Development of a Computer-Simulation Model for a Plant-Nematode System

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Abstract: A computer-simulation model (MELSIM) of a *Meloidogyne*-grapevine system is developed. The objective is to attempt a holistic approach to the study of nematode population dynamics by using experimental data from controlled environmental conditions. A simulator with predictive ability would be useful in considering pest management alternatives and in teaching. Rates of flow and interaction between the components of the system are governed by environmental conditions. Equations for these rates are determined by fitting curves to data from controlled environment studies. Development of the model and trial simulations have revealed deficiencies in understanding of the system and identified areas where further research is necessary. *Key Words: Meloidogyne, Vitis,* population dynamics, pest management.

Interest in the application of systems analysis and computer simulation to the study of plant-pathogen systems is growing (23, 24, 25, 33). Progress in finding analytical solutions for complex models of biological systems was limited before the advent of high-speed computers (10, 20, 32). The use of modeling and computer-simulation techniques is increasing in other areas of agricultural and biological research (2, 4, 15, 18). The modeling approach is a valuable tool in scientific procedure, especially if the intention of the research is to gain an understanding or control of an ecosystem. Components (such as ecosystems) of the universe are too complex to be grasped and controlled without abstraction (16).

The modeling approach to studies of nematode population dynamics has resulted in models describing overall effects during an average season (7, 14, 17). Final nematode population density or crop yield is expressed in terms of the initial population without regard for intermediate environmental phenomena. The descriptiveness and adaptability of these models are limited by the necessity of producing analytical solutions. Computer-aided numerical integration techniques allow step-by-step simulation of the interaction between the organisms (24), and actual environmental conditions affecting them can be considered at each step. The effects of environmental disturbance or pesticide application can also be considered at each step. The approach lends itself to the simulation of pest management experiments and testing pest management alternatives (13, 30). It is useful in drawing attention to areas where knowledge is weak, and is helpful in directing research programs and in providing insights and training in epidemiological concepts.

In this paper, the terminological definitions of Mihram (11) and Mize and Cox (12) are followed. *Simulation* is the process of conducting experiments on a model of a system. A *system* is a set of interacting or interdependent components. Its boundaries are specified by the systems analyst, and they should include all components which significantly affect total systems performance. Each system may consist of subsystems which can be studied independently while the results may still be combined (32). An *experiment* is the process of observing the performance of the system or its model under a certain set of conditions.

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MODEL FORMULATION

The system simulated is that of a plant-parasitic nematode, *Meloidogyne* spp., and a perennial plant, grapevine—*Vitis vinifera*. The model was constructed stepwise. *(i)* The essential components of the system were defined (Fig. 1). Third- and 4th-stage larvae were considered as a single component as their niche and role in the system are similar. *(ii)* Directions of flow of materials or individuals between the components were marked (Fig. 1). *(iii)* Equations defining the flow down each arrow were derived. Thus, the flow or transition from eggs to death (γ_{ED}) is proportional to

