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A POPULATION MODEL FOR TWO-SPOTTED SPIDER MITE *TETRANYCHUS URTICAE* AND ITS PREDATOR *METASEIULUS OCCIDENTALIS*

BY

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A population simulation model that was developed for the fruit tree red spider mite (*Panonychus ulmi* Koch) and its phytoseiid predator (*Amblyseius potentillae* Garman) (Rabbinge, 1976) was adapted to *Metaseiulus occidentalis* Nesbitt and *Tetranychus urticae* Koch. The model uses life-table data for *T. urticae* and *M. occidentalis* and *M. occidentalis'* numerical and functional responses. The assumptions made in the model were tested by comparing the model outcome with the results of an independent greenhouse experiment. Sensitivity analyses were also done to evaluate the implicit assumptions of the model and to determine the relative importance of the rates and parameters used. Results of the sensitivity analysis showed that time of release is critical for rapid control of the prey population. Predator-prey release ratios and frequency of releases are relatively less important. Differences in functional and numerical response and predator dispersal rate also seem relatively less important than proper timing of releases.

Biological control of mites is becoming recognized as an effective pest control method in agricultural crops (Huffaker *et al.*, 1970). Traditionally an empirical approach has been applied in inundative or augmentative releases of predators or parasites, and by trial and error the methods of release, including the frequency, the numbers and the time of release, are improved. It is desirable to shorten this procedure and to base the releases on a better understanding of the system. Perhaps simulation models can be used in conjunction with optimization techniques to develop better release methods (Shoemaker, 1977).

The goal of this project was to develop a population simulation model of the two-spotted spider mite (*Tetranychus urticae*) and its phytoseiid predator (*Metaseiulus* (= *Typhlodromus*) *occidentalis*). The model will eventually be used to devise release strategies for pesticide, resistant strains of *M. occidentalis* (Hoy, 1979), as well as evaluate the relative effectiveness of wild and selected (pesticide-resistant) predators. Laboratory experiments provided the life-table data for the two-spotted spider mite and *M. occidentalis* as well as *M. occidentalis'* numerical and functional response. The basic structure of the simulation model is the same as that for the fruit tree red spider mite (*Panonychus ulmi*) and its predator (*Amblyseius potentillae*) in the Netherlands (Rabbinge 1976). New experiments were performed

in the laboratory to measure dispersal of *M. occidentalis* and to test whether the model and its implicit assumptions (for instance unlimited prey) are applicable to the *M. occidentalis* - *T. urticae* system. The model was tested by comparing its expected results with the outcomes of independent population experiments in a greenhouse.

MATERIALS AND METHODS

Sources of the colonies used — The predator strain used for the greenhouse experiments was derived from 20—30 adult females isolated from dormant grape buds in a Fresno County, California vineyard. This strain was maintained for 12 months using *T. urticae* as prey, as described by Roush & Hoy (1978). The *T. urticae* used in the experiments were taken from a colony resident in the University of California, Berkeley greenhouses for more than 2 years.

Numerical and functional response — In order to use data on predation rate developed by Kuchlein (1966) and Fransz (1974) for *Typhlodromus longipilus* Nesbitt, we performed predation rate experiments to compare the characteristics of our *M. occidentalis* colony with their data. *M. occidentalis* and *T. longipilus* are considered nonspecific (Huffaker *et al.*, 1970). Newly emerged, gravid *M. occidentalis* females were isolated from the culture as deutonymphs and provided with a male. After moulting and mating the females were placed individually on a 3.8-cm² leaf disk of lima bean (*Phaseolus limensis* var. *limenanus* Bailey) placed upside down on wet cotton. They were provided with prey at two experimental densities. The predators remained on the leaf disk for adaptation at least 12 hr and any prey killed were replaced every 2 hr; then the females' predation rate and reproductive rate were observed continuously for 8 hr at 23° ± 1°. Eggs or adult males of *T. urticae* were used as prey during the experiment at densities of two or ten each per disk, respectively, with eight replicates per density.

Greenhouse release experiment — To test the model an experiment using *T. urticae* and *M. occidentalis* was performed under greenhouse conditions where the temperature varied between 27° and 19.5° and relative humidity between 70% and 90%. The lima beans were grown in 25-cm diam. pots with a 1:2 mixture of vermiculite and soil by volume. These were arranged in eight plots each consisting of 16 pots occupying 1 m². After the bean plants had developed a closed canopy 50 cm high, each of eight plots was infested with 30 adult *T. urticae* females. The adult females were placed on leaf disks (3 per disk) which were put haphazardly over the canopy of the plot, sticking them to the leaves with needles. Ten days after inoculation with prey, ten newly emerged adult female *M. occidentalis* were placed uniformly on four of the experimental plots, using one female per disk. Population densities of both species were determined every 3 days using 20 randomly sampled leaflets per plot. The population density and its age distribution were determined either by actual counts of mites made under a dissecting microscope or by counting the numbers of mites brushed from the leaves with a leaf brushing machine. The counts on individual leaves allowed an estimate of the distribution patterns of the predator and prey mites.

During the experiments, the total leaf area per plot was kept constant by pruning the new runners every day. The density levels of the mites during the experiments were so low so that no mites were lost due to pruning. Total leaf area was determined from two control plots and the average leaf area of 20 leaflets was determined on each sampling date, using a Li-cor (Lambda Instruments, Lincoln, Nebr.) leaf-area meter. Leaf area determinations allowed the extrapolation of the results of the detailed observations of predation rates on the leaf disks to the more complex situations of the greenhouse experiment.

Dispersal of M. occidentalis — In two additional plots heavily infested with *T. urticae*, ten adult female *M. occidentalis* were released at one place and their dispersal from that site was determined using a 1 m² grid subdivided into 10 × 10 cm units that was hung above the plot in order to map the predator's distribution. The location of the released predators was determined every 15 min after release for 6 hr. Thus the pattern of migration of the mites could be determined using mite density maps which show the frequency of occurrence of mites at different distances from the source (Table I).

