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A Simulation Model of *Heterodera schachtii* Infecting *Beta vulgaris*

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Abstract: A simulation model of a single sugarbeet, *Beta vulgaris* L., plant infected by the sugarbeet cyst nematode, *Heterodera schachtii* Schmidt, was developed using published information. The model is an interactive computer simulation programmed in FORTRAN. Given initial population densities of the nematode at planting, the model simulates nematode population dynamics and the growth of plant tap and fibrous roots. The driving variable for nematode development and plant growth is temperature.

Key words: sugarbeet, sugarbeet cyst nematode, simulation modeling, *Beta vulgaris, Heterodera schachtii.*

The sugarbeet cyst nematode, *Heterodera schachtii* Schmidt, is a damaging pathogen of sugarbeets worldwide (2,14). Control strategies typically include crop rotation and preplant nematicides, although some granular nematicides may be applied postplant. Damage thresholds have been developed for several geographical regions of the world. Within a given region, however, damage thresholds can vary with environment and growing conditions. Increased understanding of nematode population dynamics as related to plant growth is important for improved management decisions regarding nematodes in agroecosystems.

Computer simulation models have helped advance our understanding of nematode–host plant interactions (7,18,21). We report here on the development of a simulation model of *H. schachtii* infecting the sugarbeet, *Beta vulgaris.* This work was initiated in 1980, and an abstract of this work has been published (5).

Model Development

The model simulates population dynamics of the nematode on a single sugarbeet plant in a soil volume approximating the volume a single plant occupies in the field (Fig. 1). The vertical soil profile is divided into two strata, 0–20 cm and 20–100 cm, on the basis of soil temperature fluctuations and root growth patterns. Plant growth and nematode population dynamics are simulated in each stratum.

The model was constructed using the following simplifying assumptions: (a) soil moisture, pH, and texture are not considered limiting factors for plant growth or nematode development; (b) nematodes are uniformly distributed within the simulated soil profile; (c) the plant produces fibrous roots at equal rates throughout the soil profile; (d) hatching and survival of eggs are not dependent upon their position within a cyst; and (e) net movement of nematodes between soil strata is zero.

Soil moisture is an important environmental parameter determining nematode population dynamics, but because of insufficient data it is not considered as a state variable in this model. The sources of the data used to develop the simulation of specific processes within this model are listed in Table 1, and model state variables are listed in Table 2.

The model flow is depicted in Figure 2. The model is an interactive program written in FORTRAN; it requires the user to enter various parameter values and initialize state variables. The main (driver) program calls various subroutines to perform the necessary calculations, and data is passed between subroutines via common blocks. Euler integration is used to update state variables, typically using a time step of 0.05 (day). Test runs of the simulation were analyzed to determine the sensitivity

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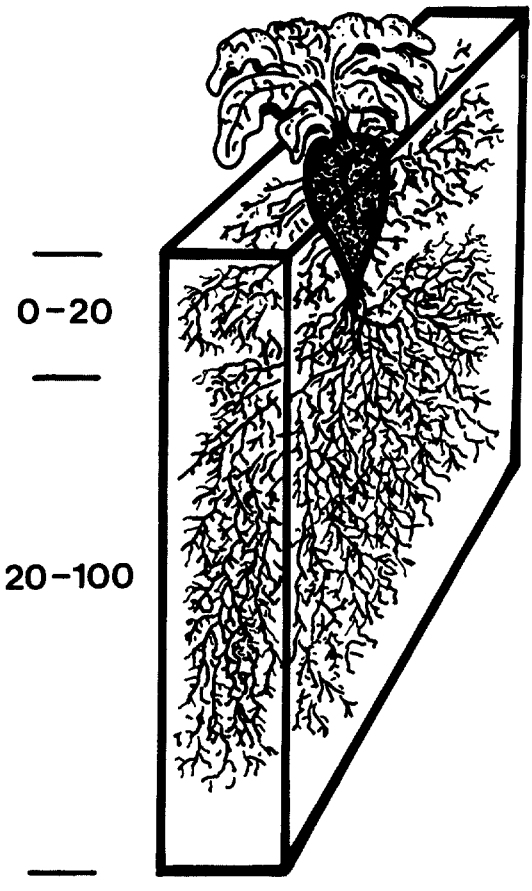

FIG. 1. A single sugarbeet plant growing in a volume of soil measuring 20 × 80 × 100 cm was depicted in this simulation model, with nematode population dynamics and plant root growth followed in top (0–20 cm) and bottom (20–100 cm) strata.

of results to time-step increment. Time steps smaller than 0.05 do not increase accuracy but significantly increase the computer time required to run the simulation.