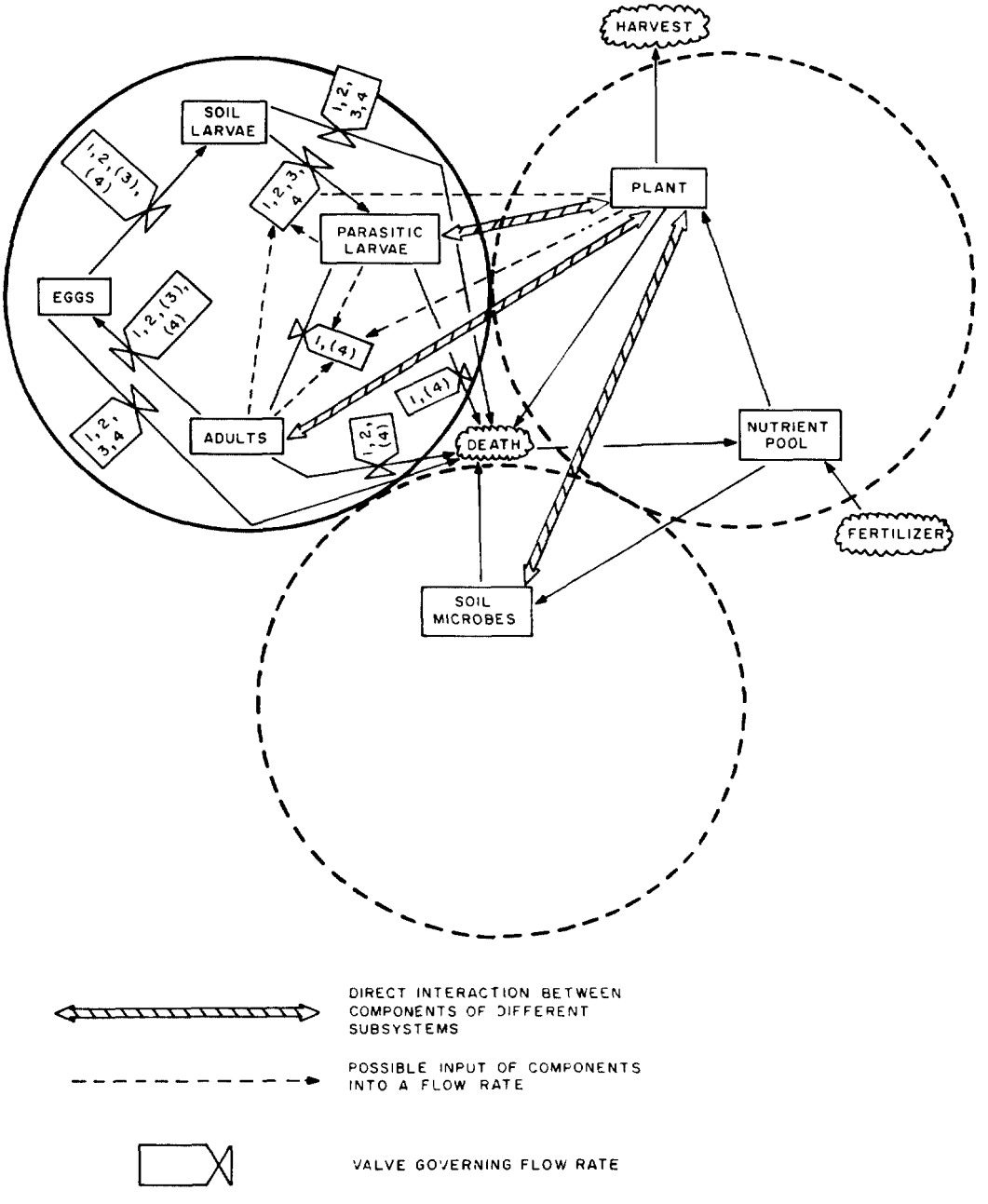

FIG. 1. Schematic representation of a *Meloidogyne*-plant system, with emphasis on details of the nematode subsystem. Extrinsic effects on rates, shown in the valves, are (i) soil temperature, (ii) soil moisture, (iii) soil oxygen, and (iv) nematicides. A number in parentheses indicates uncertainty of the effect.

the number of eggs available to die, but is independent of the number of eggs already dead.

$$\gamma_{ED} \alpha E$$

$$\text{then } \gamma_{ED} = R_1 E$$

when R_1 is the rate of death of eggs under adverse environmental conditions. Since egg death is affected by soil temperature (t) (1) and oxygen (o) (28), but not by soil moisture (29), the death rate of eggs is the sum of the death rate resulting from temperature and the death rate resulting from oxygen level.

$$\gamma_{ED} = E\,(R_{1(t,o)}) \qquad [1]$$

Similarly

$$\gamma_{ES} = R_2 E,$$

when R_2 is the hatch rate of eggs under prevailing environmental conditions. This rate is affected by temperature (t) (27), soil moisture (m) (27), oxygen (o) (28), and extremes of pH (p) (27).