TABLE I

Frequency distribution of M. occidentalis *females at different times after release from central point in 1 m² bean plots in greenhouse, based on average of five experiments*

Distance from point of release (cm)	Time after release-min				
	0	30	60	120	360
0	10	8	8	6	4
20	0	2	1	3	2
40	0	0	1	1	2
100	0	0	0	0	2
150	0	0	0	0	0

RESULTS AND DISCUSSION

Numerical and functional response — Female *M. occidentalis*' predation rate/hr on *T. urticae* eggs or males averaged 0.18 ± 0.04 and 0.2 ± 0.01, respectively, when the prey density was 2/cm² leaf area. When the prey density was 10/cm² leaf area, *M. occidentalis* females ate 0.48 ± 0.02 and 0.38 ± 0.01 eggs or males, respectively, per hour. The predator females deposited an average of 1.0 ± 0.07 or 0.8 ± 0.5 eggs/day at the lower prey density and 3.23 ± 0.07 or 1.2 ± 0.06 eggs/day at the higher prey density for females preying on eggs or males, respectively. The predation rates of our strain fell within the confidence intervals determined by Fransz's (1974) observations. At a density of 12 *T. urticae* eggs per cm² a predation rate per adult female of *M. occidentalis* of 0.5 preys killed per hour was determined, at a density of four eggs per cm² a predation rate of 0.25 was found. Therefore, we concluded that the functional and numerical responses determined for the European strain of *M. occidentalis* could be used in the model.

Leaf area determinations — The small variability in bean leaflet size (mean = 22.68 ± 1.67 cm²) justified using a "per-leaflet" expression of mite densities. The average leaf area per plot ($\bar{x}$ = 38794.2 ± 321 cm²) and the number of leaflets per plot ($\bar{x}$ = 1710.5 ± 80) was fairly uniform. The leaf area index (leaf area/soil area) of the experimental plot was about 4 during the experiment, which implies a high leaf density, as the average height of the canopy was low (50 cm).

Greenhouse release experiment — In Figs 1—2 the observed average population densities of prey and predator are shown with their confidence intervals for each sample date using a confidence limit of 90% and a two-tailed t-distribution. Fig. 1 A-D illustrates the densities per leaflet of the eggs, the juveniles, the adult females and males of *T. urticae*, respectively, in the absence of the predator. As expected, the population growth of *M. occidentalis* is exponential and does not reach an upper limit during this experiment so that it seems valid to assume the presence of unlimited food for the predator.

In Fig. 1 A-D the average densities (and their confidence intervals) of the same stages of *T. urticae* are shown in the presence of the predator. The age distribution and growth rate of the spider mite population were initially the same as when the predator was absent. But 10 days after the predator release a suppression of the prey population began, resulting in a lower final density of that population and a change in its age distribution towards younger stages. Because the period of the experiment was short and a low number of predatory mites was introduced late, the differences between the treated and untreated plots were not great, although statistically significant at the 5% level.

The growth of the predator population is shown in Fig. 2 A-D. Apparently, prey were so abundantly available that after a short interval the predator achieved an unlimited growth rate, resulting in an exponential growth curve. The experiment was stopped 42 days after infestation with *T. urticae* as by that time plant quality had declined to the point that the life-table data used in the model (Table II) were becoming invalid.

Both methods of mite counting gave corresponding results so that for average density estimations the less time-consuming leaf brush method was applied. However, individual leaf counts are necessary if mite distribution patterns are desired.

Dispersal of the predator — Table I shows that after their release, *M. occidentalis* females may move considerable distances even though sufficient food is available at the release site. It is not possible to conclude from these data whether the movement was directed or undirected. Johnson & Croft (1977) and M. W. Sabelis (*in litt.*), showed that other phytoseiid mites, like many other animals, exhibited directed and well-defined movements and behavior which were closely related to their hunger level. In the present experiment the released animals were well fed and we can assume that the directed behavioral component was absent; the remaining aimless movement can be described as a diffusion process (Pielou, 1969). Therefore, a diffusion coefficient was calculated based on formula 11.1

