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A Stochastic Model for Simulation of Interactions between Phytophagous Spider Mites and Their Phytoseiid Predators

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ABSTRACT

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A stochastic predator/prey model describing the interaction between *Tetranychus urticae* and *Phytoseiulus persimilis* is investigated via computer simulations and pilot experiments on Lima beans in a greenhouse. Most demographic events, including predation, death due to unknown causes, dispersal, and oviposition, are modelled as stochastic processes. Transitions from eggs to nymphs and from nymphs to adults are deterministic, as are management decisions (release of predators and application of miticide). Computer simulations provide adequate and realistic representations of biological processes, and the model shows stability over a range of inputs. Experimental validation of the model continues. Predictions of the model for optimal predator release or optimal timing of acaricide application have yet to be tested experimentally.

INTRODUCTION

Simulation modelling of population dynamics presents a fruitful approach to management of phytophagous spider mites (Logan, 1982; Helle and Sabelis, 1985). Most models of spider-mite demography are deterministic, and derive from classical predator/prey models (summarized by Hassell, 1978). The two-spotted spider mite, *Tetranychus urticae* Koch (hereinafter referred to as 2SSM) and its predator *Phytoseiulus persimilis* (Athias-Henriot) (hereinafter PPE) have proven especially amenable to modelling. Extensive studies on 2SSM/PPE interactions have provided considerable insight into their demog-

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raphy and adequate estimates of several demographic parameters applied to subsequent simulations (see, for example, Laing, 1968; Takafuji and Deguchi, 1980; Ohnesorge, 1981; Sabelis, 1981; Eveleigh and Chant, 1982; Shaw, 1984; Berstein, 1985). Sabelis (1981, 1985), Helle and Sabelis (1985), and Sabelis and van der Meer (1986) developed especially detailed deterministic models of PPE searching behavior.

Although the stochasticity of arthropod predator/prey systems is equally worthy of attention, the development of stochastic predator/prey models has not proceeded at a pace equal to that of deterministic models. In part, more cumbersome mathematics is involved, and, until recently, adequate computer simulations were expensive. One approach to predator/prey stochasticity is via a general model, an example being that of Bartôszyński (1977) and Bartôszyński and Buhler (1978), who assumed that the pest population followed a continuous-time pure death process between breeding seasons and that the births followed a Galton-Watson process. Chan (1984) added appropriate parameters in order to find the optimal management policy to reduce pest damage. This and other general stochastic models are tractable enough to find explicit analytic solutions to aid understanding of the gross features of interacting populations of predator and prey. However, they cannot adequately serve to model the details of a particular system such as 2SSM/PPE. Nachman (1987a,b) presented a stochastic model of the 2SSM/PPE system assuming a stable age distribution and accounting for mite oviposition, maturation, and death over 1-h time increments. Handling time became important due to the relative brevity of time-intervals.

Nachman's model was not specifically designed for pest-management optimization. Therefore the next step will be to generate simulations based upon analytical stochastic models with the ultimate goal of optimizing pest-management decisions. In the present paper we describe a stochastic simulation model of the 2SSM/PPE interaction and suggest ways to test it via manipulative experiments and simulations. We believe that the modelling approach emerging from this research has general applicability beyond management of phytophagous spider mites.

DESCRIPTION OF THE MODEL

Our model assumes a row of plants under attack by 2SSM that are in turn being eaten by PPE. Acaricide may or may not be applied. Both 2SSM and PPE pass through egg, nymph, and adult development stages; we combine all immature instars for convenience. We assume that the transitions egg ⟶ nymph and nymph ⟶ adult occur automatically after a fixed and nonrandom time spent as egg or nymph. Therefore each individual is characterized by its age, uniquely determining its form.

