

**THE INFLUENCE OF FLOWER REFUGIA AND POLLEN ON
BIOLOGICAL CONTROL OF WESTERN FLOWER THIRPS,
FRANKLINIELLA OCCIDENTALIS, BY THE PREDATORY MITE
AMBLYSEIUS CUCUMERIS; A SIMULATION STUDY**

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ABSTRACT

An interactive simulation environment for population interactions between a plant pest and its parasitoids and predators, INSIM, was used to explore the dynamic behaviour of the prey-predator system [western flower thrips, *Frankliniella occidentalis* (Pergande) - *Amblyseius cucumeris* (Oudemans)] on sweet peppers, *Capsicum annuum*. Simulated relative growth rates of thrips populations in the absence of predators varied between 0.17 and 0.20 d⁻¹, depending on availability of flowers and pollen, which is agreement with reports in the literature. Two factors were selected for explorative analysis with the model: the presence of flowers as refugia for *Frankliniella*, and the availability of pollen as alternative food for pest and predator. Pest pressure, quantified by the area under the pest progress curve, was reduced with 90% by pollen availability. The presence of flower refugia resulted in only marginally higher pest pressure, irrespective of pollen presence.

INTRODUCTION

Western flower thrips *Frankliniella occidentalis* (Pergande 1895) is a major pest problem in glasshouse crops such as cucumber, chrysanthemum and sweet pepper. Among the natural enemies used by growers for control of thrips, *Amblyseius cucumeris* (Oudemans) is used frequently (Van Houten & Van Stratum, 1993). In general success of control was found to be variable (Ramakers, 1990). Flowers are important in the [*Frankliniella occidentalis* - *Amblyseius cucumeris*] system, because they may harbour a substantial portion of the thrips population, whereas *A. cucumeris* forages very little in flowers. Thrips in flowers feed on petals as well as on pollen. *A. cucumeris* can use the pollen deposited on leaves as food. Both thrips and *A. cucumeris* can survive and reproduce on a diet of pollen only (Trichilio & Leigh, 1988; Ramakers 1990; Van Rijn & Sabelis 1990). Biological control is better on sweet peppers than on cucumbers, probably because the sweet pepper plant produces ample pollen whereas the cucumber plant is parthenocarp thus producing virtually no pollen. The level of biological control obtained with *A. cucumeris* depends on pollen as an extra supply of food (Van Rijn & Sabelis, 1992).

We used a simulation environment for population interactions between a plant pest and its parasitoid and predators, INSIM, (from INsect SIMulation; Mols, 1992) to explore the dynamic behaviour of the prey-predator system. In this paper we describe the conceptualisation and quantification of the prey-predator system and present a simulation analysis of the influence of flowers (as refugia for thrips) and of pollen (as alternative food for thrips and predatory mites) on the dynamics of the system and the level of biological control.

MATERIALS AND METHODS

Biology of thrips and predatory mite

Thrips. The life-stages of thrips are egg, first stage larva (L1), second stage larva (L2), prepupa, pupa, adult male, pre-oviposition female and reproductive female (Bunte et al, 1990; Brødsgaard, 1991). Larval and adult thrips occur on leaves and in flowers. The prepupa and pupa are found in the soil. It is assumed that the proportion of the population occurring on flowers increases proportionally with flower density: from 0 at the start of simulation (planting of sweet pepper, there are no flowers) to 0.4 at 45 days after start of simulation (full flowering) and thereafter. There is a maximum population of 48 thrips per flower (Shipp & Zarifa, 1989). The thrips populations in flowers and on leaves have the same stage composition. Both thrips and mites are found on the upper two thirds of the plant. In the model, redistribution of thrips between flowers (without predation) and leaves (with predation) occurs each time step. The distribution of thrips and mites is independent of pollen density.