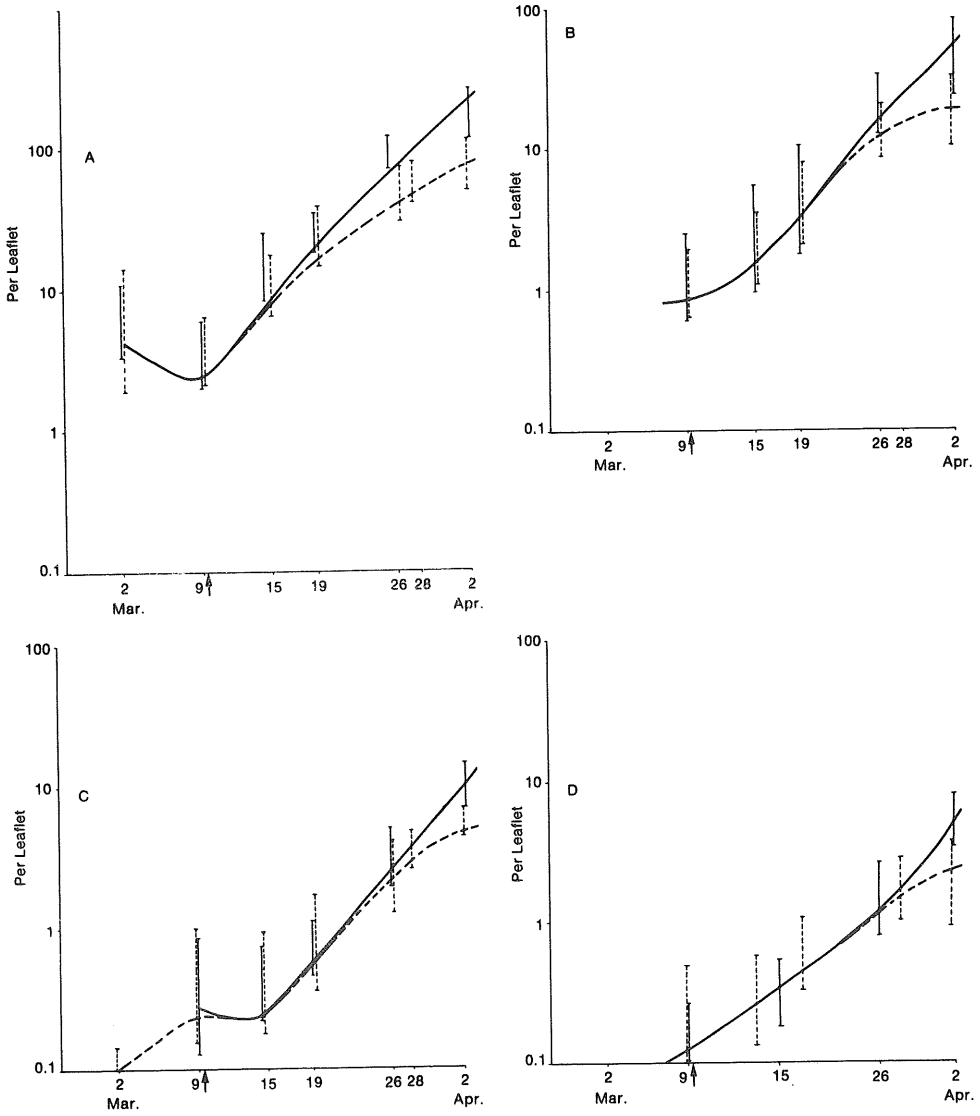

Fig. 1. Measured (solid confidence intervals α = 10% of the individual replicate means) and simulated (solid lines) population densities of *T. urticae* eggs (A), immatures (B), adult females (C), and adult males (D). Effect of releasing *M. occidentalis* upon *T. urticae* densities indicated by broken line confidence intervals, simulated *T. urticae* densities given as broken lines. Arrows: release date of *M. occidentalis*.

from Pielou (1969) using the data of Table I. This coefficient, D = 0.25 m^2 day^{-1}, was high compared with the dispersal rates found for other small animals that walk and expressed the high activity level of *M. occidentalis* after its release. Although the diffusion coefficient may be adequate for the present study, more detailed

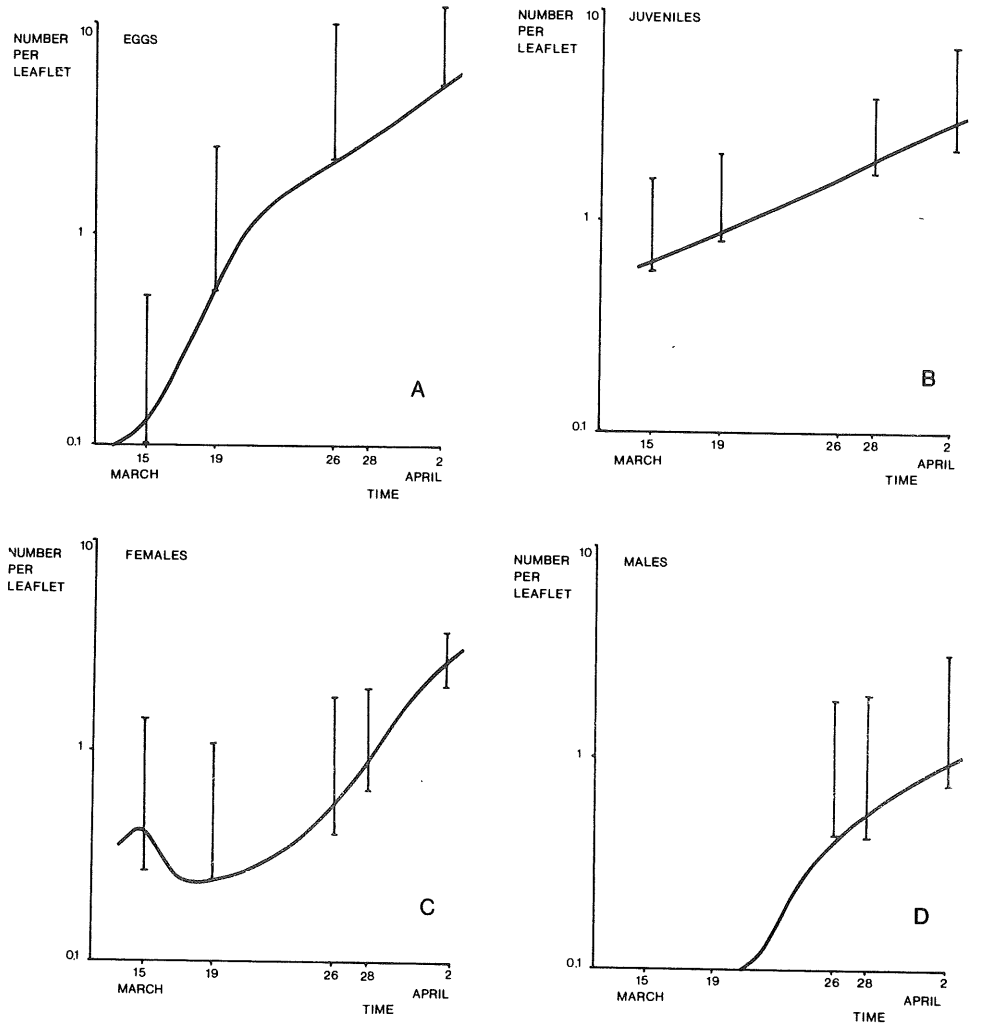

Fig. 2. Measured (confidence intervals, $\alpha = 10\%$ of individual replicate means) and simulated (solid lines) densities of *M. occidentalis* eggs (A), juveniles (B), adult females (C), and adult males (D).

observations as done by M. W. Sabelis (*in litt.*) will provide an accurate understanding of dispersal in *M. occidentalis*.