The state of the system at any time is described by: the numbers of 2SSM

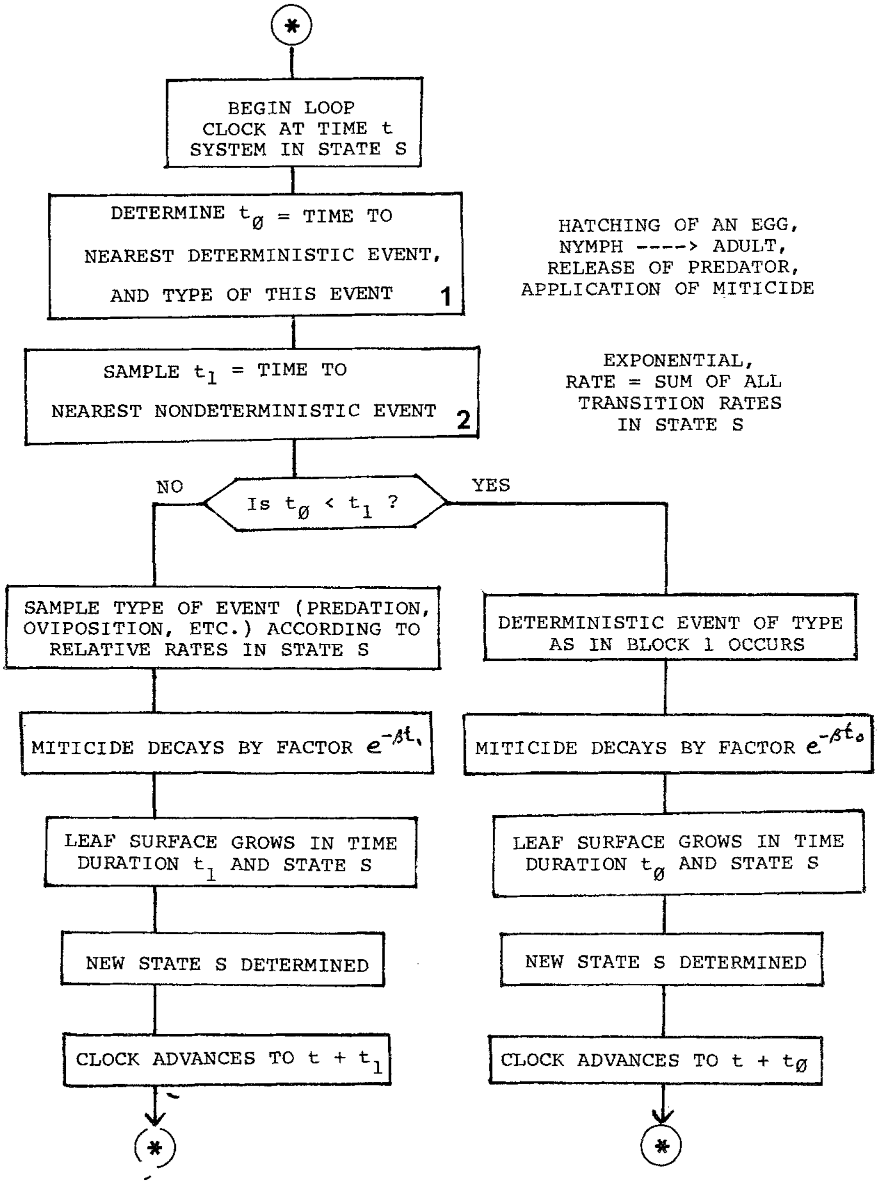

Fig. 1. Flowchart showing components of stochastic model. Computer simulates each demographic event beginning at asterisks, and recalculates residual miticide and leaf surface.

and PPE on each plant; the ages of these animals; and the leaf surface of each plant. Formally, such a description involves an array of numbers appropriately coding the above, and the model consist of assumptions which specify the (partly non-random) changes within the array. The technical details of the model will be published elsewhere; here the major features are outlined.

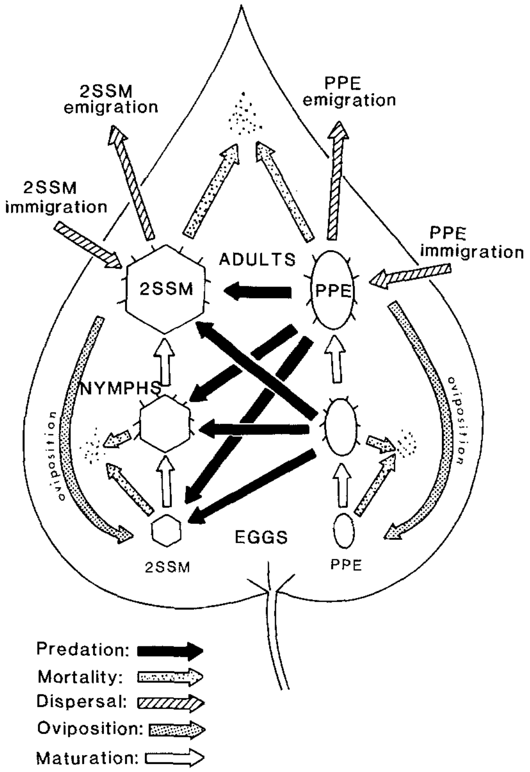

Fig. 2. Visual representation of model components on a single leaf. Open arrows indicate deterministic transitions; shaded arrows indicate stochastic transitions. Stippled areas of leaf represent dead mites. 2SSM = two-spotted spider mite; PPE = *Phytoseiulus persimilis*.

