HOW PLANTS BENEFIT FROM PROVIDING FOOD TO PREDATORS EVEN WHEN IT IS ALSO EDIBLE TO HERBIVORES

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Abstract. It is well established that plants provide alternative foods to predators of herbivorous arthropods. This provision may facilitate protection against herbivory. However, plants often cannot prevent other organisms from utilizing these foods as well. There are many examples of herbivorous arthropods that can feed on plant-provided foods such as extrafloral nectar and pollen. The question therefore arises whether individual plants still gain protection when not only the predators, but also the herbivores, can feed on these foods. We investigated this question using a mathematical model and experiments that assessed the impact of supplementary pollen on the dynamics of predatory mites (*Iphiseius degenerans* (Berlese)) and herbivorous thrips (*Frankliniella occidentalis* (Pergande)), two arthropods capable of using pollen for reproduction. Replicated greenhouse experiments showed that addition of pollen every two weeks to one young mature leaf of a male-sterile cucumber plant increased predator population growth and greatly reduced herbivore numbers.

A stage-structured predator–prey–pollen model with experimentally established parameters gave reasonably accurate predictions of population trends observed in the greenhouse experiments with and without pollen. Model analysis yielded three important results. First, herbivore (prey) equilibria always settled to lower values in the presence of pollen. Second, mean herbivore numbers during the transient phase following predator release were not always lower under pollen supply, depending on the initial numbers of predators and prey. Third, limiting the plant area covered with pollen led to a decrease in mean herbivore numbers, provided that the predators aggregated in (and thereby "monopolized") pollen patches. The latter result may explain why plants provide alternative foods at specific sites.

Key words: apparent competition; Frankliniella occidentalis; *indirect plant defense; intraguild predation;* Iphiseius degenerans; *omnivory; plant–predator mutualism; pollen; predator–prey interaction; spatial distribution; supplementary food; tri-trophic interactions.*

Introduction

Plants can influence the performance of natural enemies of their arthropod herbivores in a variety of ways. They may provide them with shelter, alternative foods, or information-conveying chemicals. The herbivores' enemies may make good use of these plant-provided facilities and, as a result, the plants may benefit by being better protected against herbivore attack. Such mutualistic interactions are never cheater proof (Bronstein 1994). Once plants invest in plant–predator mutualisms, they cannot prevent other organisms from reaping the benefits, and these organisms may well include the enemies of the plant. Indeed, there are several examples of herbivorous arthropods exploiting plant-provided shelter, chemical alarms, and foods (Sabelis et al. 1999).

We investigate whether a plant benefits from producing alternative food when this is eaten not only by predators, but also by herbivores. Plant pollen is the

source of alternative food under consideration. Clearly, pollen has evolved primarily for its role in sexual reproduction in plants, but partly as a result of mate competition, it is generally produced in large quantities and only a small fraction ends up on the stamen of another flower, thereby allowing the remaining pollen to perform other functions. One such function is to serve as a food source for mutualists, and plants may well be able to manipulate the nutritive quality and edibility to pollinators as well as to predators that may serve the plant as bodyguards. Pollen can be utilized by several groups of predatory arthropods (Sabelis and Van Rijn 1997), such as heteropteran bugs (Alomar and Wiedenmann 1996), ladybird beetles (Cottrell and Yeargan 1998, Triltsch 1997), hoverflies (Haslett 1989, Wratten et al. 1995), green lacewings (Sheldon and MacLeod 1971), and predatory mites (Van Rijn and Tanigoshi 1999*b*). However, there are also groups of herbivorous arthropods that use pollen to promote their survival and reproduction, such as chrysomelid and curculionid beetles (Jayanth et al. 1993, Jones et al. 1993), lycaenid and *Heliconius* butterflies (Gilbert 1972, Wagner and del Rio 1997), and many thrips species (Kirk 1997). We studied the impact of pollen on
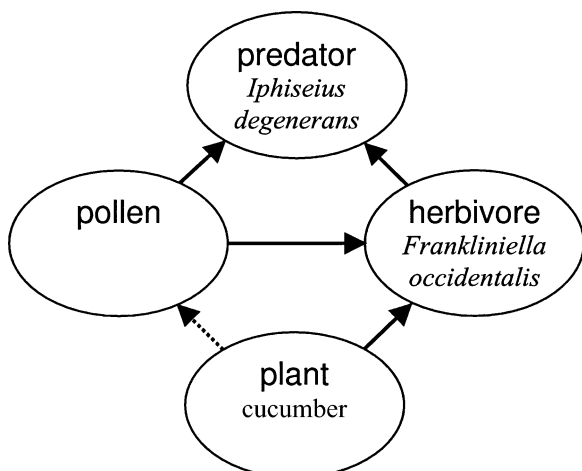
FIG. 1. Food web diagram of the experimental system. Arrows indicate flow of material.

the dynamics of the western flower thrips *Frankliniella occidentalis* Pergande (Insecta, Thysanoptera, Thripidae) and the predatory mite *Iphiseius degenerans* (Berlese) (Acari, Mesostigmata, Phytoseiidae) on cucumber plants. The thrips have been shown to increase their reproduction when fed on pollen and leaves together (Hulshof and Vänninen 1999), whereas the predatory mites are known to increase in numbers even on a diet of pollen alone (Van Rijn and Tanigoshi 1999*b*). This predator–herbivore–plant system (Fig. 1) is therefore ideally suited to answer the question whether the production of edible pollen reduces herbivore damage to the plant by promoting the effectiveness of predators, in spite of the fact that herbivores utilize pollen as well.

There is a large body of theory showing, with some rather special exceptions (Abrams and Matsuda 1993, 1996), that the addition of alternative foods or prey to the predators in a predator–prey system reduces the equilibrium level of the primary prey population (''apparent competition;'' Holt 1977, 1983, Abrams 1987, 1998). Provided that the alternative food suffices to achieve positive growth of the predator population, the prey population may even go extinct (Holt and Lawton 1993, 1994, Holt et al. 1994, Bonsall and Hassell 1997). These conclusions do not simply translate to non-equilibrium dynamics. For example, Abrams et al. (1998) showed that, under a regime of predator–prey cycles, the addition of another prey does not necessarily reduce the mean densities of the primary prey. At the population level, it may even seem as if the two prey species profit from each other's presence. Clearly, in non-equilibrium situations, one should be cautious in inferring that the addition of one prey has negative effects on the other via their shared predators. Because real populations never settle exactly at an equilibrium, it is essential to investigate under which dynamical regimes these indirect effects occur. Moreover, no such analysis has yet been made of the case in which the additional

prey (or food) is eaten not only by the predator, but also by the primary prey.

In this article, we assess the theoretical conditions under which plants will accommodate fewer herbivores when providing alternative food, in spite of the fact that not only the predators, but also the herbivores, can utilize it. We test the underlying model against observations of the effect of alternative food on the dynamics of predatory mites and herbivorous thrips in a greenhouse. Finally, we briefly discuss how our findings provide insight in the role of food provisioning in the evolution of plant–predator mutualism.

MATERIALS AND METHODS

Population experiments

The predatory mite *Iphiseius degenerans*, originally collected in Morocco in 1984, was initially reared on iceplant (*Malephora crocea* (Jacq.)) pollen by Dr. J. M. McMurtry (University of California–Riverside, California, USA) and, since 1991, on birch (*Betula pubescens* Ehrh.) pollen in our lab in rectangular PVC arenas (25°C, 62% relative humidity; Van Rijn and Tanigoshi 1999*b*). The herbivore *Frankliniella occidentalis* was obtained from a culture on cucumber (*Cucumis sativa* L.), started with a sample from a greenhouse in Naaldwijk, The Netherlands. As the alternative food source, we chose pollen from common cattail *Typha latifolia* L., because it (1) is known to be a good food source for rearing the predatory mites (Van Rijn and Tanigoshi 1999*b*), (2) is easy to collect in large quantities, and (3) retains good quality under the usually humid greenhouse conditions for several weeks (Y. M. Van Houten, *unpublished data*). The pollen was collected from plants on the University of Amsterdam campus and was then dried, sieved, and stored as described by Van Rijn and Tanigoshi (1999*b*).