Predatory mite. The life-stages of the predatory mite are egg, larva, protonymph, deutonymph, adult male, pre-oviposition female and reproductive female (Gillespie & Ramey, 1988). The nymphal and adult stages are predatory. Consumption of thrips and pollen by mites is described with hyperbolic type II functional response equations (Rabbinge, 1976). This approach considers predation and preference as a competitive process and assumes that the gut content of the predator is in equilibrium with the available density and composition of the food items (Rabbinge, 1989). In the functional response equations the contributions to the diet of the food items thrips L1, thrips L2 and pollen are determined by their respective densities (N) and two parameters characterizing the single food functional responses. These parameters are the initial slope near the origin (E), which is called the rate of successful encounter, and the plateau level (M), which represents the maximum consumption rate. The dot subscript (\cdot) denotes one of the three food items. The density of thrips per unit leaf surface is calculated by dividing thrips density per m^2 ground by two thirds of the leaf area index, to account for the preference for the younger leaf strata.

$$f(N_{L1}, N_{L2}, N_P) = M \cdot \frac{E \cdot N \cdot M}{1 + E_{L1} \cdot N_{L1} / M_{L1} + E_{L2} \cdot N_{L2} / M_{L2} + E_P \cdot N_P / M_P}$$

Here, f is the per capita feeding rate of mites. The dimension of f_{L1} and f_{L2} is thrips $\text{mite}^{-1} \text{d}^{-1}$, and of f_P is pollen $\text{mite}^{-1} \text{d}^{-1}$. Functional response parameters were estimated from data in Van der Hoeven & Van Rijn (1990). They are affected by temperature and differ among predator stages. The most voracious predator stage is the reproductive female which, at 25 °C, is characterized by the parameters: $E_{L1} = 11 \text{ cm}^2 \text{ female mite}^{-1} \text{d}^{-1}$; $M_{L1} = 16 \text{ thrips female mite}^{-1} \text{d}^{-1}$; $E_{L2} = 3.3 \text{ cm}^2 \text{ female mite}^{-1} \text{d}^{-1}$; $M_{L2} = 4.5 \text{ thrips female mite}^{-1} \text{d}^{-1}$. Pollen is difficult to quantify; hence two situations are distinguished: full pollen and no pollen. In the case of full pollen, the product $E_P N_P / M_P$ is 0.587. This estimate was obtained by comparing predation rates on L1s by adult females on leaves with and without full pollen (Van Rijn & Sabelis, 1992). In the case of full pollen, pollen was assumed to be unlimited and the product $E_P N_P / M_P$ was not affected by predation. The density of any food type does not affect the initial rate of successful encounter or maximum intake rate of other food items. There is no interaction between predators.

Adult females are divided into age-cohorts that differ in oviposition rate. The rate of egg laying of predatory mites at 25 °C and ad libitum food provision is 2.84 eggs d^{-1} for the most reproductive age cohort and 1.27 eggs d^{-1} as an average for all 15 age cohorts. Egg production decreases linearly with food intake to 0 when there is no food.

Host plant. Three plant variables are included: leaf area index, density of flowers, and availability of pollen. Leaf area index is a logistic function of time and depends on temperature:

$$L(T,t) = \frac{L_{\max}}{1 + a \cdot e^{-r(T)t}}$$

where

- L = leaf area index; m^2 (leaf) m^{-2} (ground)
 L_{\max} = maximum leaf area index; 6.4 m^2 (leaf) m^{-2} (ground)
 a = parameter expressing the relationship between L_{\max} and $L_{t=0}$ according to $a = (L_{\max}/L_{t=0}) - 1$; 32.5
 r = relative growth rate of leaf area index; d^{-1}
 t = time; d
 T = temperature; $^{\circ}\text{C}$

The relative growth rate of the leaf area index depends on temperature. The relative growth rate at each temperature is calculated using the relationship between the leaf area per plant 77 days after planting and temperature according to Bakker & Van Uffelen (1988) based on a plant density of $3.2 \text{ plants m}^{-2}$ (ground):

$$LP_{77\text{days}} = a \cdot T + b \cdot T^2 + c \cdot Ta + d$$

where

- $LP_{77\text{days}}$ = leaf area per plant, 77 days after planting; m^2 (leaf) plant^{-1}
 a = 0.2886 m^2 (leaf) $\text{plant}^{-1} \text{ } ^{\circ}\text{C}^{-1}$
 b = -0.0067 m^2 (leaf) $\text{plant}^{-1} \text{ } ^{\circ}\text{C}^{-2}$
 c = 0.0103 m^2 (leaf) $\text{plant}^{-1} \text{ } ^{\circ}\text{C}^{-1}$
 d = -2.6388 m^2 (leaf) plant^{-1}
 T = 24-h mean temperature; $^{\circ}\text{C}$
 Ta = difference between maximum and minimum temperature; $^{\circ}\text{C}$