Firstly, because the transitions egg ⟶ nymph, and nymph ⟶ adult occur after a nonrandom time, the transition laws for hatching and maturing are deterministic in the entire system. The times of releasing PPE, and/or of miticide applications, are also deterministic.

The stochastic portion of the model encompasses all remaining events, i.e. births, dispersal, and deaths (whether due to predation, miticide, or 'natural' indeterminate causes unrelated to pesticide or predation).

The flowchart (Fig. 1) outlines the general form of the model as implemented for simulation. The state description at any time t involves locations and ages (hence also forms) of all 2SSM and PPE, as well as amounts of miticide and leaf surface area of all plants. From the flowchart it is clear that the most crucial assumptions are those describing the transition intensities for stochastic events. In the initial version of our model, death rates depend upon the amount of active miticide (assuming nonresistant mites) and on food supply (leaf surface for 2SSM, density of prey for PPE). Similarly, rates of dispersal depend on availability of food, appropriately interpreted for 2SSM and

TABLE 1

Parameters for initial simulations based on the stochastic model (all values are rates per mite per day, at 25 °C, in various systems)

	2 SSM	PPE
Egg mortality		
natural death	0.011 (Sabelis, 1981)	<0.001 (Shaw, 1984)
predation	0.020 (Laing, 1968)	
Nymphal mortality		
natural death	0.006 (Sabelis, 1981)	<0.001 (Shaw, 1984)
pesticide	0.065	0 (resistant)
predation	0.04 (Bravenboer and Dosse, 1962)	
Adult mortality		
natural death	0.028 (Sabelis, 1981)	0.033 (Laing, 1968)
pesticide	0.065	
predation		
by adult PPE	0.05	
by imm. PPE	0.024	
Oviposition	2.5 (Sabelis, 1981)	2.5 (Laing, 1968)
Emigration	0.001 (Nachman, 1987a)	0.10 (Nachman, 1987a)
Maturation (days)		
egg	4 (Sabelis, 1981)	3 (Laing, 1968)
nymph	6 (Sabelis, 1981)	5 (Laing, 1968)

PPE. Oviposition rate of 2SSM is assumed constant, and PPE oviposition is a decreasing function of food supply. In the initial model, we disregard the sex of the mite, and simply assume that all adults lay eggs. This assumption is acceptable if the sex ratio remains relatively constant, or if the sizes of 2SSM and PPE populations are not sensitive to variations in the sex ratio. (The degree of sensitivity is being examined through simulation, as is density-dependent variation in sex ratio.) Although in the initial model PPE eggs and nymphs are not cannibalized, this factor may be added later.

Miticide is assumed to decay exponentially in a deterministic fashion, and to increase via reapplication at decision times. The change in leaf surface is decribed by a logistic differential equation with parameters subject to stochastic variation depending upon 2SSM population density.

Figure 2 summarizes the model visually. State variables are illustrated by outlines of leaf and mites, and arrows indicate transitions. The model attempts to capture many aspects of the demographic stochasticity of the predator/prey interaction. On the other hand, environmental stochasticity is suppressed, by making parameters constant. This assumption is probably acceptable in an environmentally controlled greenhouse. However, to check our results, we have included in the program the possibility of random fluctuation of parameters