The population experiments were carried out in 1997 at the Research Station for Floriculture and Glasshouse Vegetables (PBG, Naaldwijk, The Netherlands) in four greenhouse compartments (76 m^2 each) with cucumber plants. The compartments were separated by crop-free corridors (3.2 m wide) to prevent cross-contamination, and were provided with gauzed windows to reduce immigration of insects. The cucumber crop was maintained according to current growers' practice (PBG); temperature was computer controlled (minimum 19°C, maximum 26°C, mean 22°C). Humidity was not controlled and varied mostly between 70% and 90% relative humidity, with lower values only at the start and the end of the experiment. The main stem was trimmed beyond leaf number 19, and all side shoots were removed, except for two at the top of the main stem and the first one (or two) appearing on every side shoot. All four (to six) side shoots were allowed to grow down.

In the second week of 1997, each of the four compartments was provided with 108 cucumber plants

(*Cucumis sativa* L., cultivar Enigma). The plants, rooted in blocks of rock wool, were arranged in 12 rows. In the second and the fourth week, 60 adult females of the plant-feeding thrips *Frankliniella occidentalis* were released in each compartment. In the fourth week, four female predators (10–13 d since hatching) were introduced on every plant, which by then had 9–10 fully grown leaves. This introduction was repeated twice in the control compartments (four females per plant in weeks 7 and 10) after the predator populations were found to be nearly extinct. In the two other compartments, cattail pollen (10–15 mg/plant) was introduced every other week. Preliminary experiments showed that when cattail pollen was kept for 14 d on cucumber leaf in a greenhouse and was offered as a food source to the predators, it still allowed 75% of the juvenile mites to mature, whereas adult female mites oviposited at half the rate as on with fresh pollen (Y. M. Van Houten, *unpublished data*). The pollen was always introduced on one leaf of every plant according to the following schedule (always directly after population monitoring): (1) initially (week 4) on the eighth leaf from below, (2) leaf 16 in week 6, (3) first leaf on first side shoot in week 8, and (4) second leaf on the other first side shoot in week 10. By the end of the monitoring period (week 15), the plants had 38 leaves, on average, excluding the roughly seven leaves on the main stem that were removed when they died off.

The adult female thrips were monitored with two blue sticky traps (Koppert BV, Berkel-en-Rodenrijs, The Netherlands) per compartment. They were initially replaced once a week, but when the numbers trapped exceeded 1000/wk, the trapping period was reduced to 24 h/wk. Juvenile thrips and predator populations were estimated based on in situ observations of 8–16 representative leaves from 10 plants per compartment (one randomly selected plant per row). Initially, all leaves on a plant were checked for mites and thrips, but later, because of the increase in plant size, only one of every two or three leaves could be monitored. The leaves that had been provided with pollen were always monitored. The total population size per plant was estimated, assuming that non-sampled leaves had the same number of mites and thrips as the nearest sampled leaf (excluding the leaves with pollen). For the first six weeks, the treatment compartments were sampled weekly, whereas the control compartments were sampled every other week. Later, because of labor constraints, both treatment and control compartments were sampled at biweekly intervals in an alternating scheme.

Because treatments were administered to compartments, each with many plants, there were two replications per treatment. To test whether treatment and control differed, a repeated-measures ANOVA was carried out. For this purpose, we used leaf counts from the weeks in which both treatment and control had been monitored (weeks 5, 7, and 9) as well as from weeks 11 and 13, when we estimated the missing data from

the control by interpolation. To improve normality, all data were log-transformed. To correct for deviations from the sphericity assumption, we adjusted the degrees of freedom for the within-subject factors (time and interaction) according the conservative Greenhouse-Geisser method (Looney and Stanley 1989).

Predator–prey model

To pinpoint the conditions under which plants profit from pollen production, we constructed a predator–prey–pollen model framed in (delay-) differential equations.

The pollen (A) is assumed to be produced at a constant rate (a), removed at a rate proportional to its density by natural decay (b), and removed through consumption by thrips and predators (C):

$$\frac{dA}{dt} = a - bA(t) - C(t). \tag{1}$$

The thrips population (N) is structured into three classes: (1) vulnerable juvenile phase (small larvae); (2) invulnerable juvenile phase (large larvae, pupae in the soil, pre-ovipositing females and eggs, as the latter are inserted in the leaves); and (3) invulnerable reproduction phase (ovipositing females). By taking the egg stage together with later developmental stages, we assume that the reproductive females directly produce larvae rather than eggs, but only after a delay equal to the egg-hatching period. Thrips densities (N_i, with i indicating the class number) are expressed in number of thrips per square decimeter, corresponding to the scale of laboratory experiments. Because the densities considered are well below the plants' carrying capacity, we assume unlimited growth of the thrips population. Abiotic mortality in the juvenile phase is taken into account as an implicit reduction factor with respect to reproduction, whereas abiotic mortality in the mature phase is represented as a constant per capita rate (v) for the adults. Together with a constant (age-independent) reproduction rate, this assumption results in a net reproduction rate of the thrips (i.e., the product of reproduction and survival rates) that declines exponentially with age, which is in close agreement with experimental data (Van Rijn et al. 1995). If we assume a constant per capita developmental rate of transfer from the vulnerable to the invulnerable phase (d), the vulnerability of the thrips also declines exponentially with age, again in agreement with experimental data (Van Rijn et al. 2002*b*). The remaining, invulnerable part of the juvenile period (class 2) is assumed to be of fixed duration (τ_N). The reproduction rate of the thrips (R, corrected for sex ratio and juvenile survival) can double in the presence of sufficient pollen (Hulshof and Vänninen 1999, Van Rijn et al. 2002*b*). By assuming satiation at higher pollen densities (Type II numerical response), this effect is described by the following Michaelis-Menten (or Monod) equation:

$$R(A) = r\frac{L + A}{L + A + A_R} \qquad (2)$$

where r represents the maximum reproduction rate (at a surplus of pollen), L is the value of leaf tissue as a food source for the thrips expressed in the same units as the pollen (A) (determining the rate of reproduction in the absence of pollen), and A_R represents the food density ($L + A$) at which R is half its maximum. Even at the lowest food densities (i.e., absence of pollen), reproduction is already at about half of its maximum; thus, maintenance costs do not have to be modeled explicitly.

The rate at which vulnerable thrips suffer from predation is affected by their density (N_1) according to a saturating (Type II) functional response model (Van Rijn et al. 2002c), fitted by a Michaelis-Menten equation. Predators do not have a clear preference for either pollen or prey, but they show a lower predation rate in the presence of pollen, even at the highest prey densities (Van Rijn et al. 2002c). This is modeled by adding an interaction term to the denominator:

$$F_N(N_1, A) = f_N\frac{N_1}{N_1 + N_F + \phi A + kAN_1} \qquad (3)$$

where f_N represents the maximum predation rate, N_F is the half-saturation density of vulnerable prey, and ϕ is the food value of pollen relative to prey. The parameter k ("strength of food type interaction") determines the reduction of predation due to pollen at higher prey densities, because

$$\lim_{N_1 \to \infty} F_N(N_1, A) = \frac{f_N}{1 + kA}.$$

The assumptions just described result in the following set of differential equations for the structured prey population:

$$\frac{dN_1}{dt} = R(A(t))N_3(t) - F_N(N_1(t), A(t))P_C(t) - d_1N_1(t)$$

$$\frac{dN_2}{dt} = d_1N_1(t) - d_1N_1(t - \tau_N)$$

$$\frac{dN_3}{dt} = d_1N_1(t - \tau_N) - \nu N_3(t). \qquad (4)$$

As in the thrips model, the predator population (P) is structured into three classes: (1) nonfeeding juvenile phase (eggs and larvae), (2) feeding juvenile phase (nymphs and pre-ovipositing females), and (3) feeding and reproductive phase (ovipositing females). Mortality and development are treated similarly as in the thrips model, with a constant rate of transition, e, from class 1 to class 2, a fixed developmental delay, τ_P, for juveniles in class 2, and an adult mortality rate (representing the rate of decline in net reproduction), μ (Van Rijn and Tanigoshi 1999b). The predator rate of reproduction (G, corrected for sex ratio and juvenile

survival) is directly affected by prey and pollen density according a Michaelis-Menten function with substitutional food sources (Van Rijn et al. 2002c):

$$G(N_1, A) = \begin{cases} g\left(\dfrac{N_1 + \phi A}{N_1 + \phi A + N_G} - m\right) & \text{if positive} \\ 0 & \text{otherwise} \end{cases} \qquad (5)$$

where ϕ again represents the food value of pollen relative to prey, N_G is the half-saturation density of vulnerable prey, m represents the maintenance costs (relative to the total of maintenance and reproduction), and g is the maximum rate of reproduction (in the absence of maintenance costs).