The driver program (Fig. 3) requires the following as inputs: the time-step size upon which the iterations of numerical integration will be based—DELTAT (as a fraction of a day); the number of simulated planting seasons; the planting date and season length (in days); and the initial nematode egg population density (eggs/g soil) in each of the two strata. Initial egg density is converted within the model to total numbers of eggs in each stratum. Daily temperature data are obtained from a file of in-field temperatures or established as constant. Time-varying distributed delays are used to simulate egg development, root penetration by second-stage juveniles, and maturation of males and females within roots.

Time-varying distributed delays have been developed to model processes where pulse inputs of entities are distributed over time (1,23,24). The specific algorithms used were DELVF and DELLVF from Abkin and Wolf (1). These algorithms were selected for modeling nematode development because the length of time spent in a given developmental stage in poikilothermic organisms is variable and depends on ambient temperature. At optimal temperature, there is a minimum transition time associated with each developmental

TABLE 1. Sources of information on the development and growth of *Heterodera schachtii* and *Beta vulgaris* used to derive parameters values for the model.

Parameter	Sources
Nematode development	
J2 to adult male development	(17,26)
J2 to adult female development	(16,17,26,31)
Egg production, developmental rates	(3,12,16,25,26)
Root penetration rates	(16,27)
Nematode feeding functions	(14,15,20)
Sugarbeet growth	
Fibrous root growth	(8–10,25)
Tap root growth	(10,22,25,32,33)
Tap root/fibrous root allometric relationship	(25)

TABLE 2. State variables used in the simulation model of *Heterodera schachtii* infecting *Beta vulgaris*.

Variable name*	Definition of variable
AFEM(I)	Adult females
AMALE(I)	Adult males
CYST(I)	New cysts
DEGG(I)	Fully embryonated eggs present in the soil
DEVFEM(I)	Developing females (J2–J4 stages)
DEVMALE(I)	Developing males (J2–J4 stages)
FRW(I)	Fibrous root weight
NEMSITE(I)	Carrying capacity of most recent 7 days of fibrous root growth
PENLARV(I)	Larvae penetrating the fibrous root
SUMCYST(I)	Number of cysts present in the soil
TOTNEM(I)	Total number of actively feeding nematodes in the root system
TRW(I)	Tap root weight

* Letter in parentheses indicates that variable is monitored in both soil strata.

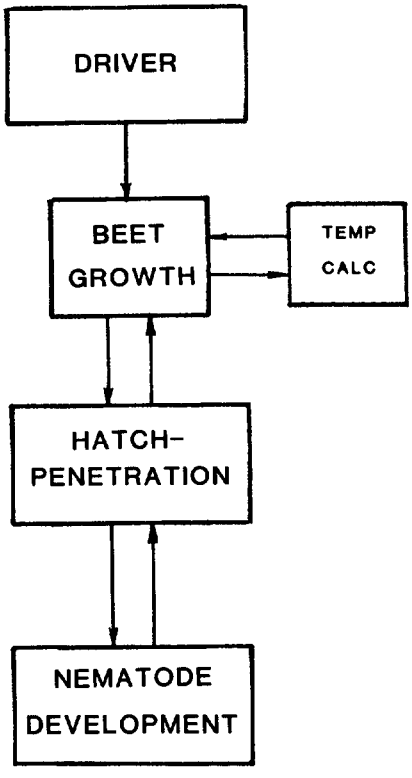

FIG. 2. Logical flow of the model, indicating interactions among subroutines (Calc = calculation).