Flower density increases linearly from 0 at day 0 (planting of sweet pepper) to a maximum of 13.7 m^{-2} at day 45 and thereafter. The maximum flower density was calculated by multiplying the daily number of new flowers per m^2 (Bakker, 1989) with an estimated life span of five days.

Pollen densities are not precisely known. Two situations are distinguished: full pollen and no pollen. In the case of full pollen, pollen is assumed to be unlimited. The stimulating effect of pollen on development, survival and reproduction of thrips is maximal for full pollen (Van Rijn & Sabelis, 1992). Full pollen occurs on flowers and on a fraction of the leaves. The fraction of leaves with full pollen depends linearly on the flower density and is 5% at full flowering. The remaining fraction of the leaves contains no pollen. Life history parameters of thrips and predatory mites on leaves are calculated as weighted averages of the parameters on pollen-covered and pollen-free habitats. A fraction of 5% of the leaves was chosen because at this fraction and with pollen as only food item, the relative growth rate of the predatory mites is zero. Ramakers (1990) and Van Rijn & Sabelis (1990) found that the density of predatory mites remains constant in the absence of thrips.

Simulation of the prey-predator system [*Frankliniella occidentalis* - *Amblyseius cucumeris*] on sweet peppers

The dynamic interaction between prey and predator is simulated using INSIM (Mols, 1992). INSIM is a software environment for generic simulation of temporal population dynamics using the state-variable approach (Rabbinge & De Wit, 1989). This approach presumes that the state of a

system can be quantified at any moment, and that changes in states can be described by mathematical equations. This leads to models in which states, rates and driving variables are distinguished (Rabbinge & De Wit, 1989).

States are quantities, such as the density of a species. The state variables of the prey-predator system are the life-stages of thrips and predatory mite and the leaf area index. Rate variables represent flows between states. The rate variables are development rate, mortality rate, predation rate, rate of reproduction and leaf area growth rate. Driving variables, or forcing functions, characterize the environment. The driving variables are temperature, pollen and flower density. Female-male ratio at the beginning of the adult stage is an auxiliary variable and is 0.67 for thrips (Higgins & Meijers, 1992) and 0.63 for the predatory mite (e.g. Castagnoli & Simoni, 1990).

After calculating the values of all rate variables, the new states are calculated by rectangular integration (Leffelaar & Ferrari, 1989). The time interval used for the integration, 0.05 d, was set smaller than one-tenth of the smallest 'time-coefficient' to avoid instabilities. Rates are mutually independent.

The boxcar train method (Goudriaan & Van Roermund, 1989) is used to simulate development through the various life-stages. Two types of boxcar trains are used, the fractional and the escalator boxcar train. The fractional boxcar train is used to account for temperature dependent development rate and variation in that rate between individuals in a particular stage. The escalator boxcar train accounts for temperature effect on development rate but does not account for variation among individuals. The escalator boxcar train is used to simulate age-dependent reproduction in the adult female stage.

Estimation of relationships and parameters

Published and unpublished data were used to quantify linear or curvilinear relationships between and all rate variables and temperature, and to quantify the maximum effect of pollen. Mean and relative dispersion of the development times were quantified. The effect of pollen was assumed to be independent of temperature. Different mathematical equations were used to quantify the relationships and the equation with the best coefficient of variation was chosen.

Simulation studies: validation and sensitivity analysis

There is no published information on the dynamics of the interaction between *F. occidentalis* and *A. cucumeris* on sweet peppers that is suitable for model validation. This is because in the published studies, lack of critical information on temperature and/or initial densities of prey and predator hamper meaningful comparison to simulation results. The only validation that we could use is a comparison of relative rates of population growth of thrips and mites in each others absence to estimates in the literature. These simulations were made for 25 °C.