Adult predator mortality increases at very low food densities (Van Rijn and Tanigoshi 1999a), and is modeled by the inverse of a Michaelis-Menten function:

$$\mu(N_1, A) = \mu_\infty\frac{N_1 + \phi A + N_\mu}{N_1 + \phi A},$$
$$\text{with } \mu(N_1, A) \le \mu_0 \qquad (6)$$

where μ_0 and μ_∞ are the mortality rate at very low and very high prey densities, respectively, and N_μ ($\ll N_G$) is the prey density at which the inverse function (i.e., mean adult life-span) is half its maximum.

These assumptions result in the following set of differential equations for the structured predator population:

$$\frac{dP_1}{dt} = G(N_1(t), A(t))P_3(t) - eP_1(t)$$

$$\frac{dP_2}{dt} = eP_1(t) - eP_1(t - \tau_P)$$

$$\frac{dP_3}{dt} = eP_1(t - \tau_P) - \mu(N_1(t), A(t))P_3(t). \qquad (7)$$

In the equations for pollen (A) and thrips (N), the juvenile predators are assumed to consume only a fraction (j) of what the adults consume (Cloutier and Johnson 1992), so that the effective number of predators consuming either pollen or thrips is defined as

$$P_C = jP_2 + P_3. \qquad (8)$$

Similarly, the effective number of thrips consuming pollen is defined as

$$N_C = l_1N_1 + l_2N_2 + N_3 \qquad (9)$$

where l_i is the consumption rate of the juvenile phase i relative to that of the adults.

The pollen consumption function is assumed to be symmetrical with the predation function F_N:

$$F_A(N_1, A) = f_A\frac{\phi A}{N_1 + N_F + \phi A + kAN_1} \qquad (10)$$

where f_A represents the maximum rate of pollen consumption.

The few experiments that have been carried out on pollen feeding (Kirk 1987, Flechtmann and McMurtry 1992) allow us to assume that the adults of both predator and prey feed at similar rates, so that the total rate of pollen consumption (C) is given by

$$C = F_A(0, A)N_C + F_A(N_1, A)P_C. \tag{11}$$

All calculations were done for the system-specific parameter values listed in Table 1.

So far, we have assumed well-mixed populations of pollen, prey, and predators. In our greenhouse experiments, however, pollen was only available on a restricted part of the plant. To model local pollen availability, the interaction space was divided into an area with pollen and one without. The proportion of the leaf surface area with pollen was assumed to be constant (α) throughout the interaction period. The proportions of the thrips and predator population within the area with pollen (respectively, β and γ) were assumed to be flexibly determined by the individual's adaptive choice between foraging in the area with pollen or in the area without. To make that choice, the predators must respond to food (pollen plus prey) density only, whereas the thrips have to balance food (leaf and pollen) density against predation risk. We assume that predators and prey cannot hop to whichever of the two areas is best at a given moment. Because thrips and their predators move on a two-dimensional plant surface, they can only assess the quality of the environment at close range. Therefore, they are thought to move randomly and, when their direct environment is profitable, to prolong the time spent there.

Assuming for the predators that the per capita rate of migration from an area is inversely related to the food density within the area (θ_1 and θ_0 for areas with and without pollen, respectively), the proportion of predators in the area with pollen (γ) is described by the following ODE:

$$\frac{d\gamma}{dt} = -\frac{1}{\theta_1}\gamma + \frac{1}{\theta_0}(1 - \gamma). \tag{12a}$$

Assuming, in addition, that redistribution is achieved at a much shorter time scale than changes in population size, the actual distribution will be close to its equilibrium:

$$\gamma^* = \frac{\theta_1}{\theta_0 + \theta_1} = \frac{\beta N_1 + \phi A}{N_1 + \phi A}. \tag{12b}$$

Assuming for the herbivores that the rate of migration from an area is inversely related to food density (ρ_i) as well as survival probability (σ_i), and making the same time-scale assumption, the equilibrium proportion of herbivores in the area with pollen is described by

$$\beta^* = \frac{\rho_1\sigma_1}{\rho_0\sigma_0 + \rho_1\sigma_1} = \left(\frac{\rho_0}{\rho_1}\frac{\sigma_0}{\sigma_1} + 1\right)^{-1} \tag{13a}$$

where the food densities in the areas with and without pollen, respectively, are given by the following:

$$\rho_1 = \alpha L + \phi A$$

$$\rho_0 = (1 - \alpha)L. \tag{13b}$$

The probability of surviving the vulnerable prey stage (with duration $1/d$) in area i when local predation risks are close to q_i can be approximated by

$$\sigma_i = \exp\left(-\frac{1}{d}q_i\right). \tag{13c}$$

The maximum predation risks (not diluted by high prey numbers) in the areas with and without pollen, respectively, are

$$q_1 = \frac{\gamma}{\alpha}P_C\frac{f_N}{Nf + \phi A}$$

$$q_0 = \frac{1 - \gamma}{1 - \alpha}P_C\frac{f_N}{Nf}. \tag{13d}$$

The division in two subspaces necessitates modifications (indicated by arrows) of the following elements of the population dynamical model (defined by Eqs. 1, 4, and 7):

(1) C (consumption of pollen),

$$F_A(0, A)N_C + F_A(N_1, A)P_C$$

$$\rightarrow F_A\left(0, \frac{A}{\alpha}\right)\beta N_C + F_A\left(\frac{\beta}{\alpha}N_1, \frac{A}{\alpha}\right)\gamma P_C$$

(2) R (thrips reproduction),

$$R(A) \rightarrow \beta R(A) + (1 - \beta)R(0), \text{ and}$$

(3) F, G, and μ (predation, predator reproduction, and mortality), here indicated by U,

$$U(N_1, A) \rightarrow \gamma U\left(\frac{\beta}{\alpha}N_1, \frac{A}{\alpha}\right) + (1 - \gamma)U\left(\frac{1 - \beta}{1 - \alpha}N_1, 0\right).$$

The model equilibria have been studied with CONTENT, a software package for numerical bifurcation analysis (Kuznetsov et al. 1996). The transient dynamics have been studied by (fixed time step) simulations ran in Mathcad 2000 (Mathsoft Engineering and Education, Cambridge, Massachusetts, USA), initializing the herbivore population by assuming preceding exponential growth ($r_m = 0.13/d$) at a stable age distribution, and initializing the predator population by assuming instant introduction of adults only.

RESULTS

Population experiments

In pollen-treated compartments, the predators increased in numbers immediately after their release, whereas in the control compartments, their numbers declined to virtually zero within a few weeks. The second predator introduction in the control compartments (in week 7; Fig. 2a) was more successful because the prey density had increased sufficiently by then to allow the predator population to increase. This increase was

TABLE 1. Default parameter values used in pollen–herbivore–predator model.