$$\text{Then } R_2 = R_{2(t,m,o,p)} \qquad [2]$$

$$\gamma_{ES} = E(R_{2(t,m,o,p)})$$

The death rate of soil larvae (second stage larvae) (R_3) is affected by soil moisture (m) (26) and by soil temperature (t) (21), but not by oxygen levels (o) (28).

$$\gamma_{SD} = S(R_{3(t,m)}) \qquad [3]$$

The transition from soil larvae to parasitic larvae (γ_{SP}) involves an interaction between components of the plant and nematode subsystems. Unless a plant root is present, the flow cannot take place and it is influenced by the amount of root available for infection. The amount available will depend upon the size of the root and the number of larvae and adults already inside it. The epidemiological concepts of Van der Plank (19) are used to describe this relationship. If the proportion of the root already infected is X, then (1-X) of the root remains available for infection. The value (1-X) varies constantly and is dependent upon the growth rate of the infecting nematode population and the rate of root growth. This value is an important factor throughout the construction of this model as the vigor of the plant also depends upon the amount of root as yet noninfected and functioning optimally.

$$\gamma_{SP} = R_4 S(1\text{-}X)$$

The rate of infection (R_4) is influenced by soil temperature (t) (27), soil moisture (m) (27), oxygen (o) (22), soil particle size (s) (27), and soil cohesion (c) (27). It may also be affected by resistance level (r) of the root system.

$$\gamma_{SP} = S(1\text{-}X)R_{4(t,m,o,s,c,r)} \qquad [4]$$

The flow of parasitic larvae to their death (γ_{PD}) depends upon the infection level of the root system (x). Since larvae that develop into males have no further input in population increase, this development is regarded as death for the purposes of the model. The death of parasitic larvae is also affected by soil temperature (t) (3), but probably not by moisture or oxygen since the larvae are within the root system.

$$\text{Then } \gamma_{PD} = P\,R_{5(t,x)} \qquad [5]$$

The rate at which parasitic larvae develop into adults (γ_{PA}) depends upon the vigor of the plant from which they obtain their nutrition (3) and thus is proportional to (1-X). It is also affected by soil temperature (t) (3) and soil oxygen level (o) (22), and may be affected by the resistance level (r) of the plant.

$$\text{Then } \gamma_{PA} = PR_{6(t,o,r)}(1\text{-}X) \qquad [6]$$

As with parasitic larvae, flow from adult females to death probably is dependent upon infection levels. It is affected by soil temperature and there is a natural death rate at completion of the life cycle.

$$\gamma_{AD} = A\,R_{7(t,n,x)}. \qquad [7]$$

The rate at which eggs are produced by adult females is probably affected by vigor of the plant as expressed by (1-X) and plant resistance level (r). It is affected by oxygen level (o) (22) and probably by soil temperature (t).

$$\gamma_{AE} = A\,R_{8(t,o,r)}(1\text{-}X) \qquad [8]$$

A simplified model of plant growth is used for current purposes. Since the nematode model is designed for use with various plant subsystems, the plant model will not be discussed in detail. The plant growth algorithm for grapevines is based upon degree-hours accumulated by the plant on a seasonal basis (31). In the model, plant

growth rate is also proportional to the vigor and growth rate of the root system. Rate of root growth is affected by soil temperature (t) (31), oxygen (o) (22), soil moisture (m) (31), soil nutrient status (nut), and the proportion of the root system remaining fully functional (1-X).