To investigate the importance of pollen as alternate food and of flowers as refugia in the prey-predator system, we compared the dynamic behaviour of four versions of the model:

- A - pollen - flower refugia
- B - pollen + flower refugia
- C +pollen - flower refugia
- D +pollen + flower refugia

The dynamics of the system was measured with four criteria:

- 1 the time taken to reduce the density of feeding thrips (all stages except egg, prepupa and pupa) below an arbitrary 'extinction' threshold of 0.01 m⁻² (ground)
- 2 the maximum density of feeding thrips
- 3 the time of maximum density of feeding thrips
- 4 pest pressure, defined as the area under the density trajectory of feeding thrips over time

These simulations were made for temperatures measured in a sweet pepper greenhouse at the Glasshouse Crops Research Station in Naaldwijk, The Netherlands, in 1992. Adult female *A. cucumeris* were introduced at a density (m^{-2} ground) equal to that of thrips larvae. Predators were introduced on day 45 as was done by Van Houten & Van Stratum (1993). In Dutch sweet pepper greenhouses, growers introduce predatory mites around 45 days after planting because thrips becomes numerous.

RESULTS AND DISCUSSION

Validation. There is quite good agreement between simulated and published relative rates of population growth (RGR) of *F. occidentalis* and *A. cucumeris*. For thrips, the simulated relative rate of growth was 0.17 d^{-1} for models A and D. For model D, initiated at very low prey density (so that space in flowers does not become limiting), a maximum RGR of 0.20 d^{-1} is achieved. Published RGRs vary from 0.16 d^{-1} (in cotton without flowers and pollen; Trichilio & Leigh, 1988) to 0.22 d^{-1} (in cotton with flowers and pollen). In cucumber (with no pollen) a RGR of 0.17 d^{-1} , exactly equal to the simulation estimate, was found by Van Rijn et al. (in press). Confirmative results were also obtained for the predator *A. cucumeris*. On diets of pollen and *F. occidentalis*, respectively, we found RGRs of 0.20 d^{-1} and 0.18 d^{-1} . Published estimates are 0.20 d^{-1} (Van Rijn & Van Houten, 1991) and 0.14 d^{-1} (Van Rijn & Van Houten, 1991). Simulated and observed RGR of *A. cucumeris* on pollen are equal. The difference between the simulated and observed RGRs attained on thrips, 0.14 and 0.18, is acceptable because of the approximate nature of the observed RGR. Overall, we conclude that life cycle parameters used in the model produce relative population growth rates in a single species situation that are similar to relative growth rates observed in reality.

Coarse sensitivity analysis. Thrips become extinct ($< 0.01 \text{ m}^{-2}$ (ground)) in all versions of the model, but the underlying dynamics are fundamentally different in the model versions with and without pollen. In the model versions without pollen, the system shows a prey-predator cycle (Figs 1A&B). Thrips density first increases, the predatory mites catch up and cause then a rapid decline in prey density. Subsequently the predators themselves go into decline because of lack of food. With pollen, the predators do not go into decline, but they maintain a certain density on the alternative food provided by pollen on leaves (Figs 1C&D). In the situation without pollen, the presence or absence of a flower refugium for thrips makes only a marginal difference for their dynamics (Figs 1A&B). With the refugium, the initial growth rate of thrips is a little higher, but due to more food, the growth rate of mites is also higher. The overall result is a higher and earlier density peak of thrips. Thrips subsequently become extinct earlier than in the situation without refugium. The pest pressure in the situation with refugium is 27% higher than in the situation without refugium, $2.9 \cdot 10^6$ thrips days m^{-2} versus $2.3 \cdot 10^6$ thrips days m^{-2} respectively. A similar effect of the refugium is seen in the model versions C and D with pollen. Here, the availability of pollen brings mite density on a stable level in 60 days (Fig. 1D), resulting in a steady - and slow - reduction of thrips density. Compared to model D, mite density in the model without flower refugium (C), is somewhat lower during the first 60 days. This results in a slight population peak of mites after 90 days, which then causes a decline of thrips density that is considerably faster in model C than in model D. Model versions C and D (with pollen) have 90 to 89% lower pest pressures than model versions A and B, without pollen. These simulations lead to the conclusion that in this system, pollen as an alternative food for predators, is an important factor contributing to predator maintenance and successful biological control, even though pollen is also an alternative food for the pest. The presence of pollen does not appear to decrease biological control by competing with thrips for being fed upon by the mites. It is interesting to note that there is an inverse relationship between the time until pest extinction (the 'speed' of biological control) and pest pressure (the 'level' of biological control).