MODELING EFFORT

The model consists of four sections which describe the population densities of *T. urticae* and *M. occidentalis*, their interactions, and the environmental conditions that affect the rate variables of the model.

Section 1 — *Tetranychus urticae*

The population growth and development of *T. urticae* is given (Fig. 3) using a

TABLE II

Life table data of T. urticae *and* M. occidentalis *used in the model*

	Temperature °C			
	18	24	32	Authority
Tetranychus urticae				
DPE*	7.0 ± 0.4	6.0 ± 0.7	2.2 ± 0.5	Laing 1969, a, b Tanigoshi *et al.*, 1975
DPJ	10.0 ± 1.2	6.5 ± 0.9	3.6 ± 0.9	Tanigoshi *et al.*, 1975
POF	2.5 ± 0.6	2.1 ± 0.5	1.3 ± 0.3	Tanigoshi *et al.*, 1975
LSM	16.7 ± 4.1	12.5 ± 3.5	8.3 ± 2.9	Tanigoshi *et al.*, 1975
LSF	33.0 ± 12	25.0 ± 10	15.0 ± 5	Tanigoshi *et al.*, 1975
Max. Life span, ♀♀	70	45	30	Lee & Davis, 1968
Length age class	14	9	6	Lee & Davis, 1968
RR1	3	5	6	Lee & Davis, 1968
RR2	5	6	8	Tanigoshi *et al.*, 1975
RR3	4	3	5	Tanigoshi *et al.*, 1975
RR4	2	2	3	Lee & Davis, 1968
RR5	0.8	1.5	1	Tanigoshi *et al.*, 1975
RM1	0.004	0.004	0.05	Sabelis, *in litt.*
RM2	0.002	0.023	0.048	Sabelis, *in litt.*
RM3	0.07	0.066	0.172	Sabelis, *in litt.*
RM4	0.11	0.13	0.19	Sabelis, *in litt.*
Metaseiulus occidentalis				
DPE	6.25 ± 0.9	2.5 ± 0.6	2.0 ± 0.4	Tanigoshi *et al.*, 1975
DPJ	6.67 ± 0.9	4.0 ± 0.5	2.9 ± 0.25	Sharma, 1976 Tanigoshi *et al.*, 1975
POF	4.0 ± 0.8	2.33 ± 4.0	1.11 ± 0.25	Tanigoshi *et al.*, 1975
LSF	18.87 ± 8.0	14.29 ± 4.0	12.5 ± 3.0	Tanigoshi *et al.*, 1975
LSM	13.35 ± 3.65	10.0 ± 3.16	8.3 ± 2.9	Tanigoshi *et al.*, 1975
RR	1.45	2.1	2.9	Tanigoshi *et al.*, 1975
Fecundity	27.36	30.01	36.25	Tanigoshi *et al.*, 1975

* DPE = Development Period Eggs; DPJ = Development Period Juveniles; POF = Pre-Oviposition period Females; LSM = Life Span Males; LSF = Life Span Females; MLSF = Maximum Life Span Females; RR1-RR5 = Reproductive Rate in eggs/day in age class 1—5; RM1-RM4 = Relative Mortality Rate in day^{-1} in age class 1—4.

simplified relational diagram (Forrester, 1961). The developmental stages are lumped into five groups: the eggs, the juveniles, the preovipositional females, the males and the mature females. For each group a series of age or developmental classes (state variables) is used to calculate the dynamically changing age structure of the population and to mimic the dispersion in time during development (Goudriaan, 1973, Rabbinge, 1976). Developmental rates derived from the literature are included in the model as a function of temperature. Mortality during development due to abiotic factors is very low

$$\text{Relative MORtality rate: RMOR} = \frac{\ln Y_1 - \ln Y_2}{\Delta t}$$

in which Y_1 is the number of animals in the development class at the beginning, Y_2 the number that is transferred to the next class and Δt is the average residence time in this developmental class. The relative mortality rates for the different groups at different temperatures are given in Table II. The rate of ageing of the females, the dispersion in time during ageing and the age dependence of reproductive rate are simulated using a method described by Rabbinge (1976). During this process some of the mites die and disappear from the system and the reproductive rate is calculated on a per age class basis. Five age classes are