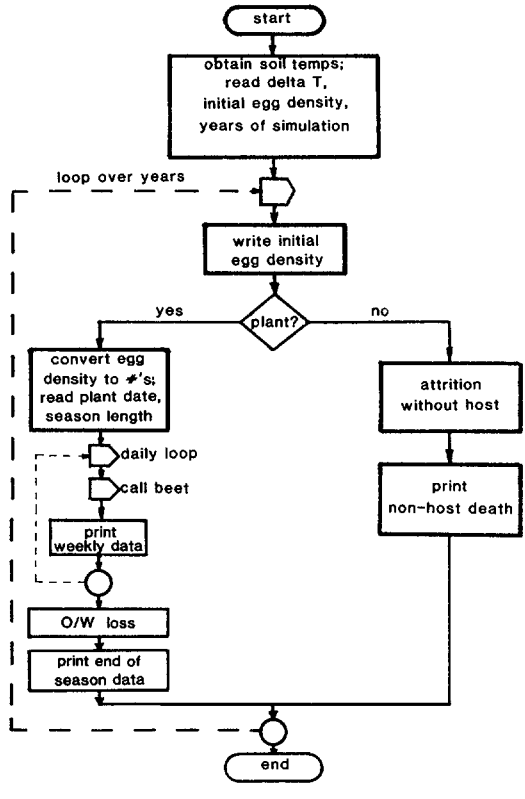

FIG. 3. Flowchart of the main program of a simulation model of a single sugarbeet plant growing in a known volume of soil, indicating required user inputs and flow options within the model (delta T = time step for Euler integration as fraction of a day; O/W = overwinter).

stage of the nematode. As temperature conditions become suboptimal or supraoptimal, the time required for transition through a specific stage increases.

Temperature subroutine: Ambient temperature in the soil profile is considered to be the driving variable for nematode and plant growth and development. Records of field temperatures obtained from Unionville, Mich., in 1979 provide the field temperature data for the model. Using daily maximum and minimum soil temperatures (at 15 cm deep), temperature fluctuations in the soil profile are simulated as a sinusoidal diurnal fluctuation with fluctuation magnitude diminishing with soil depth (4). A damping function simulating the effect of increasing leaf area index on diurnal soil temperature fluctuations was superimposed on the sinusoidal fluctuation. With these routines, instantaneous average temperature is available for each stratum. If desired, the subroutine can be altered so each stratum has a constant temperature, allowing simulation of experimental conditions.

Beet growth and development subroutine: Beet tap root and fibrous root growth rates are related to soil temperature (8–10,22,25,32,33). Root growth is initially limited to the top soil stratum. After roots penetrate the second stratum, optimal root growth is divided between each of the two strata. The total fibrous root weight is determined by summation of fibrous root weight in each stratum. The relationship of relative fibrous root growth rate to temperature was derived (9,10,25) to allow modification of root growth in relation to temperature. Fibrous root weight—FRW(I)—increase is described by linear functions derived from Fick (9,10):

$$\text{FRW growth rate} = 0.0421 \text{ g/day} \quad \text{if FRW} < 1.05 \text{ g.}$$
$$\text{FRW growth rate} = 1.4200 \text{ g/day} \quad \text{if FRW} \geq 1.05 \text{ g.}$$

State variables are updated for each stra-

tum at each iteration of the model, which is indicated by the array index (I).

Fibrous root weight is initialized as 0.0001 g in strata one to avoid having a numerator of zero in the equations. The beet growth subroutine uses data provided by the temperature subroutine to obtain a temperature correction factor—TEMPFAC—for fibrous root growth rate. The instantaneous change in fibrous root weight—DELFRW(I)—is calculated for each stratum as

$$\text{DELFRW(I)} = \text{RATE} * \text{TEMPFAC(I)} * \text{DELTAT},$$

where RATE is the optimal fibrous root growth rate and TEMPFAC is the correction for deviation from optimal growth rates dependent on temperature. The fibrous root weight is updated as

$$\text{FRW(I)} = \text{FRW(I)} + \text{DELFRW(I)}.$$

Fibrous roots are depicted as remaining suitable for invasion by the nematode for 7 days before processes such as suberization render them unsuitable. This estimate was derived from Kampfe (19). The most recent 7 days of fibrous root biomass is maintained as the variable SUM(I). The nematode carrying capacity of fibrous roots is calculated by dividing SUM(I) by the minimal root volume required for nematode development (20). The number of feeding sites available for nematode colonization, the carrying capacity—NEMSITE(I)—is calculated as