Then root-growth rate =

$$R_{9(t,o,m,nut)}(1\text{-}X) \qquad [9]$$

Since X appears in several equations and is a variable dependent upon the proportion of the root system infected, it is necessary to have an equation to calculate the value. If we consider that each unit of root growth is capable of supporting T nematodes before growth cease, then the nematode-carrying capacity of the root (weight W) is TW. The proportion of the root infected will be the number of nematodes present divided by the carrying capacity, i.e. X = N/TW. However, there are two components of the nematode subsystem within the root (Fig. 1), and it seems unlikely that each component would carry the same weight in regard to its effect on the root system. If I assume that parasitic larvae (P) have an effect only β as great as that of adults (A), then, N = (A + βP).

$$X = (A + \beta P)/TW \qquad [10]$$

From the equations for the flow along each arrow in Fig. 1, a differential equation for the amount of change occurring in each compartment during a short period of time (dt), given the environmental conditions during that time period, can be developed. The change in each compartment is the sum of the flows into and out of the compartment. For the egg compartment, using equations 1, 2, and 8:

$$\frac{dE}{dt} = AR_8 - ER_2 - ER_1 \qquad [11]$$

Soil larvae compartment, equations 2, 3, and 4:

$$\frac{dS}{dt} = ER_2 - SR_3 - S(1\text{-}X)R_4 \qquad [12]$$

Parasitic larvae compartment, equations 4, 5, and 6:

$$\frac{dP}{dt} = S(1\text{-}X)R_4 - PR_5 - P(1\text{-}X)R_6 \qquad [13]$$

Adult compartment, equations 6 and 7:

$$\frac{dA}{dt} = PR_6 - AR_7 \qquad [14]$$

Root growth compartment, equation 9:

$$\frac{dG}{dt} = R_9(1\text{-}X) \qquad [15]$$

By using techniques of computer-aided numerical integration, these simultaneous differential equations can be solved and the size of each compartment defined at any point in time. Numerical integration techniques involve solving the differential equation after each time period (dt) and then updating the compartment size before repeating the calculation. Thus, for the equation $\frac{dN}{dt} = RN_t$ for the time interval dt,

$dN = dt\ (RN_t)$,

$$N_{(t+1)} = N_t + dN.$$

Since the growth curves for each component of the system are developed in small time increments (dt), and since the rates ($R_1 - R_9$) involved in these equations are affected by environmental conditions, new sets of environmental conditions which modify the rates for that time period can be specified for each dt. If a series of equations which predict the value of the rates under each set of environmental conditions is incorporated in the computer program, the system can be used to simulate field conditions.

The next step in the modeling process is to develop regression equations for the rates of flow down each arrow. Curves were fitted to the data of several authors to produce the required rate equations. In fitting the curves, the data were considered biologically as well as mathematically. (It is possible to fit a line passing through every point on a graph, but the line produced may be biologically unlikely). In some cases, interpretation of data was rather liberal to adapt it to the model, and, where data were not readily available, estimates were made. Rates are expressed on a per hour basis. One approach would be to define the rates by multiple regression equations based on a series of environmental variables. Thus, the hatch rate of eggs:

$$R_2 = \alpha_o + \alpha_1 T + \alpha_2 M + \alpha_3 O + \alpha_4 P$$

where T, M, O, and P represent soil temperature, soil moisture, oxygen level, and pH respectively. Unfortunately, this approach is often not applicable to biological systems; also data for development of such equations are not available. Data are available, however, for development of rate equations based on one variable. This rate can be modified according to the effect (from 1.0 → 0) of the other environmental factors influencing it. Fortran notation of the variables will be used at this stage to distinguish them in each equation. Correlation coefficients are given where possible as a measure of fit of the curves to the data points. Data are available to express