Parameter	Description	Value and units	Notes[†]
Pollen dynamics			
α	Proportion of leaves with pollen	0.1 (ratio)	2
a	Pollen supply rate	0.1×10^4 pollen grains·dm^{-2}·d^{-1} or 5×10^4 pollen grains·plant^{-1}·d^{-1}	3
b	Instantaneous loss rate	0.2 grains/d	4
f_A	Maximum rate of pollen consumption by thrips and predators	0.07×10^4 pollen grains·adult^{-1}·d^{-1}	5
Prey (*F. occidentalis*) biology			
d_1	Developmental rate vulnerable prey phase (young larvae)	1/3 (per day)	6
τ_N	Developmental time invulnerable prey phase (eggs, older larvae, pupae, pre-ovipositing females)	15 d	7
r	Maximum rate of net reproduction, at surplus of pollen	4.0 offspring·adult^{-1}·d^{-1}	7
A_R	Food (leaf plus pollen) density at which its effect on prey reproduction (R) is half its maximum.	0.3×10^4 pollen grains/dm^2	8
L	Food value of leaf tissue in terms of pollen density	0.3×10^4 pollen grains/dm^2	9
ν	Instantaneous decline in adult net reproduction rate	0.11 (per day)	7
Functional responses			
f_N	Maximum rate of thrips predation	4.0 prey·adult^{-1}·d^{-1}	10
N_F	Prey density at which predation is half its maximum	1.5 prey/dm^2	11
k	Weight of interaction between prey and pollen density, responsible for the reduction of consumption of either pollen or prey	0.11 dm^2/10^4 pollen grains	12
ϕ	Value of pollen relative to prey in terms of predation, predator reproduction, and survival	0.34 prey/10^4 pollen grains	11
j	Consumption rate of juvenile predators relative to adult predators	0.25 (ratio)	13
$i_{1,2}$	(Pollen) consumption rate of juvenile thrips stages (1 and 2) relative to adults	0.2 (ratio) 0.6	14
Predator (*I. degenerans*) biology and numerical response			
e	Developmental rate, nonpredatory phase (eggs and larvae)	1/3.7 (per day)	15
τ_P	Developmental time predatory phase (nymphs)	6.3 d	15
g	Maximum rate of net reproduction (in absence of maintenance costs)	1.5 offspring·adult^{-1}·d^{-1}	16
m	Maintenance costs (relative to the total of maintenance and reproduction)	0.2 (ratio)	17
N_G	Prey density at which net reproduction is half of its maximum (in absence of maintenance costs)	1.0 prey/dm^2	18
μ_∞	Minimum adult mortality rate	0.05 (per day)	16
μ_0	Maximum adult mortality rate	0.2 (per day)	19
N_μ	Prey density at which adult mortality is half its maximum	0.08 prey/dm^2	20

† (1) Data for *N. cucumeris* were used when not available for *I. degenerans*. Rates measured at 25°C were multiplied by 0.8 to be valid for 22°C (using 11°C as threshold; Van Rijn et al. 1995). (2) See Fig. 3b. (3) 10–15 mg cattail pollen/14 d; 5×10^4 pollen/mg. (4) After 14 d, pollen quality in terms of predator reproduction ($G(0,A)$) is decreased by 50% (Y. M. Van Houten, *unpublished data*), which corresponds with a 95% decrease in pollen density in 14 d. (5) For grain size 7000 µm^3 (Kirk 1987: Fig. 4): 500/d at 20°C (compare Flechtmann and McMurtry 1992). (6) Van Rijn et al. (2002*b*). (7) Van Rijn et al. (1995); see also (9). (8) Smaller than for adult predators: 0.3/ϕ; see (18). (9) $L = A_R$ because pollen doubles reproduction rate (Hulshof and Vänninen 1999). (10) Van Houten et al. (1995). (11) Van Rijn et al. (2002*c*). (12) Maximum predation = $f_N/(1 + kA) = 0.36 f_N$ for $A = 15 \times 10^4$ pollen/dm^2 (Van Rijn et al. 2002*c*). (13) Cloutier and Johnson (1992). (14) Proportional to body mass (Van Rijn et al. 2002*b*) and feeding period (Van Rijn et al. 1995). (15) Van Rijn and Tanigoshi (1999*b*). (16) Exponential regression of net reproduction data (Van Rijn and Tanigoshi 1999*b*). (17) Van Rijn et al. (2002*a*). (18) For oviposition, 0.3 (see 11); for juvenile survival, +0.7 (see 20). (19) Van Rijn and Tanigoshi (1999*a*). (20) Estimated from the initial predator decline in the absence of pollen.

exponential, with a growth rate equal to 0.14/d; hence, the predator numbers in the control compartment soon approached the level in the pollen-treated compartments where the predator population stabilized, probably due to competition for food (thrips and pollen). Thus, although the number of predators did not differ between treatments at the last sampling date, the pollen introductions resulted in significantly higher numbers of predators during the first eight weeks (Table 2), which was due to a fast initial increase of predators when thrips density was still low. The initial difference in population growth partly resulted from a higher pred-
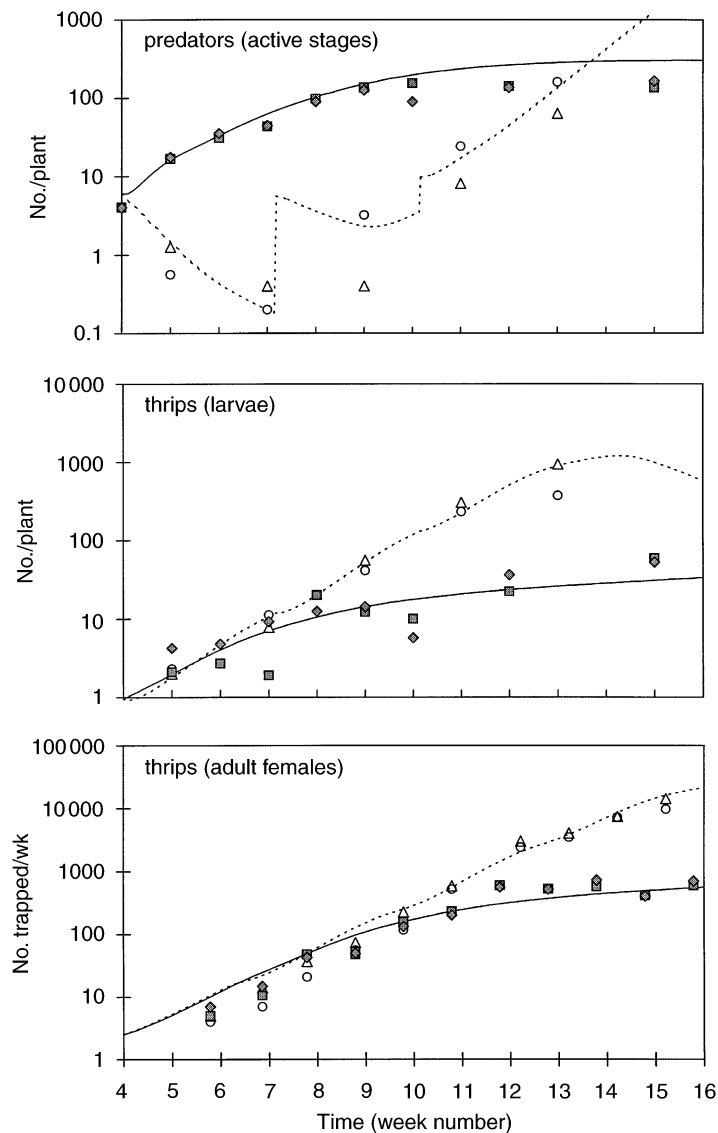
FIG. 2. Population dynamics of predatory mites (all mobile stages) and western flower thrips (larvae and adult females) in the presence and absence of cattail pollen on cucumber plants. Experimental results are indicated by symbols (closed symbols for treatment and open symbols for control). Simulation results are indicated by lines (solid for treatment and dotted for control). As in the experiments, simulations concern numbers per plant. Whenever rates are density dependent, densities result from dividing numbers by plant surface, which itself is an increasing function of time, approximated by the fitted logistic function: $S(t) = 108 [1 + \exp(-0.06 (t - 10))]^{-1}$ (dm^2, t in days since predator release). Adult thrips densities were converted into numbers trapped per week (bottom panel) by multiplying by 18 dm^2/wk, based on the fit at higher densities. The proportion of the area with pollen, α, is fixed at 0.1. Initial numbers were two thrips per plant (all stages according to stable stage distribution) and six adult predators per plant (representing males and females, equivalent to the four females that were released in week 4). Predator introductions were repeated in the control experiments in weeks 7 and 10. Note the y-axis log scale.

ator recruitment under the pollen treatment, as is evident from the sharp rise to a 3:1 juvenile : adult ratio in week 5, compared to the low 1:5 level in the controls. Later on, the juvenile : adult ratios converged to 1:1 in both treatment and control.

In the control compartments, the thrips population increased more or less exponentially during the first eight weeks, with a growth rate (0.108–0.122 larvae/d and 0.134–0.140 adult females/d) close to the intrinsic rate of population increase at 22°C (0.13 thrips/d; Van Rijn et al. 1995). The population growth rate of thrips larvae in the pollen-treated compartments was initially only slightly lower than in the control compartments (0.055–0.091 larvae/d), but became much lower after five weeks (0.007–0.022/d). This yielded significant differences in mean population levels (Table 2) and, in

the course of population change (i.e., interaction with time, Table 2), between treatment and control.