$$\text{NEMSITE(I)} = \text{SUM(I)}/7.0 * 10^{-5}.$$

At this point the program calls up the hatching and penetration subroutine which uses the information on fibrous root weight to simulate nematode egg hatch and penetration of roots by juveniles. When the program returns to the beet growth subroutine, the nematode total damage function—NEMAFED(I)—is passed back and the new change in fibrous root weight due to nematode feeding is calculated as

$$\text{FRW(I)} = \text{FRW(I)} - \text{NEMAFED(I)}.$$

After initial fibrous root growth, the tap root begins to grow. Tap root weight—TRW(I)—is obtained using a temperature dependent allometric ratio of tap root weight to fibrous root weight derived from Radke and Bauer (25) and Ulrich (33). Tap root growth is exponential during the early growth phase and reaches a linear growth phase after approximately 95 days at 25 C (25,32,33).

Hatching and penetration subroutine: When soil temperatures are above 10 C, fully developed eggs present in the soil—DEGG(I)—are stimulated to hatch by the proximity of fibrous roots (34). If FRW(I) ≤ 0.17 g, then

$$\text{PHATCH(I)} = 0,$$

where PHATCH(I) represents the proportion of fully developed eggs that will hatch. This constraint is to simulate host plant stimulation of egg hatch (29,34). PHATCH(I) is considered an increasing linear function of FRW(I) until FRW(I) equals 2.1 g, after which PHATCH(I) = 1.0. Fully developed eggs hatch according to

$$\text{HEGG(I)} = \text{DEGG(I)} * \text{PHATCH(I)},$$

where HEGG(I) is the number of eggs which hatch. The number of eggs that are developed is updated

$$\text{DEGG(I)} = \text{DEGG(I)} - \text{HEGG(I)}.$$

When soil temperature is above 10 C, the proportion of developed eggs that hatch is determined from the size of the available fibrous root in each stratum. The number of eggs entering the penetration delay (simulating hatch and penetration) is obtained from

$$\text{SEGG(I)} = 0.35 * \text{HEGG(I)} * [\text{NEMSITE(I)} - \text{TOTNEM(I)}] \div \text{NEMSITE(I)},$$

where SEGG(I) is the average proportion (35%) of juveniles that can successfully penetrate the root (16,27). The remainder of the equation represents the number of potential feeding sites available in the fibrous root system minus the number of actively feeding nematodes already present—TOTNEM(I). Penetration of juveniles into the roots is limited by the fibrous root carrying capacity, as determined in the beet growth subroutine, and by the number of nematodes already present in the fibrous root. If the capacity is large, relative to the number of nematodes in the root, most juveniles enter the growth and

development delays. If the carrying capacity and the number of nematodes in the root are nearly equal, few or none of the juveniles can penetrate.

The time required for penetration of the root system is simulated using a time-varying distributed delay based on temperature. The temperature correction factor for the penetration delay is obtained from an array of temperature-dependent relative penetration rates derived from Johnson and Viglierchio (16) and Raski and Johnson (27). SEGG(I) is passed into the penetration delay. The minimum penetration time is 4 days at optimal temperature of 23 C (16). The delay in penetration increases to 7 days at 30 C and approximately 400 days at 10 C. The delay output is PENLARV(I), the number of juveniles that have successfully penetrated the root system. This subroutine passes the information to the nematode development subroutine.

Nematode development subroutine: The number of juveniles that have successfully entered the plant root system—PENLARV(I)—is divided into future males and females:

$$\text{DEVFEM2(I)} = 0.5 * \text{PENLARV(I)},$$
$$\text{DEVMAL2(I)} = 0.5 * \text{PENLARV(I)},$$

where DEVFEM2(I) and DEVMAL2(I) represent developing females and males, respectively, assuming a 1:1 sex ratio (17). Temperature-dependent developmental arrays for male and female growth are used to determine the lengths of the male and female delays. The minimum developmental times for males and females are 18 and 20 days, respectively, at optimal temperature (25 C) (17). Male development requires 41 days and female development 33 days at 30 C. The minimum temperature threshold for development of males and females is 10 C (17,27). The maximum temperature threshold for males is 35 C and for females 30 C (17). At maximum and minimum temperatures development ceases. DEVFEM(I) and DEVMALE(I) represent the total numbers of developing females and males in the root system; they are obtained by summing the contents of the male and female developmental delays. Males no longer feed after leaving the root system (26). The model assumes adequate insemination of females regardless of population density due to the promiscuous nature of males and the attractiveness of females (11–13). This assumption may be unrealistic at low population densities.