$$R_2 = RHT \times EMEH \times EOEH \times EPH \quad [16]$$

RHT—the rate of egg hatch resulting from temperature—is expressed as the proportion of development/h; the equation is from Ferris and Small (6) $RHT = 0.0115\ T - 0.0009T^2 + 0.00003T^3 - 0.0000003T^4 - 0.0567$ (r = .93). EMEH—the effect of soil moisture on egg hatch adapted from Wallace (27) $EMEH = 0.0137M - 0.00016M^2 + 0.3476$ (r = .62). EOEH—the effect of oxygen on egg hatch is adapted from Wallace (28) $EOEH = 0.3997e^{[0.0437(0)]}$ (r = 0.99). The oxygen level of the soil is related to the diffusion rate, which is probably not impaired until soil moisture levels are very high (24). EPH—the effect of pH on egg hatch (9, 27), is fairly optimal within the range of most agricultural soils but decreases the hatch below pH 5. $EPH = 1.8205\ P - 0.14P^2 - 4.942$ (r = 0.96). Note that if soil moisture, oxygen level, and pH are optimal, EMEH, EOEH, and EPH have a value of 1.0 and the hatch rate is at its maximum for that temperature. If any factor is suboptimal, its effect is less than 1.0 and there is a slowing effect on the rate. This approach assumes that the experiment determining the curve for RHT was conducted at the optimum range for each of the other factors.

In the case of death rates, e.g. R_1, since the death rate increases as more environmental factors become suboptimal, a rate can be determined for each factor and the effect on the total death rate will be additive. Thus:

$$R_1 = RDET + RDEO \quad [17]$$

RDET—the death rate of eggs (egg deaths/egg/h) resulting from temperature (1) $RDET = 0.0187\text{-}0.0019T\text{-}0.000047T^2$ (r = 0.98). RDEO—death rate of eggs resulting from lack of oxygen. Wallace (28) showed that 6 days without oxygen is lethal to *Meloidogyne javanica* eggs; thus RDEO = 1/144 = 0.0069/egg/h. This rate is somewhat unrealistic as it assumes linearity of the effect. Further experimentation is required.

$$R_3 = RDSLT + RDSLM \quad [18]$$

RDSLT—death rate of soil larvae resulting from temperature (larval deaths/larva/h) (21) $RDSLT = 0.00104 + (e^{9.06T})/(12 \times 10^5)$. RDSLM—death rate of soil larvae resulting from lack of moisture (larval deaths/larva/h). It is considered that low soil moistures are lethal to soil larvae, and that this effect will only occur below 10% of the moisture-holding capacity. At these moisture levels, the following equation is used: $RDSLM = 0.021\text{-}0.0021M$. Further research is needed to investigate this relationship.

$$R_4 = RINF \times ETIN \times EMIN \times EOIN \times EPS \times ECO \times ERESIN \quad [19]$$

RINF—max rate of infection under ideal conditions (number entering/larva/h). Since there are no suitable data available, if it is assumed that, under ideal conditions, all the larvae capable of penetrating the root would establish infection sites within 7 days, then RINF is estimated in the region of 0.005. ETIN—effect of temperature on infection $ETIN = 0.4336T - 0.0085\ T^2 - 4.611$ (r = 0.97). This curve is based on a combination of data from Wallace (27) on the effect of temperature on larval movement and invasion. EMIN—effect of moisture on invasion which is based on data by Wallace (27) on larval movement at different moisture levels. $EMIN = 0.0503M - 0.0045\ M^{1.5}$. EOIN—effect of oxygen level on invasion (20). $EOIN = 0.0279 + 0.0469$ (0) (r = 0.99). EPS—effect of particle size on infection, which is based on data for larval movement and invasion (27). $EPS = 0.0048\ P - 0.000006\ P^2 - 0.0702$ (r = 0.80). ECO—effect of soil cohesion on infection $ECO = 0.4064 + 0.0005C$ (r = 0.93), based on data for larval movement (27). ERESIN—the effect of the resistance level of the host on

the rate of infection, which is dependent upon the plant variety used.

$$R_5 = RDPLT + RDPLST \quad [20]$$

RDPLT—death rate of parasitic larvae resulting from temperature (deaths/larva/h) is based on data of Davide and Triantaphyllou (3) on percent males at various temperatures. RDPLT = $0.000625e^{(-0.1726T)}$ (r = 0.95). RDPLST—death rate of parasitic larvae, or development to males, resulting from starvation under crowded conditions. Davide and Triantaphyllou (3) showed that, under crowded conditions, approximately 50% of the larvae became males, a rate of 0.0014/larva/h based on a standard development period of 15 days at 25-30° C. For the purposes of the model, crowded conditions are defined as occurring when $X > 0.9$; RDPLST is multiplied by X when $X > 0.9$, so that it proceeds at a maximum rate only when $X = 1$.