The populations of adult female thrips also showed initially equal growth rates in treatment and control, but started to deviate from week 11 onward, nearly three weeks later than for the larvae, a delay close to the developmental time at 22°C. Including all 10 trapping periods, the mean population levels and especially the population changes were significantly different between treatment and control (Table 2). The pollen treatment ultimately resulted in a 20-fold reduction in the number of thrips larvae (in week 11–12) and the number of adult females (in week 15).

By the end of the experiment, these differences in thrips numbers clearly resulted in different damage levels. In the pollen-treated compartments, the leaves were

TABLE 2. Repeated-measures ANOVA of the effects of pollen supply on biweekly (log-transformed) estimates of population size of thrips larvae and predatory mites, and on weekly (log-transformed) trap catches of adult female thrips.

Factor	Predators			Thrips larvae			Thrips adults		
	df	F	P	df	F	P	df	F	P
Treatment	1, 2	133	0.007	1, 2	21.0	0.044	1, 2	32.6	0.029
Time	4, 8	24.3	0.038	4, 8	74.1	0.005	9, 18	902	<0.0001
Treatment × time	4, 8	9.8	0.087	4, 8	14.3	0.038	9, 18	77.3	0.0009

Notes: P values for time and interaction effects are based on adjusted df values (with the given epsilon) for deviations from sphericity (Greenhouse-Geisser method). For predators, $\varepsilon = 0.25$; for thrips larvae, $\varepsilon = 0.34$; for thrips adults, $\varepsilon = 0.21$.

virtually free of thrips damage, whereas in the control compartments, ≥25% of the leaf surface was damaged by thrips, which is expected to result in a similar reduction in photosynthetic capacity (Childers 1997). Moreover, the number of fruits distorted due to feeding by thrips varied from <20% for the treated to nearly 100% for the control compartments. By the end of the experiment (week 17), the cumulative herbivore density in the control compartments was ~2100 thrips-days/leaf, which exceeded the threshold level of 1900 thrips-days/leaf (9.4 thrips-days/cm²), reported to reduce plant growth and fruit yield significantly (Welter et al. 1990). In the pollen-treated compartments, the thrips were kept well below this level (110 thrips-days/leaf).

In summary, the presence of pollen significantly increased the effectiveness of the predatory mites in controlling the thrips population, despite the fact that both thrips and predators can utilize pollen as a food source. Note that the pollen treatment did not even increase the thrips population growth when predator density was still low. One clue as to why pollen introductions promoted the predators and not the thrips was hidden in their vertical distribution within the plant (Fig. 3a). Apparently the leaves with pollen harbored much of the population of predatory mites (>90% in the first few weeks, later declining to 40%; Fig. 3b). Individual leaves continued to arrest predators for at least five weeks after pollen supply. The thrips larvae, on the other hand, did not really concentrate on the pollen-treated leaves (0–20% were on pollen-treated leaves, which represented ~10% of all leaves; Fig. 3). The thrips were always most abundant in the top of the plant, and the percentage on pollen-treated leaves became significant only when top leaves were provided with pollen (from week 9 onward). As a consequence, the predators profited more from the local pollen supply than did the thrips, whereas they apparently still visited thrips-infested leaves frequently enough to exert control.

Predator–prey model: validation and predictions

Model validation.—To test against the experimental observations, we carried out simulations with our model extended to include plant growth during the experimental period. Virtually all parameters were based on independent measurements in the laboratory or on a priori knowledge of experimental conditions (5×10^4 pollen grains per plant per day, ~10% of the leaves supplied with pollen, at 22°C). The only exceptions were the two parameters determining the dependence of adult and juvenile predator survival on food density (N_μ and partly N_G). These parameters are difficult to measure at sufficiently low prey densities. Hence, they were fitted by a least squares method such that the simulations correctly mimicked the initial decline (weeks 5–9) in the predator population observed in the *absence* of pollen. These curve-fitted parameters had very little impact on the dynamics later in the season, as well as in the *presence* of pollen, because juvenile and adult mortality became less dependent on prey density whenever food (prey and/or pollen) density was high.

With these modifications, the simulated dynamics corresponded well with the observed dynamics of predator and prey (Fig. 2). Although pollen supply was ended after eight weeks in the population experiments, the pollen supply rate was kept constant in the model, which explains the higher final predator population. For the thrips, the model simulations gave an accurate description of the differences between treatment and control. However, the number of adult thrips on the sticky traps showed a faster increase than predicted by the model, which indicates a density-dependent trap chance, e.g., due to an increased flight activity at higher thrips densities.

For the predators, the simulated distribution over leaves with and without pollen also agreed fairly well with the observations (Fig. 3b). Initially, when thrips density is low, the majority of predators stay on leaves with pollen, but when thrips density increases, the percentage of predators on leaves with pollen drops from >90% to ~40%. However, the model predicts that the thrips should completely avoid leaves with pollen (because of the high numbers of predator there), whereas the observations show that some (4–20%) of the thrips do occur on leaves with pollen. There may be two causes for these differences between model predictions and observations. First, from week 9 onward, pollen was supplied on the now full-grown top leaves of the
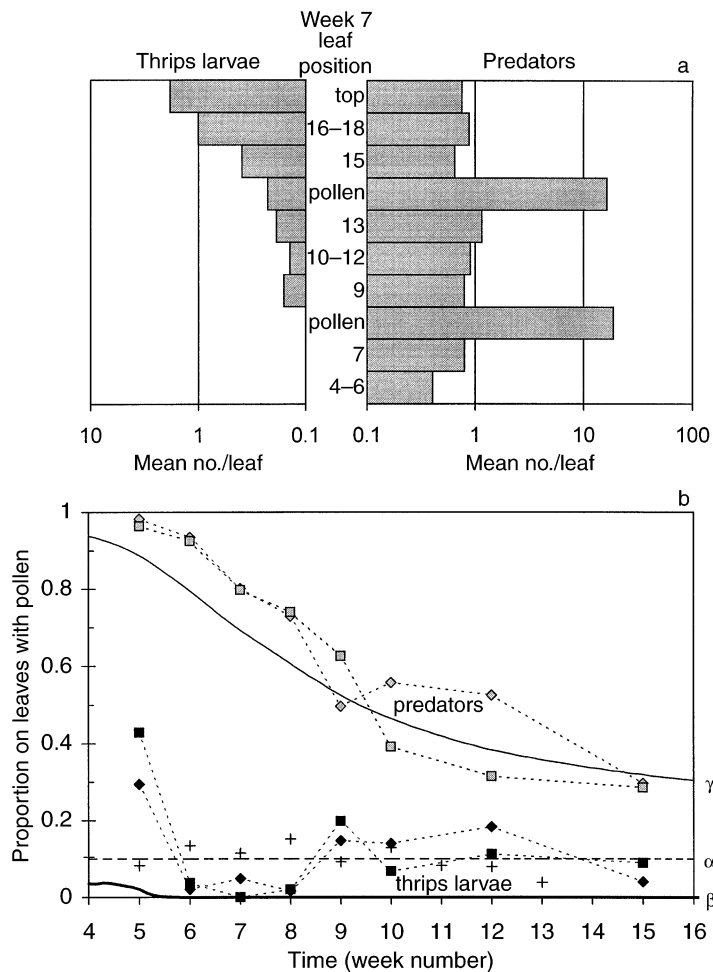
FIG. 3.   Distribution of herbivores and predators over leaves with and without pollen. (a) Snapshot (at week 7) of the vertical distribution of predatory mites and western flower thrips larvae on cucumber plants, with pollen on leaves 8 and 14; note the *x*-axis log scale. (b) Change in proportion of thrips and predator populations present on leaves with pollen. Squares and diamonds indicate results from two replicate experiments (dotted lines), and solid lines indicate model results: black symbols and heavy line for herbivores (β); gray symbols and thin line for the predators (γ). Crosses indicate the actual proportion of leaves that were supplied with pollen <5 wk before the count, and the dashed horizontal line represents their mean value used in the model ($\alpha = 0.1$).

plant, which are also the preferred leaves for the thrips. This may have increased the coincidence between thrips and pollen. Second, the observations refer to larvae of both first and second stages. This is important because first stages stay near their birth site, and mothers avoid ovipositing near predators (P. C. J. Van Rijn, *personal observation*), whereas second-stage larvae may well move to a leaf with pollen as soon as they are big enough to be invulnerable to the predators. In the model, however, all stages were assumed to have the same distribution over leaves with and without pollen.