Eggs are attributed to adult females as they leave the female development delay—AFEM(I):

$$\text{EGG(I)} = \text{AFEM(I)} * 250,$$

where EGG(I) represents newly deposited eggs, with an average of 250 eggs attributed to each female (31).

A temperature-dependent developmental array is used to drive another delay simulating the process of egg development. Egg development requires 8 days at 25 C (16), whereas minimum and maximum thresholds are estimated as 11 C and 35 C, respectively.

EGG(I) enters the egg development delay, and TEGG(I) is the output of the development delay, representing fully developed eggs. For every 250 fully developed eggs, an adult female is removed from the feeding population and added to the population of cysts—CYST(I):

$$\text{CYST(I)} = [\text{TEGG(I)} * \text{DELTAT}]/250.$$

The number of cysts present in the soil—SUMCYST(I)—is updated as,

$$\text{SUMCYST(I)} = \text{SUMCYST(I)} + \text{CYST(I)}.$$

The number of females which are still feeding in the root system is calculated as

$$\text{SUMAFEM(I)} = \text{SUMAFEM(I)} + \text{AFEM(I)} * \text{DELTAT} - \text{CYST(I)}.$$

The pool of developed eggs in the soil—DEGG(I)—is updated using

$$\text{DEGG(I)} = \text{DEGG(I)} + \text{TEGG(I)} * \text{DELTAT}.$$

Simulation of the development of males follows the same logic as for females, but the mean delay time and temperature-dependent developmental rates are different. The output of the male development delay is AMALE(I), and adult males are deleted from the feeding population.

An attempt was made to include an attrition factor in the nematode development delays to simulate the death of some

juveniles during development in the root. This attrition factor was considered to reflect deaths caused by overcrowding, parasitism, partial resistance of the host, or improper positioning of the nematode in the root. Because of the poorly defined nature of such an attrition factor (30), its use in the model was ineffective.

The male and female nematode feeding functions used in the model were derived from Griffin (14,15) and Santo and Bolander (28). The nematode feeding function—NEMFED(I)—is first calculated for feeding females using

$$\begin{aligned}\text{NEMFED(I)} = [&\text{DEVFEM(I)} * 2.3 \\ &* 10^{-8}\ \text{g/nema}] \\ &+ [\text{SUMAFEM(I)} * 2.3 \\ &* 10^{-8}\ \text{g/nema}].\end{aligned}$$

The feeding function is modified by a factor—FEEDFAC—that considers the phenology of the plant such that the impact of nematode feeding is greater on younger plants (14,15).

If FRW(I) < 14.0 g, then

$$\text{FEEDFAC(I)} = (-19.0/14.0) * \text{FRW(I)} + 20.0.$$

If FRW(I) ≥ 14.0 g, then

$$\text{FEEDFAC(I)} = 1.0.$$

The actual female feeding function is then calculated as

$$\begin{aligned}\text{NEMFED(I)} = &\text{NEMFED(I)} \\ &* \text{FEEDFAC(I)}.\end{aligned}$$

The nematode feeding function for males is calculated as

$$\begin{aligned}\text{NEMAFED(I)} = &\text{DEVMALE(I)} \\ &* 3.8 * 10^{-10}\ \text{g/nema}.\end{aligned}$$

Males are considered to cause less plant growth reduction than females. The modifier FEEDFAC is again used to alter the nematodes' impact on young plants. The total nematode feeding on the plant is then calculated as

$$\begin{aligned}\text{NEMAFED(I)} = &\text{NEMFED(I)} \\ &+ \text{NEMAFED(I)},\end{aligned}$$

expressed as fibrous root weight lost. This information is returned to the beet growth and development subroutine, and the model continues iteration until the season length specified by the user is reached.