$$R_6 = RDVT \times EODV \times ERESDV \quad [21]$$

RDVT—rate of development of parasitic larvae as a result of temperature (proportion of development/h) (3), expressed as the proportion of the total development completed per iteration at various temperatures. RDVT = $0.00034T - 0.000004\ T^2 - 0.0036$ (r = 0.99). EODV — $0.000004\ T^2$ — oxygen level on development (20). EODV = (0)/((0) + 0.3012) ERESDV—effect of the resistance level of the plant on the developmental rate of parastic larvae.

$$R_7 = RDAT + RDAN + RDAST \quad [22]$$

RDAT—death rate of adults as a result of temperature (deaths/adult/h); for lack of available data, it is assumed that this rate is equal to the death rate of parasitic larvae resulting from temperature, RDPLT. RDAN—natural death rate of adult females under ideal conditions (deaths/adult/h). The assumption is made that a female will live for about 100 days, and RDAN is preliminarily set at 0.0004/female/h. RDAST —death rate of adults as a result of starvation (deaths/adult/h). This parameter is assumed to be similar to the one for parasitic larvae, RDPLST, and set with the same limitations.

$$R_8 = REPT \times EOEP \times ERESEP \quad [23]$$

REPT—rate of egg production as a result of temperature (eggs/female/h). No data could be found relating the egg output rate of females to temperature. Temporarily, the assumption is made that a female will produce 8 eggs/day under ideal conditions on grapevine roots, and REPT is assigned a maximum value of 0.33 eggs/female/h and multiplied by ETIN (the effect of temperature on larval movement and invasion) on the assumption that similar optima may be involved. EOEP—the effect of oxygen on egg production (22) EOEP = $0.1357\ (0) - 0.0039(0)^2 - 0.1662$ (r = 0.99).

$$R_9 = RPGT \times EORG \times EMRG \times EGN \quad [24]$$

RPGT—rate of root growth as affected by temperature. The curve for grapevine roots is derived from data by Kliewer et al. (8), Winkler (31), and estimates. It is expressed in terms of the net assimilation rate (N.A.R.) at different temperatures. EORG —effect of oxygen on root growth, from the data of Van Gundy and Stolzy (22). EMRG —effect of moisture on root growth, modified from Winkler (3). EGN—effect of nitrogen on plant growth is estimated from Winkler (31).

PROGRAMMING CONSIDERATIONS

The general form of the computer program for the model follows the flow chart (Fig. 2). Initially, the parameters of the system are defined with regard to soil type, pH, penetrability, plant variety-nitrogen status, etc. and subroutines are called to calculate the rates dependent upon these variables. Initial values for the state variables (number of eggs, soil larvae, etc.) are entered, and then the iteration cycle is commenced. Environmental data (soil moisture, temperature, nitrogen or nematicide application) are read in for each iteration period. Subroutines are called to calculate rates and modify state variables on the basis of this environmental input. Finally, the change occurring in each state variable compartment is calculated and the compartments updated at the end of the iteration period.

Within the ENVRAT subroutine, which calculates the rates determined by soil temperature, moisture and oxygen levels, calculations of the available oxygen are made.