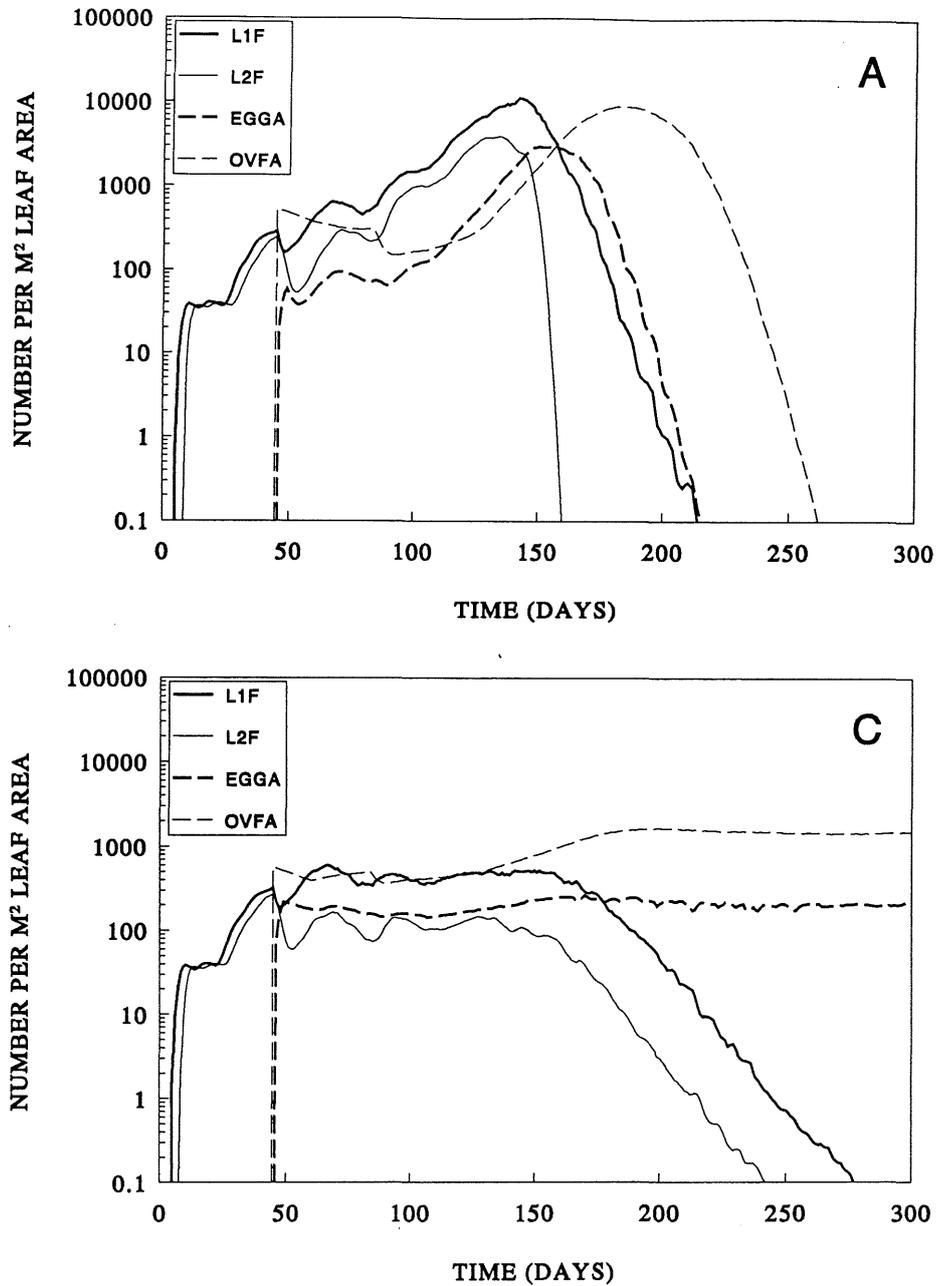
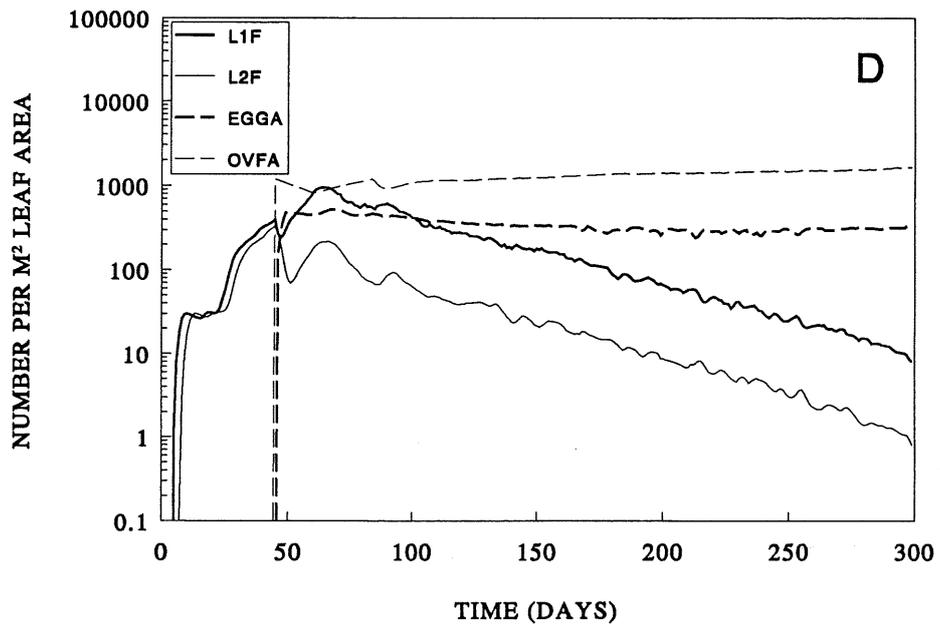