The greenhouse experiments suggest that the addition of pollen, although both predator and prey can utilize it, directly promotes population growth of the predatory mites and indirectly (via the predator) stops the growth of the herbivorous thrips population. These effects are indeed borne out from analyzing the pollen–prey–predator model, as we will show first for the equilibrium state and then for the case of transient dynamics.

Equilibrium state.—Because our homogeneous model is of the Lotka-Volterra type, the prey equilibrium

(see the Appendix) is not affected by prey-related traits, but is determined by the predators' numerical response (Holt 1977, Oksanen et al. 1981). Feeding on pollen promotes predator reproduction and therefore decreases the herbivore equilibrium, even down to zero, given a high enough rate of pollen supply (Fig. 4a). Although the presence of pollen also decreases the rate of predation on thrips and increases herbivore reproduction, these effects do not affect the herbivore equilibrium. Thus, feeding by the herbivore on the same food source as the predator does not alter the apparent competition principle.

At intermediate supply levels ($a = 0.1$; Fig. 4a, c, d), concentrating the pollen in a small part of the environment will further reduce the herbivore equilibrium (Fig. 5b). Because the predator population now aggregates in an area with higher pollen density (Figs. 4c and 5d), the overall population growth will be higher, which, according to the apparent competition principle, will result in a lower herbivore density (Figs. 4d and 5e). At high pollen supply levels, the herbivore is not driven to extinction as in the homogeneous case (Fig. 4a), but is suppressed to a level that asymptotically
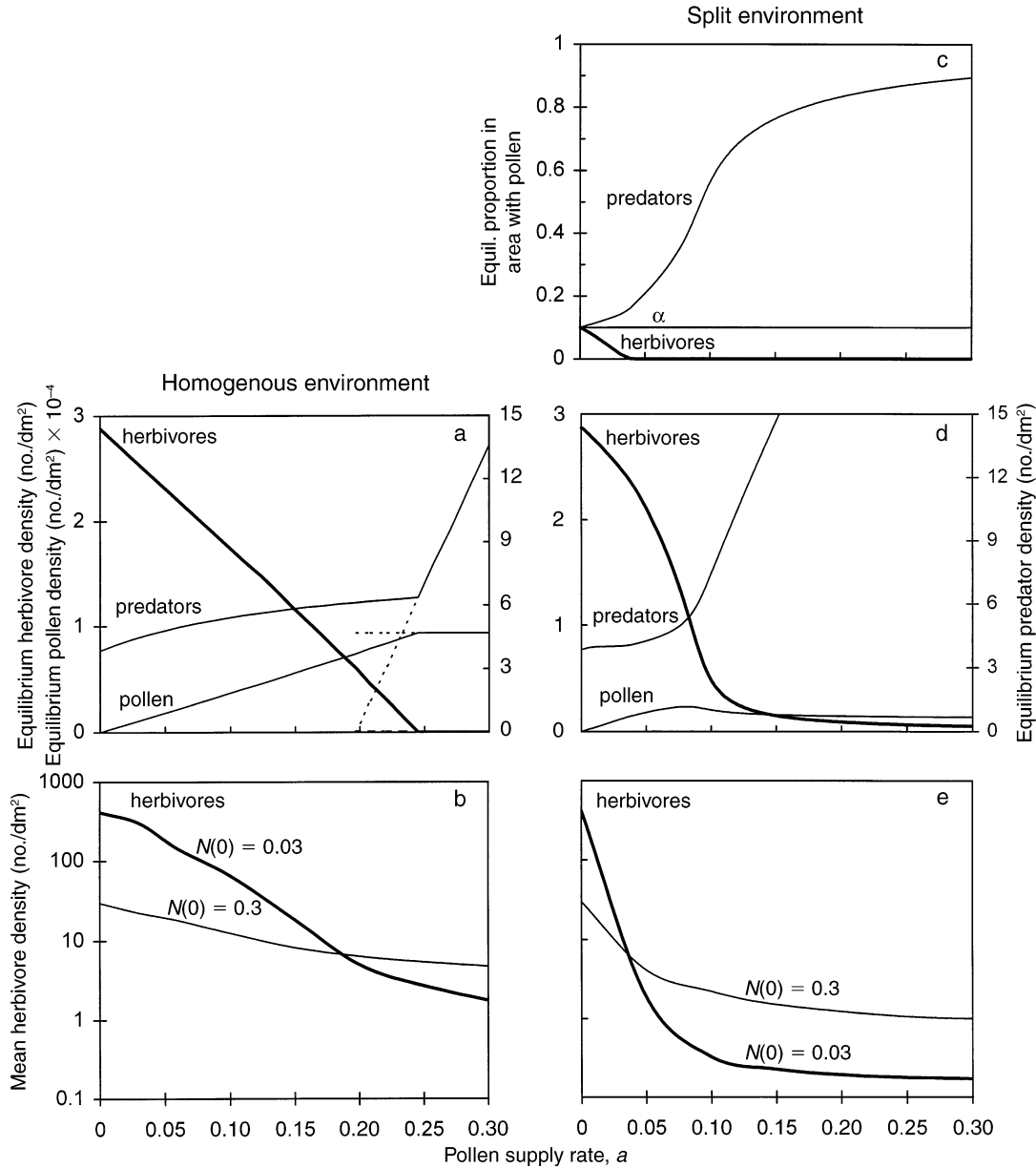
FIG. 4. The effect of the pollen supply rate, a, on equilibrium and transient dynamics of the pollen–herbivore–predator model in (a, b) a homogeneous environment ($\alpha = 1$) and (c–e) a split environment ($\alpha = 0.1$). The upper panels represent equilibrium population densities, (a, d) and equilibrium distributions (c). Note that pollen density values (a, d) must be multiplied by 10^4. Dashed lines indicate unstable equilibria. The bottom panels (b, e) represent the mean herbivore densities ($\bar{N}$, at log scale) during the first 100 d after predator release for two initial herbivore densities, $N(0)$: $0.03/dm^2$ and $0.3/dm^2$. The initial predator density (0.1 adults/dm^2) and the lowest herbivore density correspond with those in the experiments, assuming a plant size of $\sim$60 dm^2.

approaches zero with increasing pollen supply (Fig. 4d). This is the result of the herbivores all seeking refuge in the area without pollen, where a lower predator density can be found (Figs. 4c and 5e).

Transient dynamics.—The system moves toward the equilibrium for a wide range of initial values because of the extended invulnerable phase of the prey (Murdoch et al. 1987, Abrams and Walters 1996). The con-