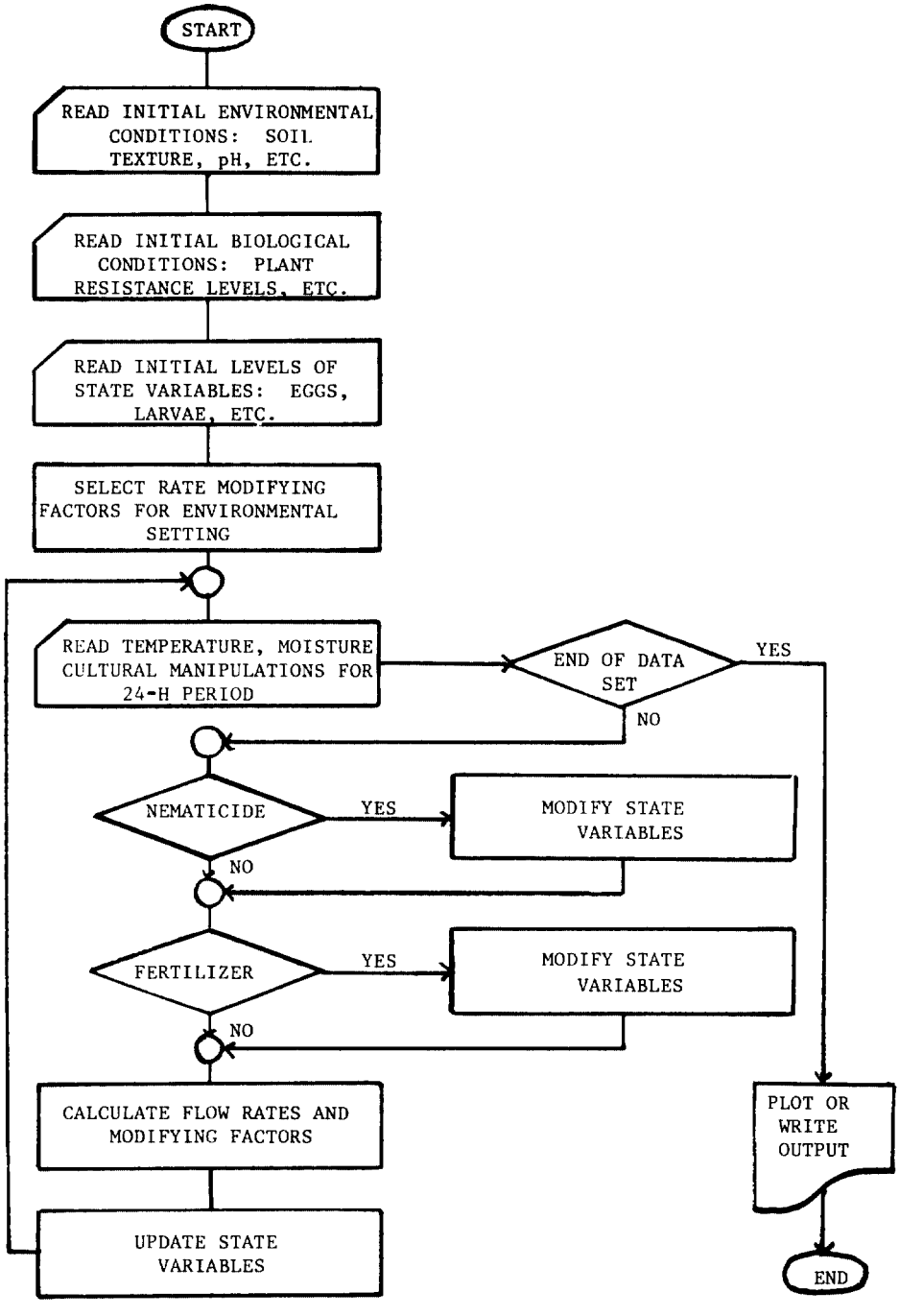

FIG. 2. Flow chart of the computer program of a *Meloidogyne*-plant simulator.

Available oxygen is considered as being at a maximum value (21%) until soil moisture levels have risen to a stage at which oxygen diffusion rates might be affected (26). A soil moisture level of 80% of the moisture-holding capacity is arbitrarily chosen. Above this moisture level, the following equation applies: AVOX = 1./(M-80). AVOX—available soil oxygen. This parameter has the value 1.0 when oxygen concentration is 21% below a soil moisture level (M) of 80% of holding capacity.