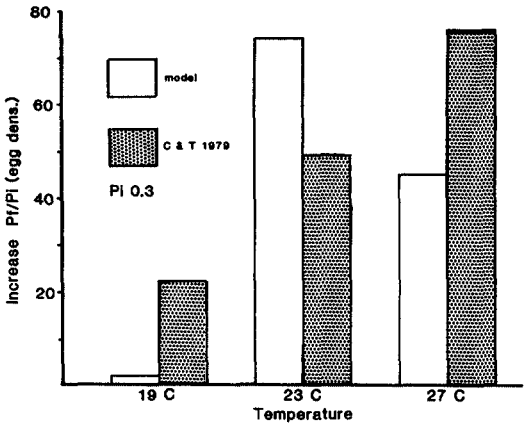

FIG. 4. Comparison of model output to data from Cooke and Thomason (5) showing nematode population increase (Pf/Pi, in eggs/g soil) over 105 days of plant growth at constant temperatures and an initial population density of 0.3 eggs/g soil.

RESULTS AND DISCUSSION

Although the model is deterministic, it is capable of complex dynamics depending upon the initial population density of the nematode and soil temperatures.

Sensitivity analyses: An analysis was conducted to determine the sensitivity of nematode population increase and tap root growth to modification of the per capita nematode damage to the plant. The base value per capita damage was compared with 0.1 times and 10 times the base value. The simulated reproductive rate of the nematode was insensitive to changes in the base value, but the increase of 10 times had an overly severe impact on tap root growth.

The sensitivity of tap root growth to modification of the length of time the fibrous root system remained available for nematode penetration was analyzed. The base value of 7 days was compared to 1 day and 21 days, with an initial population density of 1.0 egg/g soil at a constant temperature of 21 C. The differences in tap root weights between the 1-day and 7-day lengths was not significant, but the 21-day length resulted in an unrealistic decrease in tap root growth. On the basis of the analyses, we believe the base values used for these parameters are set at reasonable values, given the model's structure.

Validation: The rate of increase of nematode population density generated by the model was compared to two data sets not

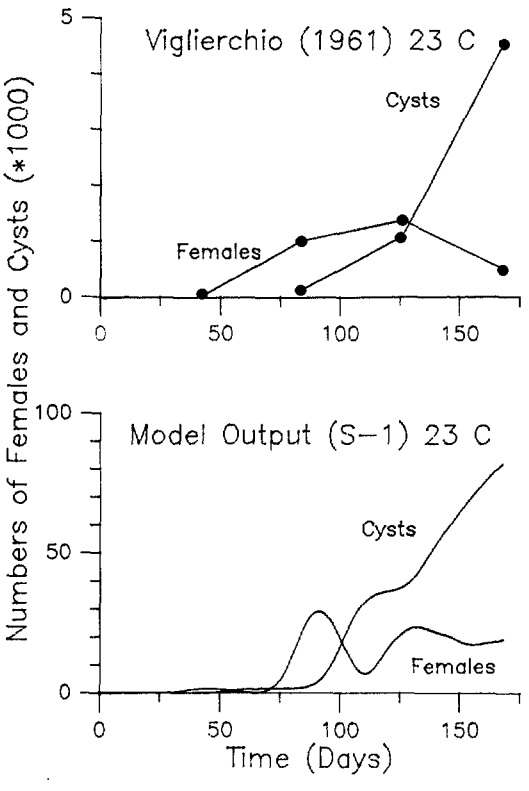

FIG. 5. Comparison of model output (stratum 1; 0–20 cm) to data from Viglierchio (34) showing the increase in white female *Heterodera schachtii* and cysts (in soil and roots) during 150 days of plant growth at a constant temperature of 23 C and initial population density of 1.0 egg/g soil.

used in the construction of the model. Comparison with data from Cooke and Thomason (6) for population increase at constant temperatures is depicted in Figure 4. The rate of nematode population density increase generated by the model did not compare favorably with their results. At 19 C the model rate of increase was lower, at 23 C higher, and at 27 C lower than values obtained by these authors. It is not possible to identify a specific data set or assumption used in construction of the model that accounts for the disagreement. An obvious problem with the model is that it was developed using information from many different studies, each conducted under specific conditions.