clusions for equilibrium conditions, however, do not apply directly to the case of transient predator–prey dynamics, because now the growth enhancement of the prey population (due to pollen feeding by the prey), as well as the reduction of predation rate (due to pollen feeding by the predator) come into play (Van Rijn and Sabelis 1993). If we consider the mean numbers of predator and prey (herbivore) over the first 100 days,
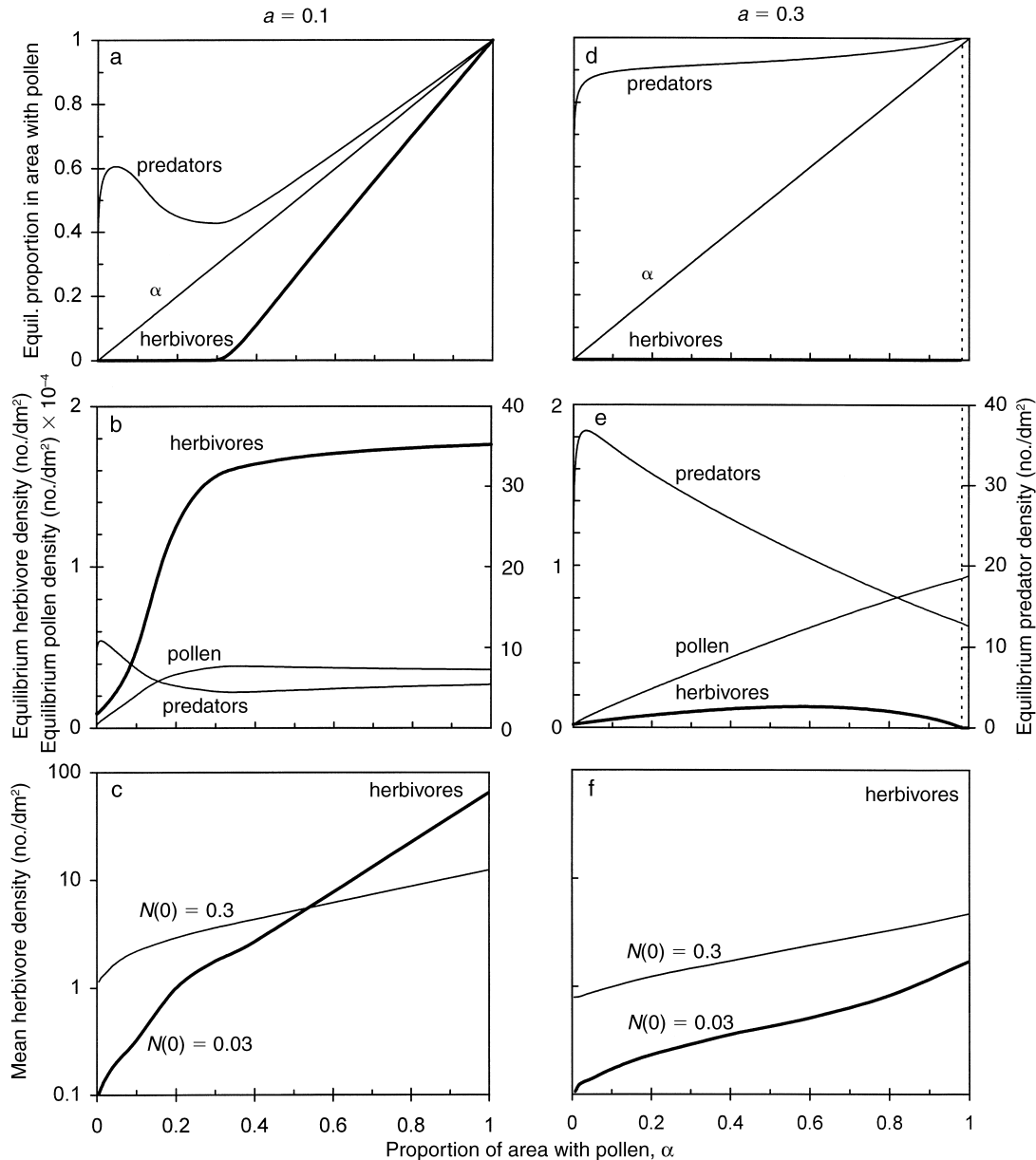
FIG. 5. The effect of concentrating pollen on part of the plant surface, α, on equilibrium and transient dynamics of the pollen–herbivore–predator model for two pollen supply rates: $a = 0.1$ (default; panels a–c) and $a = 0.3 \times 10^4$ grains·dm^{-2}·d^{-1} (panels d–f). The upper and middle panels represent equilibrium distributions (a, d) and equilibrium population densities (b, e). The dashed vertical line indicates the parameter value ($\alpha = 0.98$) at which the equilibrium herbivore density becomes zero. The bottom panels (c, f) represent mean herbivore densities ($\bar{N}$, at log scale) during the first 100 d after predator release for two initial herbivore densities, $N(0)$: 0.03/dm^2 and 0.3/dm^2. The initial predator density (0.1 adults/dm^2) and the lowest herbivore density correspond with those in the experiments, assuming a plant size of ~60 dm^2.

simulations for the case of a homogeneous environment show that there is an initial predator density below which the mean herbivore density will be higher, rather than lower, in the presence of pollen (Fig. 6; $\alpha = 1$). This is because the herbivore initially profits from the pollen both by its increased reproduction and by a decreased risk of being eaten by predators. In this way, the herbivore initially has a higher population growth

rate and therefore causes the plant to incur more damage in the presence of a supply of pollen. Above a critical initial predator density, the mean density of the predators will be higher in the presence of pollen and that of the herbivores will be lower (Fig. 4b), which is qualitatively similar to the equilibrium case.

In a split environment, one with and one without pollen, the critical predator density is shifted to much
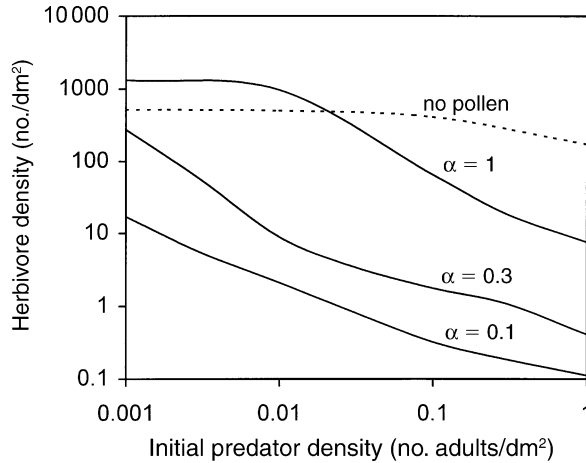
FIG. 6. The effect of initial predator population, $P(0)$ (adults released only) on mean herbivore density during the first 100 d after predator release without pollen (dotted line) and with pollen (solid lines) supplied at different proportions of the plant surface (α). The initial herbivore population, N_0, is $0.1/\text{dm}^2$, with a stage distribution stable at unlimited growth ($a = 0.1 \times 10^4$ grains·dm^{-2}·d^{-1}). Note the log scale on both axes.

lower values (Fig. 6); decreasing the area with pollen (α), while keeping pollen supply constant, further reduces mean herbivore density (Figs. 5c, f, and 6). These effects arise because (1) the predators tend to aggregate in the area with pollen, (2) the herbivores avoid the area with pollen to escape from the associated higher predation risk, and thus (3) the predators, not the herbivores, monopolize pollen as a food source. Should the herbivores not avoid predators in the area with pollen (e.g., $\beta = \alpha$), even lower mean herbivore densities would be achieved (Fig. 7c).

DISCUSSION

Perspectives for biological control

That supplementary foods such as nectar, sugar, and pollen can promote biological pest control has been advocated for a long time (McMurtry and Scriven 1966, Schiefelbein and Chiang 1966, Kennett et al. 1979, Hagen 1986, Van den Meiracker and Ramakers 1991, Bakker and Klein 1992, McMurtry 1992). However, clear experimental evidence has been lacking. Our study has shown convincingly that supplying pollen can greatly improve the control of thrips with predatory mites in greenhouses. That this result is obtained in a system in which both predator and herbivore can utilize the food source further widens prospects for application. Moreover, an accompanying model, parameterized on the basis of laboratory experiments, provides us with insight into the underlying mechanisms.

One crucial aspect is the distribution of the alternative food supply. So far, little or no attention has been paid to how alternative foods are distributed in a crop. Foods have either been dusted or sprayed to
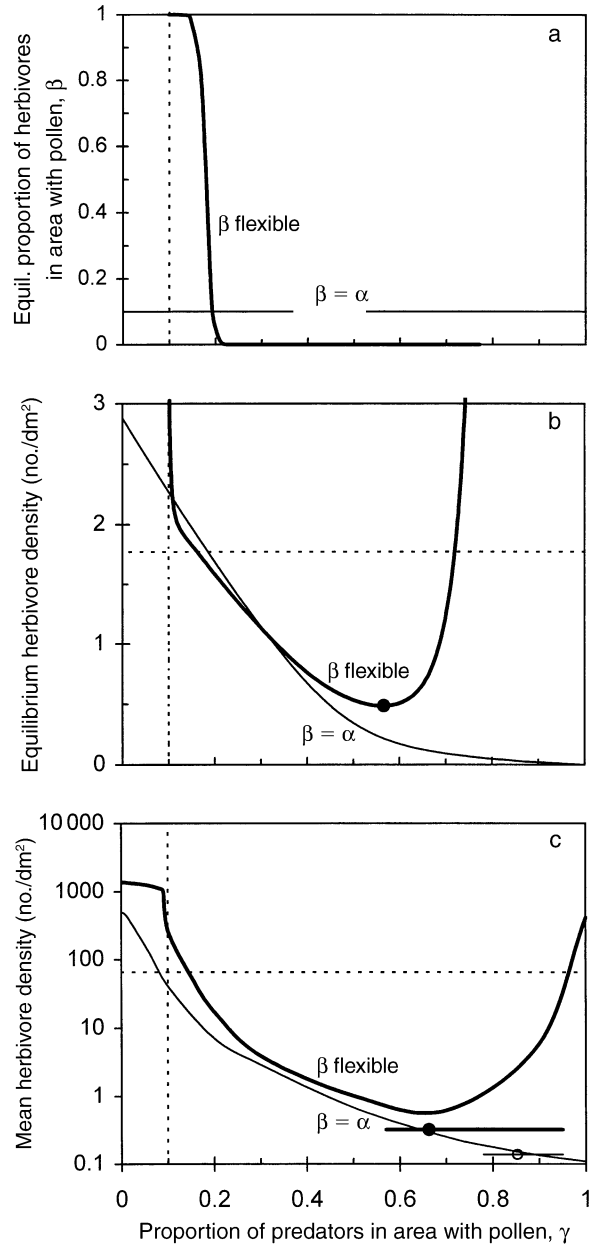