For programming purposes, equations 11 and 13 are broken into constituent parts to allow calculation of the development of eggs and parasitic larvae in age groups. This sequence prevents apparent hatch or development to adults from occurring before development is completed.

Temperature and moisture conditions vary with soil profile. The program could be modified to calculate the growth curves of the state variables in three regions of the soil profile at each iteration, the upper 10 cm, 10-30 cm, and below 30 cm. Soil physical factors (pH, cohesion) are regarded as similar throughout the profile.

Another refinement in the program would be to recognize that some of the rate equations are based on a narrower range of the independent variable than might be encountered in the field. A warning message could be printed when the simulator is operating outside of the experimental data base.

DISCUSSION

A trial simulation, using experimental and estimated parameters, of a *Meloidogyne* population on grapevines compares qualitatively and quantitatively with actual population data for eight months of the year (Fig. 3). Environmental data used in the simulation were measured in the vineyard at the time of the population studies (5). The model parameters are derived from results on several *Meloidogyne* spp. from different geographic areas; also, there were several *Meloidogyne* spp. in the vineyard studied. Differences in physiological response to environmental conditions could increase error in simulations. Plant-growth simulations are not shown, but simulated yields approximated those in the vineyard. Nematode density data for the upper 60 cm of soil were used for comparison on the assumption that this is where most of the feeder roots are located and that it is a region of relatively homogeneous environmental conditions, with the exception of temperature.

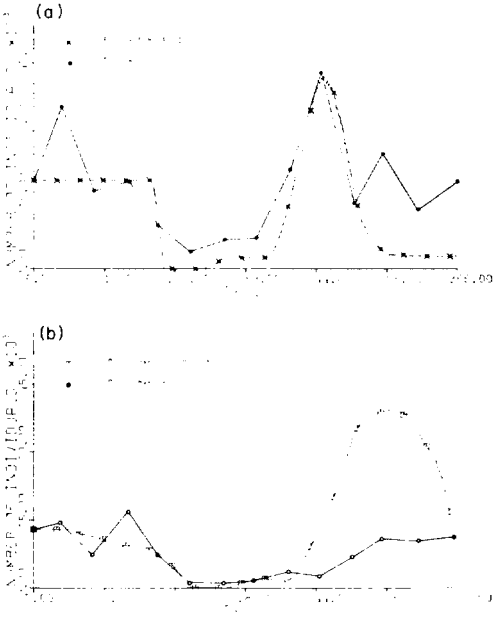

FIG. 3. Comparison of a trial simulation of a *Meloidogyne*-plant system with field data. A) Eggs. B) Second-stage larvae.

Deficiencies in my understanding of the grapevine/root-knot system, as expressed in the model, are evident in the latter part of the simulation (Fig. 3). The higher number of eggs in the vineyard (Fig. 3-A) may be due to decreased hatch during the fall, or continued egg production despite the physiological slowing of the plant. Similarly, the lower actual larval numbers (Fig. 3-B) indicate a possible decreased egg hatch, continued larval invasion of roots at this time of the year, or the effect of biological control mechanisms not included in the model. The most probable deficiency is in the difficult area of nematode/plant interaction and the effect of the annual rhythm of host physiology on this interaction. The need for further research in this area is indicated.

The modeling approach enables a holistic understanding of the system by placing the interrelated factors in perspective. It demonstrates the relative importance of the state and input variables to the behavior of the system. Hypotheses tested in a few seconds with a verified model may avoid prolonged, costly experimentation. Manipulatable aspects of the agro-ecosystem whose effects can be tested with the present simulator include alteration of soil moisture, nutrient status, pH and aeration, host variety, and timing and frequency of pesticide application. Experimentation in deficient areas will improve reliability and predictive ability of the

simulations. As models of other subsystems (including models of other nematode species, mycorrhizal fungi, and other soil microorganisms) of the agro-ecosystem are developed, they can be included in the total system and the interactions can be studied.

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