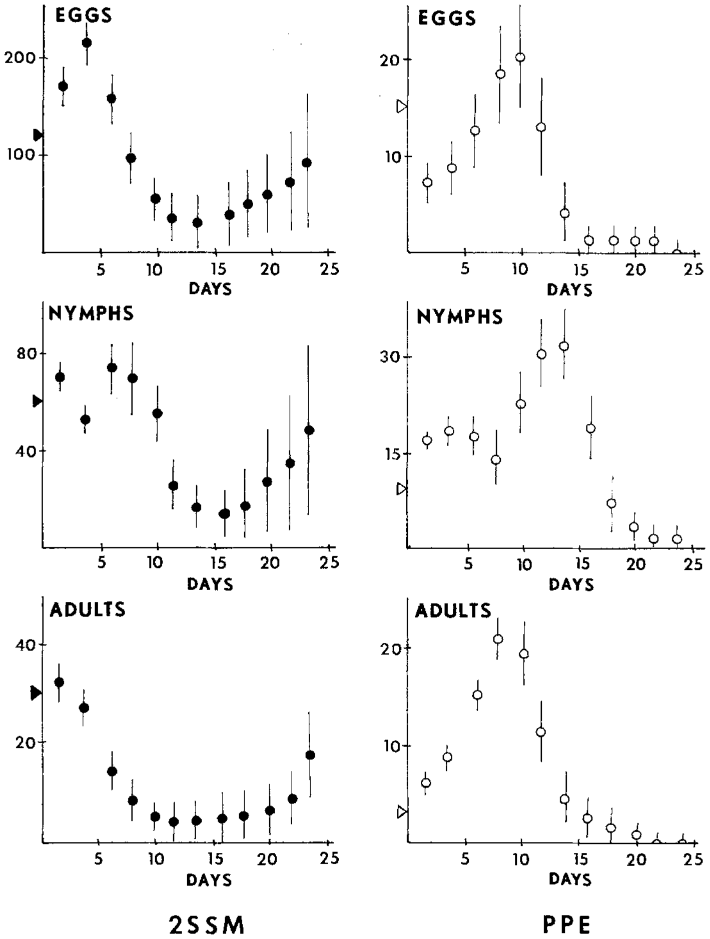

Fig. 3. Sample output from 100 simulations on Pyramid computer. Data are mite totals on 5 plants; bars are ± SD. Input densities are indicated by arrows. Parameters are as in Table 1 except that no pesticide was used. 2SSM = two-spotted spider mite; PPE = *Phytoseiulus persimilis*.

about their means. By comparing outcomes with constant and varying parameters, we plan to determine the adequacy of suppressing environmental stochasticity.

SIMULATION

The model was programmed (by DKP) on a Pyramid 90X minicomputer, and initial simulations used parameters (Table 1) from published research on various systems, or from our own preliminary estimates if literature values were unavailable. Figure 3 illustrates a sample output based on 100 simulations each involving an array of 5 plants. One hundred trials of the model simulated for a 50-day growing season with maximum density of 5000 2SSM used 45 min of CPU time. The program is currently under conversion for use on a Cray X-MP/24 which should reduce computer speed 50-fold. As can be seen, the model provides some biological realism in that nymph and adult populations follow those of eggs and the impact of PPE on 2SSM is evident. There is reasonable stability at least over short time intervals simulating 3 or 4 weeks, the time-span of greatest interest to a manager of greenhouse crops.

Facets of the model are being refined during initial collection of experimental data and additional computer simulations. We anticipate that a refined version of the model will be applicable to a production-scale experiment on commercial greenhouse cucumbers managed according to optimal pesticide application and release of PPE predicted via computer simulations.

EXPERIMENTAL VERIFICATION

To apply the general model to the 2SSM/PPE interaction we use 2-week-old Lima bean (*Phaseolus limensis* MacF.) plants in linear arrays of 5 plants each. Each plant is limited to 5 leaves; additional leaves are trimmed. Each array is isolated within a plastic and organdy cage 80 cm × 30 cm × 30 cm. Within each array, adult 2SSM from stock cultures are released onto the plants. Thirty 2SSM are released onto each plant centrally located within an array, 15 onto each of the two adjoining plants, and none on each of the end plants.

After 14 days, adult PPE are released into the caged arrays as follows: one array with 4 PPE on the 2 end plants only, one with 8 PPE on the central plant only, and one with 4 PPE on each plant adjoining, but not on, the central plant. Each release scheme is replicated 5 times. Control arrays without PPE are also replicated 5 times.

At 3-day intervals following initial inoculation of 2SSM, eggs, nymphs, and adults of each mite species are censused, and adult 2SSM are sexed. The extent of yellowing and webbing produced by 2SSM is measured, photographed, and optically analyzed with a Dapple Image Processing System as an index of leaf damage. Results are compared with output from computer simulations.

In a subsequent experiment, similar arrays of 5 plants will be subjected to modified treatments including application of hexacis at recommended rates. Miticide-resistant or miticide-susceptible PPE will be released also. (The precise arrangement of 2SSM and PPE releases are dependent on the outcome of the first set of experiments.)

DISCUSSION

The use of stochastic models in pest management is generally untried, and application of stochastic modelling to spider-mite predator/prey systems is a recent development. The combination of demographic and environmental stochasticity may render most arthropod predator/prey systems inherently unpredictable over moderate time intervals. Under the controlled conditions of the greenhouse, however, environmental stochasticity is often suppressed, thus improving predictability. The 2SSM/PPE interaction has shown a good fit to numerous deterministic models (e.g. Sabelis, 1981; Shaw, 1984; Bernstein, 1985) and is ideal to test the present model experimentally. Future research will concentrate upon those parameters having the greatest impact on fluctuations in 2SSM and PPE. The ultimate goal is a refined model that provides predictive capability to optimize release of predators and/or application of a pesticide to enhance the efficiency of agricultural production. Adoption of refinements will depend primarily upon their effect on the problem of spidermite control. Given intensification of greenhouse production, increasing unreliability of chemical pesticides when used alone, and increasing costs of inputs in crop production, this modelling approach presents a valuable tool in enhancing the efficiency of agricultural production as well as in the understanding of demographic processes within arthropod populations.

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