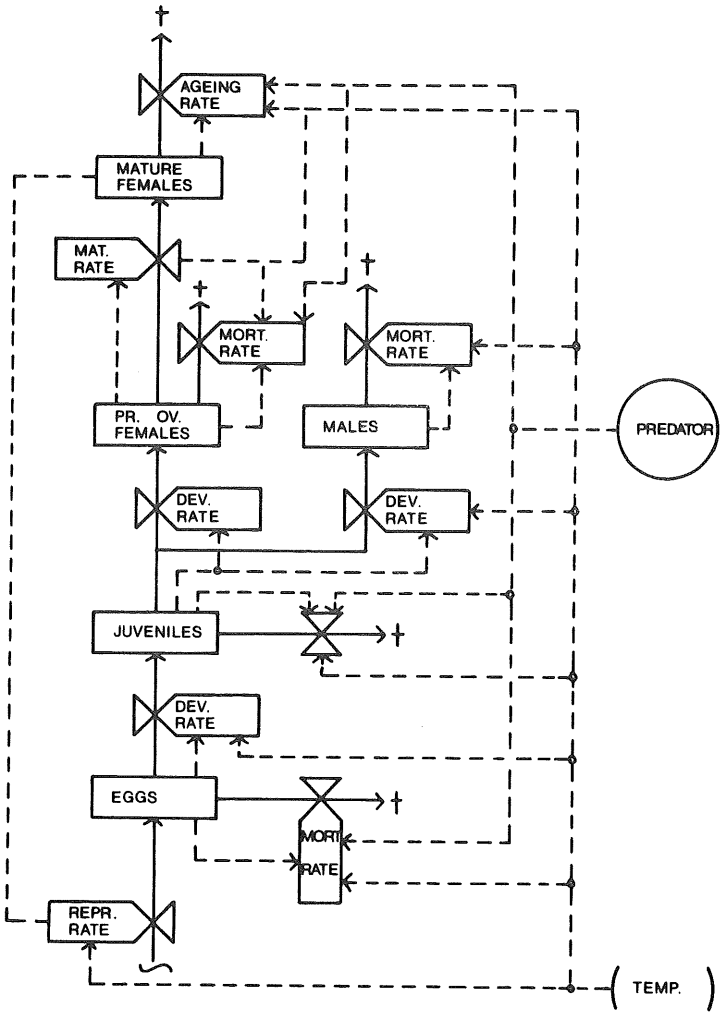

Fig. 3. Relational diagram of *T. urticae*: rectangles; +: state variables, valves indicate rates of changes, circles: auxiliary variables; parameters underlined, driving variables given between brackets and material or information flows given by solid or broken lines, respectively.

distinguished for the mature females; the size of the class and the reproductive rates of those groups are presented in Table II.

Section 2 — *Metaseiulus occidentalis*

The life history of *M. occidentalis* is similar to that of *T. urticae*. As in *T. urticae*, development is considered in five groups: eggs, juveniles, preovipositional females, males and mature females. Rates of development, ageing and reproduction are given in Table II based on literature data.

Section 3 — *Prey-predator interactions*

All stages of the prey and four stages of the predator are involved in the prey-predator interactions. The preference of the predator for different stages of the prey depends on the developmental and physiological stage of the predator. Juvenile predatory mites do not readily accept the adult stages of *T. urticae* and prefer prey eggs. Adult *M. occidentalis* attack eggs and all mobile stages of the prey, but also prefer the younger stages, although the satiation level of the predator affects this preference. Because the functional and numerical responses of our strain of *M. occidentalis* were similar to those obtained by Fransz (1974), we used his data on feeding response or ratiation level. Fransz (1974) showed that *M. occidentalis* reaches a steady state at each point of the functional response curve in which the satiation level oscillates with a small amplitude. In that steady state a unique relationship exists between the predation rate for each prey stage and the satiation level of the predator so that the functional response curve may be used as an input relation for the model. The functional response curves for the different stages of predator-prey combinations are processed (Rabbinge 1976) to find the relative predation rates (predation rate divided by the prey density) for each combination dependent on the predator's satiation level. Prey preference and the changes in predation rates with changes in satiation of the predator are thus included. The increase in the predator's satiation level is the sum of the predation rates for each of the prey stages multiplied by their respective prey values. These values were based on their surface-volume ratio and were calibrated with data given by Rabbinge (1976). The decrease in the predator's satiation level is due to digestion and this rate is assumed to be proportional to the actual satiation level and the relative digestion rate; its temperature dependence was assumed to be the same as that of *A. potentillae*. At 10, 15, 20, 25 and 30°, the relative rate of digestion of prey by *A. potentillae* is 0.1, 0.4, 0.8, 1.0 and 1.5 day^{-1}. Thus the effect of temperature on the prey-predator interactions works through the relative digestion rate and the relative predation rates.

Since the size of the system affects relative predation rates, the ratio of leaf area of the leaf disk to the leaf area of the experimental plot was used as a multiplication factor of the relative predation rates. To account for the dispersal of *M. occidentalis* in space and its dependence on the distribution of the prey, a prey density-dependent correction factor for the relative predation rates was introduced, based on the dispersal studies. This density-dependent correction factor was 0.5, 0.75, 1 and 1 for prey densities/leaflet totaling 0.1, 10, 20 and 100 *T. urticae*/leaflet, respectively. The predator's apparently directed search behavior

outside areas with high prey densities causes a more than proportional relative predation rate when prey densities are low but prey are clustered.

T. urticae exhibits more clustering and colony formation than *P. ulmi* (Rabbinge, 1976). An average prey density of less than two *T. urticae* per leaflet corresponds with a negative binomial distribution pattern that evolves into a more random distribution as the average density increases (Table III). With *T. urticae* highly

TABLE III

Distribution characteristics of T. urticae *and* M. occidentalis *populations during greenhouse experiments. (x = mean, k = measure of clustering calculated using maximum likelihood method (Bliss & Fisher, 1953))*

Time (days after start of experiment	Repli-	*T. urticae*				*M. occidentalis*			
		♀♀		Eggs		♀♀		Eggs	
	cate	x	k	x	k	x	k	x	k
8	1	0.01	<0.01	2.9	0.24	—	—	—	—
	2	0.02	0.2	6.3	0.33	—	—	—	—
	3	<0.01	<0.01	5.2	0.33	—	—	—	—
	4	0.01	<0.01	7.3	0.43	—	—	—	—
22	1	1.2	0.9	16.8	1.0	0.1	<0.01	—	—
	2	1.0	0.7	8.4	0.6	0.05	<0.01	—	—
	3	0.9	0.5	9.3	0.4	0.06	<0.01	—	—
	4	1.7	3.5	15.8	0.6	0.02	<0.01	0.2	<0.01
30	1	6.0	3.6	55.7	3.2	2.0	5.8	4.5	6.2
	2	6.9	8.2	81.5	3.5	1.2	15.9	5.1	4.6
	3	6.5	3.4	53.5	3.4	1.5	3.2	3.7	3.4
	4	4.5	2.0	71.3	1.8	1.1	5.3	3.7	2.7

clustered at low densities, *M. occidentalis* loses time moving from one prey colony to another. For this reason the level of clustering expressed as k-value (Pielou, 1969), is introduced as such in the relative predation rate. In fact, the process of leaving and arriving at prey colonies and the associated behavior when going to another colony should be included in the model. The extrapolation of the simple prey-predator system from the laboratory to the simple greenhouse situation is also complicated at high predator densities by the phenomenon of mutual interference, which may diminish the relative predation rate. However, the situations for which calculations were made concerned relatively low predator densities. Moreover, lack of information on these effects at those densities meant that the effects of mutual interference had to be ignored in the present model.