Comparison of the simulated production of cysts and females (in roots and soil) with that obtained by Viglierchio (34) is depicted in Figure 5. The numbers of cysts and females produced differ. The model soil volume is larger, however, so although the initial egg population densities are the same, the absolute number of eggs in the simulated system are greater. The data from Viglierchio (34) represent point estimates of population structure, whereas the model results are continuous (Fig. 5) making it difficult to compare the two, despite their apparently similar basic dynamics.

Phenomena such as sex-ratio shifts and differences in fecundity caused by changes in host quality are poorly understood but still affect nematode population dynamics. Such factors are not included in the model; therefore, model realism is limited.

Computer simulation models are becoming increasingly useful as aids in comprehending complex interactions occurring in biological systems and may be especially useful in the analysis of host–pathogen relationships (21). A benefit of simulation is the recognition of information gaps and previously unsuspected interactions and feedback mechanisms within the system. Our model is useful as a guide and framework for further research.

Construction of this simulation model has identified the need for further study of the cyst nematode–sugarbeet relationship. A deficiency of quantitative information on nematode development and reproductive rates and feeding processes limits the accuracy and usefulness of the model. Well-defined information on the growth of the fibrous root system, particularly the allometric relation between fibrous and tap root growth under field conditions, is desired.

Specifically, we have identified several questions which, when answered, may allow further development of this model. The following points require further elucidation: 1) nematode carrying capacity of the root system and the average root volume required for maturation of males and females under variable environmental conditions, 2) effects of nematode population density and plant growth on the fecundity and sex ratio of the nematode, 3) hatching behavior of eggs as temperature and moisture change at the end of the growing season, and 4) attrition rates for male and female nematodes within the root, based on nematode population density, temperature, and plant growth. An improved mod-

el could have predictive value and use in the management of cyst nematodes in infested fields.

