity (16). Attraction of larvae to root tips could be incorporated in the simulator if conclusive quantitative data were available.

In the modified simulation model, numbers of nematodes per unit weight of root and plant damage are related through the epidemiological rationale of Vanderplank (15). The effect of increased density was originally expressed arithmetically, each additional nematode having equal influence on plant growth (2). Applying Seinhorst's (13) damage function to the relationship, the proportion of the root not damaged after infection by one nematode is $(1 - 1/TW)$, where T is the number of nematodes per unit weight of root at which growth ceases, and W is the root weight. Then, the proportion of the root not damaged by $(A + P)$ nematodes is:

$$(1 - 1/TW)^{(A + \beta P)}$$

where A is the number of adult females, P the number of third- and fourth-stage larvae, and $\beta$ the ratio of the damage caused by a parasitic larva to that caused by an adult female. This function now becomes the value $(1 - X)$ in the simulation model (2); it represents the proportion of root which is healthy and available for plant and nematode growth. At each iteration in the simulation, the root weight and number of nematodes are calculated and updated and $(1 - X)$ is reevaluated.

*Effects of seasonal changes in host physiology:* There is an annual cycle of vine (*Vitis vinifera* L.) growth, related to temperature and season, expressed in differential root, shoot, and berry growth, and translocation of carbohydrates to and from the roots (17). Freeman and Smart (7) observed a periodic pattern of root production in grapevines with aerial and subterranean parts competing for assimilates. Active root development began several weeks after bud burst and the start of shoot elongation, and continued until after berry maturity. It is a reasonable assumption that growth activity aboveground can be used as a measure of physiological activity within the plant at the beginning of the annual growth cycle. This would include physiological activity of root tissues because water uptake and mobilization of stored assimilates must occur at this time. Productive activity (growth and reproduction) of the nematode parasitic stages is related to the physiological activity of the plant (1) as intensive host metabolic activity is generated at the site of host-parasite interaction (9). Accordingly, a host physiology function has been incorporated in the simulator. The grapevine growth algorithm is based upon degree-hours accumulated by the plant on a seasonal basis (2). The host physiology function is calculated from the rate of plant growth (vegetative and fruit) at any time relative to the maximum rate of growth during the season and is modified by root growth activity. Thus,

$$P_t = (G_t/G_{max})(R_t/R_{max})$$

where $P_t$ is the effect of host physiology at time t, $G_t$ represents the total aboveground growth rate and $G_{max}$ the maximum growth rate possible according to the degree-hour

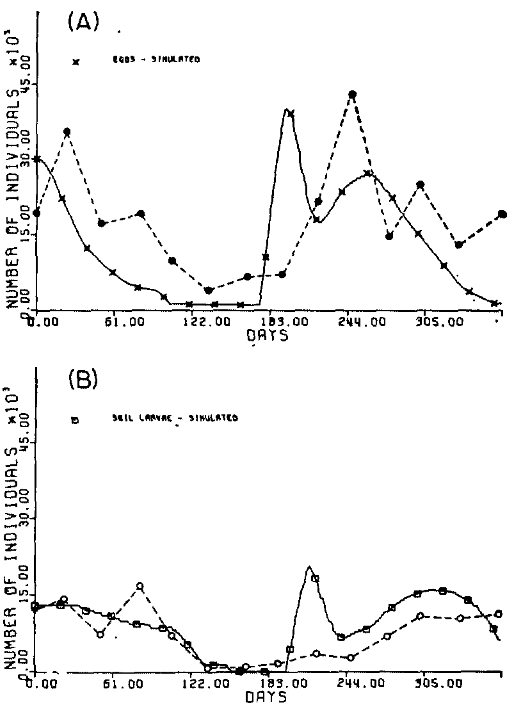

FIG. 1-(A-B). Simulated population data for *Meloidogyne arenaria* after model refinement, compared with field validation data. *A)* Eggs. *B)* Second-stage larvae. Broken lines indicate data from field samples for 1973.

curve, $R_t$ and $R_{max}$ are equivalent values for root growth rates. The function influences the development and productivity of nematode parasitic stages as a multiplier in the relevant equations. This arrangement permits consideration of the inherent decrease in vine metabolic activity as dormancy is approached in the fall.

## RESULTS AND DISCUSSION

Refinement of the simulation model improved its predictive ability (Fig. 1-A, 1-B), particularly regarding second-stage larvae in the soil. Simulations now show two peaks in the egg population curve, although the predictions are offset from observations. Data of Milne and DuPlessis (10) and Tyler (14) suggest that about 20,000 heat units (Centigrade degree-hours above 10 C) are required to complete the life cycle. There are 25,000 heat units from the simulated date of first overwintering egg-hatch (day 95) to the start of the first simulated egg population peak (Fig. 1-A), and another 25,000 units from that peak to the next (day 260). The heat units available appear sufficient for two completions of the life cycle before dormancy of the vines. There were indications of a double peak in the initial sample but not in simulations with the original model (2). The appearance of the simulated initial peak earlier than detected in samples, indicates a need for current studies on rates of parasitic larval development and on rates of egg production by females.

A point of weakness in the model is the lack of data on the variability inherent in the nematode life cycle. Not all larvae in the vicinity of the root penetrate simultaneously, because of genetic and spatial variances. Data on larval penetration (8, 14) could be manipulated into a penetration probability function relative to physiological time. A proportion of *M. arenaria* eggs hatched more slowly than the majority, so that eggs from the same age cohort could be expected to produce larvae over a considerable period (4). Similarly, variation occurs in the time of larval development to adult females, and probably in the length and pattern of egg production, because of genetic variability and differences in the suitability of infection sites. These factors will have a profound influence on the nematode population curve and on the interaction with the host. Few data are currently available, and rates used in the model frequently represent maxima rather than the range of observations. Consideration of this variability should result in delay of the simulated egg production peaks so that they approach coincidence with observed values.

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