Section 4 — *Driving variables*

All rates in the model are affected by abiotic conditions, especially by temperature. The instantaneous temperature was derived from a sinusoidal curve drawn through the daily maximum and minimum greenhouse air temperature measured at bench height at the place where the beans were grown. During the

greenhouse experiments, air temperatures oscillated between 27° and 19° with a very regular pattern. Relative humidity was not included in the present model, since only very low or very high humidities (less than 40% or more than 95%) over long periods appear to have detrimental effects on the prey or predators (Rabbinge, 1976). This was never the case in the greenhouse experiments and these effects were neglected.

The program was executed with time steps of 0.1 day, the size of this time step being dictated by speed of change of the system (De Wit & Goudriaan, 1978). Here, the inverse of the relative predation rate for prey eggs at 30° governs the rate with which the system changes. Larger time steps will cause deviations from the actual performance of the system and may even result in oscillations (Rabbinge, 1976).

Results of the model calculations

Results of the model calculations are compared with those obtained in the greenhouse experiment (Figs 1—2). Fig. 1 A-D shows the results when no predators were released. The actual growth rate and the relative composition of the *T. urticae* population in the simulation correspond quite well with the experimental results. These simulation results were reached without any adaptation of input data. Fig. 1 A-D shows similar results when the effect of the predator release is included. These results were also reached with the unadapted model in which the factor that accounts for the prey distribution is introduced. The simulated curve falls within the confidence intervals of the greenhouse measurements for nearly all cases. A better fit could have been obtained by changing some of the estimated input relations or parameters but this was not done, since the model would then become a sophisticated method of curve fitting. Apparently the dependence of the relative predation rates on the satiation level of *M. occidentalis* and the prey utilization values derived from the surface-volume ratio of *T. urticae* are as valid in this model as they were in the original (Rabbinge, 1976). The satiation level of *M. occidentalis* is low in the beginning of the simulation but develops later to higher values due to increases in the prey population. This phenomenon would explain why *M. occidentalis*' development and reproduction are retarded initially (Fig. 2 A-D). However, the predator's satiation level increases rapidly to its maximum value and the relative predation rates then diminish; preferences in prey utilization change and only eggs and larvae are eaten. This behavior can be seen in the simulations (Fig. 5) where the cumulative predation of two prey stages is presented. Although the relative contribution of the younger prey stages to the total population may be low, the consumption rate of the younger prey stages is (at a high satiation level) more than proportional to their actual density. In the simulations (Fig. 4) a maximum density for *T. urticae* adult females is reached 45 days after the start of the experiment and after 57 days the number of *T. urticae* eggs is maximal. At those moments predator densities are fairly high (> 2 adult females per leaflet) and the number of killed prey is enormous (Fig. 5 A-B).

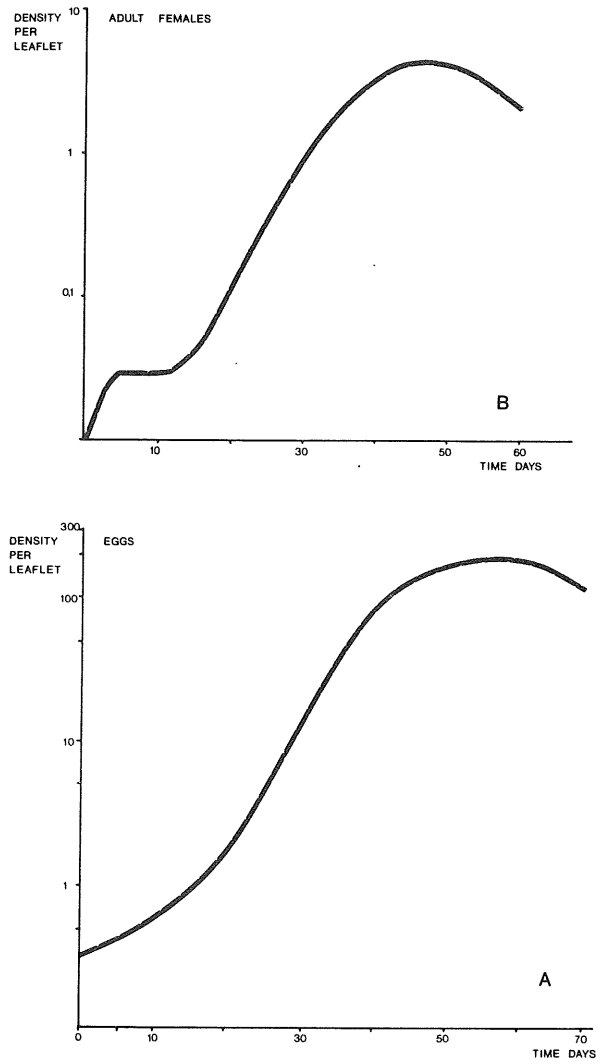

Fig. 4. Calculated densities of *T. urticae* females (A) and eggs (B) when *M. occidentalis* was released on day 10.