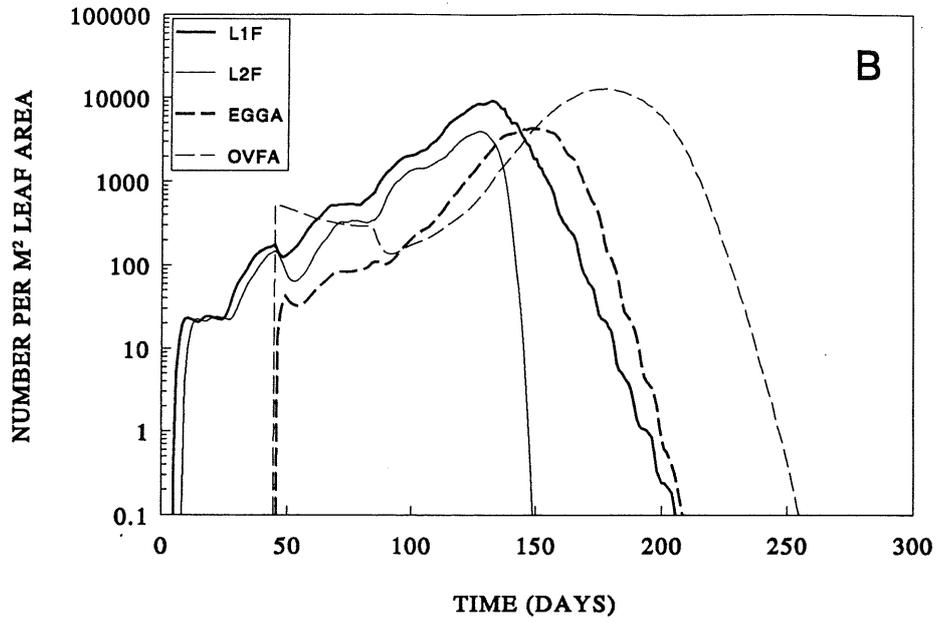