Literature Cited

1. Abkin, M. H., and C. Wolf. 1976. Distributed delay routines: Del, dels, delf, dellf, delvf, dellvf. Computer library for agricultural systems simulation. Document 2. Department of Agricultural Economics, Michigan State University, East Lansing.
2. Altman, J., and I. J. Thomason. 1971. Nematodes and their control. Pp. 335–370 *in* R. T. Johnson, J. T. Alexander, G. E. Rush, and G. R. Hawkes, eds. Advances in sugarbeet production: Principles and practices. Ames: Iowa State University Press.
3. Banyer, R. J., and J. M. Fisher. 1971. Effect of temperature on hatching of eggs of *Heterodera avenae.* Nematologica 17:518–534.
4. Campbell, G. 1977. An introduction to environmental biophysics. New York: Springer-Verlag.
5. Caswell, E. P., A. E. MacGuidwin, K. T. Milne, C. E. Nelsen, and I. J. Thomason. 1981. A simulation model of *Heterodera schachtii* infecting *Beta vulgaris.* Journal of Nematology 13:434 (Abstr.).
6. Cooke, D. A., and I. J. Thomason. 1979. The relationship between population density of *Heterodera schachtii,* soil temperature, and sugarbeet yields. Journal of Nematology 11:124–128.
7. Ferris, H. 1976. Development of a computer-simulation model for a plant-nematode system. Journal of Nematology 8:255–263.
8. Fick, G. W., W. A. Williams, and R. S. Loomis. 1971. Recovery from partial defoliation and root pruning in sugar beet. Crop Science 11:718–721.
9. Fick, G. W., W. A. Williams, and A. Ulrich. 1972. Parameters of the fibrous root system of sugar beet (*Beta vulgaris* L.). Crop Science 12:108–112.
10. Fick, G. W., R. S. Loomis, and W. A. Williams. 1975. Sugar beet. Pp. 259–295 *in* L. T. Evans, ed. Crop physiology. New York: Academic Press.
11. Golden, A. M. 1959. Significance of males in reproduction of the sugar-beet nematode (*Heterodera schachtii*). Plant Disease Reporter 43:979–980.
12. Green, C. D., D. N. Greet, and F. G. W. Jones. 1970. The influence of multiple mating on the reproduction and genetics of *Heterodera rostochiensis* and *H. schachtii.* Nematologica 16:309–326.
13. Greet, D. N., C. D. Green, and M. E. Poulton. 1968. Extraction, standardization and assessment of the volatility of the sex attractants of *Heterodera rostochiensis* Woll. and *H. schachtii* Schm. Annals of Applied Biology 61:511–519.
14. Griffin, G. D. 1981. The relationship of *Heterodera schachtii* population densities to sugarbeet yields. Journal of Nematology 13:180–184.
15. Griffin, G. D. 1981. The relationship of plant age, soil temperature, and population density of *Heterodera schachtii* on the growth of sugarbeet. Journal of Nematology 13:184–190.
16. Johnson, R. N., and D. R. Viglierchio. 1969. Sugar beet nematode (*Heterodera schachtii*) reared on axenic *Beta vulgaris* explants. I. Selected environmental factors affecting penetration. Nematologica 15: 129–143.
17. Johnson, R. N., and D. R. Viglierchio. 1969. Sugar beet nematode (*Heterodera schachtii*) reared on axenic *Beta vulgaris* root explants. II. Selected environmental and nutritional factors affecting development and sex-ratio. Nematologica 15:144–152.
18. Jones, F. G. W., R. A. Kempton, and J. N. Perry. 1978. Computer simulation and population models for cyst-nematodes (Heteroderidae: Nematoda). Nematropica 8:36–56.
19. Kampfe, L. 1960. Die raumliche Verteilung des Primarbefalls von *Heterodera schachtii* Schmidt in den Wirtswurzeln. Nematologica 5:18–26.
20. Kerstan, U. 1969. Die Beeinflussung des Geschlechterverhaltnisses in der Gattung Heterodera. II. Minimallebensraum-selektive Absterberate der Geschlechter-Geschlechterverhaltnis (*Heterodera schachtii*). Nematologica 15:210–228.
21. Loomis, R. S., and S. S. Adams. 1983. Integrative analyses of host–pathogen relations. Annual Review of Phytopathology 21:341–362.
22. Loomis, R. S., A. Ulrich, and N. Terry. 1971. Environmental factors. Pp. 19–48 *in* R. T. Johnson, J. T. Alexander, G. E. Rush, and G. R. Hawkes, eds. Advances in sugarbeet production: Principles and practices. Ames: Iowa State University Press.
23. Manetsch, T. J. 1976. Time-varying distributed delays and their use in aggrevative models of large systems. IEEE transactions on systems, man, and cybernetics 6:547–553.
24. Manetsch, T. J., and G. L. Park. 1974. System analysis and simulation with applications to economics and social systems. Part 2. East Lansing: Michigan State University.
25. Radke, U. K., and R. E. Bauer. 1969. Growth of sugar beets as affected by root temperatures. Part 1: Greenhouse studies. Agronomy Journal 61:860–863.
26. Raski, D. J. 1949. The life history and morphology of the sugarbeet nematode, *Heterodera schachtii.* Phytopathology 40:135–151.
27. Raski, D. J., and R. T. Johnson. 1959. Temperature and activity of the sugarbeet nematode as related to sugarbeet production. Nematologica 4:136–141.
28. Santo, G. S., and W. J. Bolander. 1979. Interacting effects of soil temperature and type on reproduction and pathogenicity of *Heterodera schachtii* and *Meloidogyne hapla* on sugarbeets. Journal of Nematology 11:289–291.
29. Shepard, A. M. 1959. The invasion and development of some species of *Heterodera* in plants of different host status. Nematologica 4:253–267.
30. Shepard, A. M. 1960. A study on the apparent decay of eggs within cysts of *Heterodera schachtii* Schm. and *H. gottingiana* Libscher, and of free larvae in the soil. Nematologica 5:103–110.
31. Thomason, I. J., and D. Fife. 1962. The effect of temperature on development and survival of *Heterodera schachtii* Schm. Nematologica 7:139–145.
32. Ulrich, A. 1952. The influence of temperature and light factors on the growth and development of sugarbeets in controlled climatic environments. Agronomy Journal 44:66–73.
33. Ulrich, A. 1954. Growth and development of sugar beet plants at two nitrogen levels in a controlled temperature greenhouse. Proceedings of the American Society of Sugarbeet Technologists 8:325–338.
34. Viglierchio, D. R. 1961. *Heterodera schachtii,* hatching properties of field importance. Journal of the American Society of Sugarbeet Technologists 11: 294–301.