Sensitivity analyses with the model

A sensitivity analysis evaluated the assumptions implicitly made in the conceptualization of the model and determined the relative importance of the rates and parameters used. One parameter at a time was changed, leaving all other input values of the model the same (Table IV). The *T. urticae* population curve is represented by the maximum density of females and the day at which this maximum is reached in comparison with the "standard curve" obtained in the greenhouse experiment. Table IV also presents a ratio of simulated prey egg

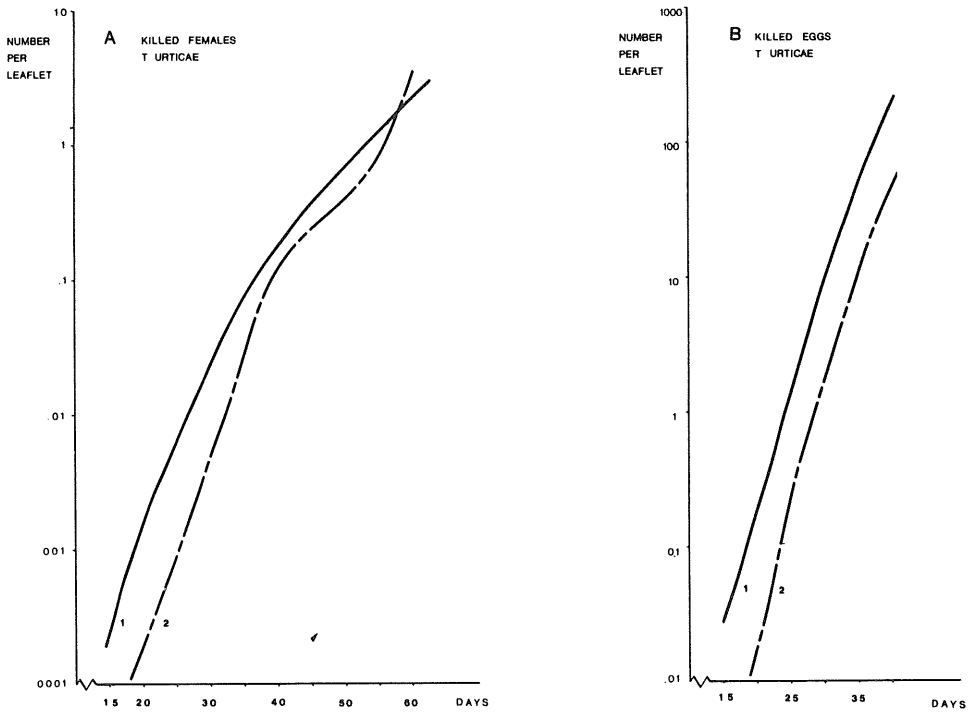

Fig. 5. Cumulative number of *T. urticae* females (A) and eggs (B) killed by *M. occidentalis*/leaflet as calculated with the model in which (1) is basic curve and (2) is result of calculations for a system 10 × in size.

density/"standard" curve and the simulated density of the female predators 50 days after the start of the experiment or simulations.

Output control

Runs made with the unmodified model but using time steps of 0.01 day and 0.5 day were compared with those made with the standard 0.1 day. Improvement in results due to the smaller time step was less than 2% and thus the use of the time step of 0.1 day is adequate. With a time step of 0.5 day the results differed by more than 15% from the computation using time steps of 0.1 day.

Input information and initialization

To test the sensitivity of the system for frequency, time, and ratio of predators and prey at the time of releases, computer runs were made in which all these elements were tested independently (Table IV). The time of release was thus shown to be of critical importance for adequate control of the prey population. Early releases effected control of the spider mite population before it started its population boom. The predators in this system will stay alive, but due to lack of food their development is delayed and their reproductive rate is reduced so that

TABLE IV

Sensitivity analyses with T. urticae *and* M. occidentalis *population model compared to data from greenhouse experiment. Only analyses showing a deviation greater than 5% of standard curve given*

Treatment	Time predators released (days after expt. begun)	No. adult ♀♀ released	Max.density prey ♀♀ leaflet	Day max. density reached	No.predator ration*	♀♀ at day 50 per leaflet
1. Simulated greenhouse Expt. (STANDARD)	12	10	5	45	1.0	5
2.1 Initial conditions, one release at	0	10	0.8	35	0.75	8
2.2 Initial conditions, one release at	0	30	0.2	25	0.1	15
2.3 Initial conditions, 2 releases at	12.24	2.40	8	50	1.5	4
2.4 Initial conditions, 2 releases at	12.24	5.40	7	50	1.5	3
2.5 Initial conditions, 2 releases at	12.24	30.40	2	40	0.9	5
3.1 Reproduction dec. 0.5 × due to dec. food utilization efficiency	12	10	15	55	1.5	1.0
3.2 Develop. rate dec. 0.5 × due to dec. food utilization efficiency	12	10	30	60	2.0	0.8
4. System size increased 10 ×	12	10	60	65	2.0	1.5
5.1 Predation by females neglected	12	10	>15	>70	3.0	2.5
5.2 Predation by juveniles & ♂♂ neglected	12	10	10	50	2.5	2.5

* Ratio: Density prey eggs in treatment/Density prey eggs in standard at day 50.

the final predator population is low, i.e., one adult female per leaf after 50 days rather than the five obtained for the "standard" situation. This result is also given in Table IV. The ability of the predator to control its prey was less sensitive to the predator-prey ratio or to the frequency of predator releases.

Predation

Runs were made in which the predatory activities of 1) females, or 2) juveniles and males were ignored to test their relative importance. All *M. occidentalis* stages contributed considerably to predation although about 40% of all the *T. urticae* eggs and juveniles were eaten by adult females, as is shown in the calculated cumulative number of killed prey (Table V). Although the age class composition of the predator population is such that the fraction of adult predator females is low, their

contribution to predation per animal is relatively high. From these results it seems justified to conclude that a decrease in juvenile and male predatory activity is less severe than a decrease in the females' predatory activity.