Fig.1 Coarse sensitivity of the simulation model for the effects of the presence of pollen and flowers on pest and predator dynamics. Figs A-D give simulated dynamics of first (L1F) and second stage (L2F) larvae of thrips, *F. occidentalis*, and of eggs (EGGA) and reproductive females (OVFA) of the predatory mite *A. cucumeris* on leaves of sweet pepper in four versions of the simulation model.



Model versions are: **A** - pollen & - flower refugia; **B** - pollen & + flower refugia; **C** + pollen & flower refugia; and **D** + pollen & + flower refugia. Day 0 is the planting date of sweet pepper. Mites are introduced on day 45 at a density equal to that of thrips.

Fine sensitivity analysis. In the fine sensitivity analysis we investigated the relationship between pest pressure and the value of three parameters: the fraction of leaves with full pollen (standard value: 5%), the maximum number of thrips per flower (standard value: 48) and the fraction of thrips occurring in flowers, space permitting (standard value: 40%). Parameters were increased and decreased with 10% with respect to their standard value. The elasticity is defined as the relative change in pest pressure, divided by the relative change in the parameter value. We present only the average of the two elasticities.

Increasing the fraction of leaves with full pollen causes a major reduction in pest pressure, as indicated by elasticities of -2.46 in model C (- flower refugia) and -3.40 in model D (+flower refugia). The large influence is no surprise because the fraction of leaves with full pollen determines whether mites can maintain their density in the absence of thrips. On leaves without pollen, mites starve and become extinct. On leaves with full pollen, they increase exponentially without limitation (pollen is unlimited). At the plant level, consisting of a mixture of pollen-covered and pollen-free leaves (with instantaneous redistribution of mites between these categories), the situation is intermediate. At the standard proportion of 5% leaves with full pollen, the relative growth rate of mite populations without thrips as prey is close to zero. At higher or lower proportions of leaves with full pollen, there is respectively exponential growth or decline of mites in the absence of thrips. In actuality, the availability of pollen to predators on leaves is quite uncertain and should be further investigated experimentally.

The influence of the maximum number of thrips per flower on pest pressure depends on the absence or presence of pollen, with elasticities of 0.43 in model B (-pollen) and -0.33 in model D (+pollen). The (unexpected) negative effect of increasing the maximum number of thrips per flower in model D is caused by higher predator densities resulting from higher rates of pest flux from flowers onto leaves. Pest flux onto leaves was increased because of higher pest densities in flowers in combination with higher absolute growth rates in flowers.

In model D (+pollen), pest pressure is positively dependent on the fraction of thrips foraging in flowers, with an elasticity of 1.10. In model B (-pollen), however, the elasticities obtained by decreasing and increasing the parameter value, respectively, were of opposite sign. By decreasing the fraction of thrips in flowers, the rate of reproduction of the predator just after introduction increases, leading to lower peak prey densities. Increasing the fraction of thrips in flowers leads to a shorter predator-prey cycle with almost the same peak density.

CONCLUDING REMARKS

Both field work and the simulations described here demonstrate the large effect of pollen on biological control. More empirical information is now needed to test the model in detail. Despite its largely hypothetical status, the model has distinctive merit. At the current state of quantitative information at the process and systems levels, the model serves as an integrative vehicle to make explicit hypotheses on the major processes and their role at the system level. By emphasizing what is not known, empirical research is guided to questions most urgently requiring elucidation. At later stages, when gaps in knowledge are filled, the model may serve a role in deriving guidelines for judicious application techniques of predators. Simulations may answer questions as to how many predators should be released and when, and whether biological control may be improved by using more than one species of natural enemy or supplementing pollen or other alternative food sources for predators. A validated simulation model, can also be used to investigate further the effects of environmental factors, such as temperature, humidity and daylength, thus bridging the gap between crop production and crop protection oriented activities. Finally, because of its process-oriented nature, the simulation model is a useful tool in teaching. Students can use the model to develop their insight into the population dynamical processes underlying biological pest control. Such application of the model using INSIM as a user-friendly interface, is currently tested out by the Dutch Agricultural Colleges.

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