TABLE V

Simulations of cumulative number of prey killed per leaflet after 40 days at greenhouse experimental tempeatures

	No. killed prey		
	eggs	juveniles	adult females
When all stages of *M. occidentalis* are active predators	194	10.8	1
When only female *M. occidentalis* are active predators	73	7.2	0.16

Rates of mortality, development and reproduction

a. *Multiplication factors.* To test the importance of the factor that accounts for prey distribution, runs were made in which this factor was made bigger or smaller. This factor is only important when its effect is more than doubled or halved. Changes within 25% of the assumed value are of minor importance and do not dramatically change the course of the population curve of either predator or prey. Also the effect of changes in mortality rates due to abiotic factors is negligible; only when an increase of at least ten-fold in relative mortality rates is assumed can an affect on the population curves be seen.

b. *Numerical and functional response.* Data on the response of phytoseiid reproductive rate and developmental rate to lack of food are scarce. To test the effects of these factors on the overall behavior of the system, simulations were made in which the effect of the satiation level on the reproductive rate and the development rate of the juveniles was increased by a factor 2. The effect of the delayed developmental rate is more severe than a change in reproductive rate (Table IV), probably because the shorter developmental rate has a greater effect on population development than does the direct effect of the increase in reproductive rate.

c. *Size of the system.* All of the calculations described above concerned the greenhouse experimental system. Changes in the size of the system were introduced by altering the ratio of the area of the experimental arena for the predation experiment and the area of the actual system. Enlarging the system tenfold, while using the same numbers of predator and prey mites results in delayed control of *T. urticae* by *M. occidentalis* (Table IV). This logical result, due to the longer search period of the predator, is shown in Fig. 6 where the satiation level of the predator is presented. The satiation level of the predator stays rather low during a longer period and thus the relative predation rates stay at their

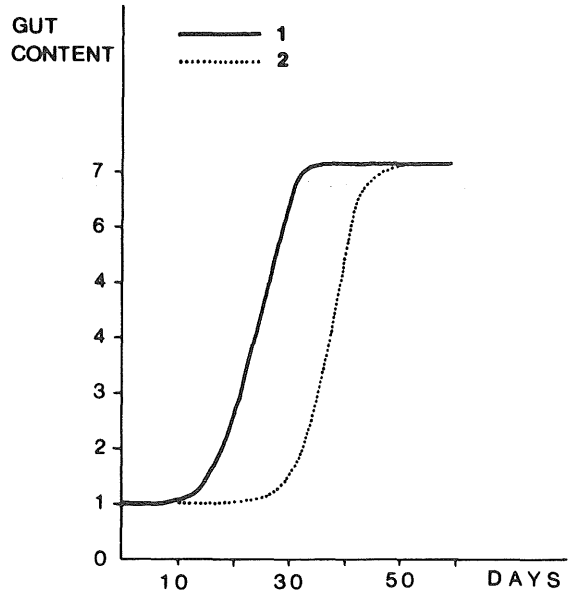

Fig. 6. Gut content of *M. occidentalis* females calculated with the model, (1) is basic curve and (2) is result of calculations for a system 10 x in size. (All stages of *T. urticae* served as prey.).

maximum for a longer period. Nevertheless, it takes the predator population a longer period to reach the growth rates that were shown in the greenhouse experiments. Thus the reproductive rate and developmental rate of *M. occidentalis* juveniles are delayed in the beginning and consequently the population growth of the predator is delayed.

GENERAL DISCUSSION

The presented simulations and their comparison with independent greenhouse measurements show that the *P. ulmi - A. potentillae* model (Rabbinge, 1976) may be adapted for use with *T. urticae* and *M. occidentalis*. Apparently the introduced functions and relations do describe the system sufficiently accurately so that extrapolation to other prey-predatory mite combinations is possible. Moreover, structural changes between both systems seem of minor importance. Under the conditions of this model, predator movement from one colony to another can be sufficiently described by one density-dependent correction factor, but further confirmation under field conditions is required before the model can be considered completely reliable as a tool for evaluating field experiments.

Based on the model it appears that timing of predator releases will be critical to achieve the most rapid control and rates of release, differences in functional and numerical response and predator dispersal rate seem relatively less important. However, before the model is used to determine predator-prey ratios or timing of

releases, field tests must be carried out to validate the model for this larger arena size.

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ZUSAMMENFASSUNG

EIN POPULATIONSMODELL FÜR DIE GEMEINE SPINNMILBE, TETRANYCHUS URTICAE *UND IHREN RÄUBER* METASEIULUS OCCIDENTALIS

Ein Simulationsmodell, das für die Populationen der Obstbaumspinnmilbe (*Panonychus ulmi* Koch) und ihren Feind (*Amblyseius potentillae* Garman) entwickelt worden war (Rabbinge, 1976), wurde *Metaseiulus occidentalis* Nesbitt und *Tetranychus urticae* Koch angepasst. Das Modell verwendet Life-table Daten für *T. urticae* und *M. occidentalis* sowie die numerischen und funktionalen Reaktionen von *M. occidentalis*. Die im Modell gemachten Annahmen wurden getestet, indem das Modellergebnis mit den Resultaten eines unabhängigen Gewächshausversuchs verglichen wurde. Die Sensitivitätsanalyse zeigte, dass der Zeitpunkt der Freilassung entscheidend ist für eine rasche Begrenzung der Wirtspopulation. Das Räuber-Wirtverhältnis und die Häufigkeit der Freilassung sind weniger wichtig. Unterschiede in der numerischen und funktionalen Reaktion und die Ausbreitungsgeschwindigkeit scheinen ebenfalls weniger wichtig zu sein als der richtige Zeitpunkt der Freilassung.

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