FIG. 7. The effects of predator distribution, γ, on (a) equilibrium herbivore distribution, β^*, (b) equilibrium herbivore density, N^*, and (c) mean herbivore density, $\bar{N}$, during the first 100 d after predator release (log scale), according to the pollen–herbivore–predator model. The dashed vertical line indicates the proportion of the area supplied with pollen ($\alpha = 0.1$). Two herbivore distribution strategies are compared: even ($\beta = \alpha$; thin lines, open circles) and flexible adaptive (β according to Eq. 13; heavy lines, solid circles). The (mean) adaptive predator distributions are indicated by circles, and in (b), their ranges are indicated by horizontal lines. For comparison, the (mean) herbivore level in a homogeneous environment ($\alpha = 1$) is indicated by a dashed horizontal line.

achieve a more or less even distribution (Ben-Saad and Bishop 1976, Nichols and Neel 1977, Hagley and Simpson 1981), or they have been provided by introducing pollen- and/or nectar-producing "companion" plants in the crop (Smith and Papacek 1991, Hickman and Wratten 1996, Ramakers and Voet 1996). More recently, predators have been introduced together with alternative food (or nontarget prey) via open rearing units positioned in the crop (Ramakers 1990, Van Steenis 1992). How these various ways of distributing alternative food affect the biological control of plant pests has not yet been considered. Our experiments show that the local supply of pollen on otherwise pollen-free cucumber plants increases the densities of predatory mites and suppresses the growth of the herbivore population, even though the herbivore can also utilize pollen. Moreover, the analysis of our predator–prey model shows that uniform supply of alternative food leaves room for the herbivores to enhance their population growth rates and to escape from predator control, whereas local supply enables the predators to monopolize the alternative food source (Figs. 4–6).

Another much neglected aspect is the many and varied effects of supplementary foods on the behavior and life history of predators. These foods may decrease predation on the target pest, increase survival, speed up development, and promote reproduction. Moreover, they may cause retention of predators in the target crop. Which of these effects actually occurs depends on the quality and quantity of alternative food. Some authors have implicitly assumed that the effect of supplementary foods becomes manifest within one generation of the predator (Ben-Saad and Bishop 1976, Nichols and Neel 1977, Hagley and Simpson 1981). Therefore, they have ignored the impact of the foods on the predators' reproduction and have focused on the impact on predator survival and retention. Other authors have considered the effects of supplementary foods over periods longer than a single generation, so that the predator's numerical response may have played an additional role (McMurtry and Scriven 1966, Bakker and Klein 1992). The importance of the latter is illustrated by our study on predatory mites and herbivorous thrips in a cucumber crop. Because our experiments were carried out in a greenhouse and with non-endemic predators, we can exclude attraction and retention of predators from outside the crop as a cause of improved thrips control. Thus, the positive impact of pollen results only from the predators' numerical response to pollen and thrips density. This numerical response apparently outweighs the negative effects of a decrease in the functional response and the accelerated population growth of the thrips due to feeding on pollen.

Evolution of plant–predator mutualism

Given that many plants produce edible pollen, we may now ask whether plants benefit even when the pollen is eaten by the herbivores as well. If we assume that (1) a single plant harbors a population of predators and herbivores obeying the equations of our model; that (2) the mean number of herbivores on a plant provides an estimate of plant damage and, ultimately, plant fitness; and that (3) much pollen will drop down on leaves of the same plant (and is thus wasted for the plant's reproduction), then the results of our model analysis can be viewed in an evolutionary context. We showed that the plant benefits from producing edible pollen via increased protection by predatory mites, even though the pollen can also be exploited by herbivorous thrips. This result critically depends on the ability of predators to increase their population growth rate by feeding on pollen. Under equilibrium conditions, utilization of pollen will always decrease the herbivore population, irrespective of whether pollen feeding promotes predator survival, development, or reproduction, and irrespective of how the pollen is distributed over the plant. Under non-equilibrium conditions, however, the impact on the herbivore population depends not only on the benefit of pollen to the predator, but also on that to the herbivore via increased population growth rate and reduced consumption by the predators. Whether the overall effect on the plant will be positive or not will thus depend on how pollen influences the predator : prey ratio near the moment of colonization of the plant by the herbivore, and the predator's numerical and aggregative response to herbivore density on the plant.

We showed that the benefits to the herbivore can be reduced if plants provide pollen locally. In doing so, the plant stimulates predators to aggregate near pollen sites, thereby increasing the predation risk to the herbivores that would forage for pollen, and reducing the benefits of pollen to the herbivore. Herbivores will be selected to avoid sites with pollen occupied by predators. Preliminary experiments indeed showed that thrips females avoid laying their eggs on leaves occupied by predatory mites (P. C. J. Van Rijn, *personal observations*). In this way, the predators monopolize the alternative food source and achieve a higher population growth rate, thereby decreasing the herbivore population to even lower levels. However, from the plant's perspective, predators should not be too strictly arrested at sites with pollen because they would then lose their impact on the herbivores (Fig. 7). We therefore hypothesize that the secrets of the plant's indirect defenses (sensu Price et al. 1980) are hidden in how it manipulates the distribution and quality of pollen. This hypothesis might have more general implications for our insight concerning the various ways in which plants manipulate the third trophic level to their own benefit (Sabelis et al. 1999). Clearly, the plant may benefit from local supply, not only when it provides pollen, but also when it provides extrafloral nectar and protective structures (domatia). This might explain why extrafloral nectaries and mite domatia are found in specific areas, often near the leaf base (Lundström 1887,

Bentley 1977, Walter 1996), and why they often are functional only in a restricted (usually younger) part of the plant (Beattie 1985).

Omnivory and food web composition

The "predator" in our system feeds on herbivores as well as on plant material (pollen), and therefore represents a typical example of omnivory. As a consequence, the herbivore experiences both predation and exploitative competition by the predator, a combination that is called "intraguild predation" (Polis and Holt 1992). Although omnivory is now recognized as a widespread phenomenon (Polis and Strong 1996), its ecological significance is still not fully understood. Simple model systems with omnivory are largely unstable (Pimm and Lawton 1977, 1978). At low basal productivity levels, the predator cannot be maintained, and at high productivity, the intermediate prey is eliminated due to apparent competition, leaving only a relatively small parameter domain where predator and prey can coexist (Holt and Polis 1997, Mylius et al. 2001).

McCann and Hastings (1997) argued that food webs do not need to have a stable internal equilibrium in order to have a stable composition. They showed that moderate levels of omnivory can stabilize food chains that show non-equilibrium dynamics (oscillations), via period doubling reversals (see also McCann et al. 1998). However, these same models showed that systems that have a stable equilibrium lose one of its components when omnivory becomes stronger or when basal productivity increases. Mylius et al. (2001) showed that invulnerable prey stages in the prey or noncarnivorous stages in the predator, has only minor effects on the parameter domain where predator and prey can coexist at equilibrium. Our study, based on similarly structured populations, now shows that another mechanism, adaptive behaviors in prey and predator in a spatially heterogeneous environment, greatly facilitates stable coexistence. When pollen occurs only in part of the environment, increasing the pollen supply rate (technically similar to basal productivity) no longer results in full elimination of the prey, but only in suppression to low prey levels (Fig. 4a,c,d). Bifurcation analysis of our model showed (Fig. 5e) that predator and prey will coexist for any distribution of the resource (pollen) that deviates slightly from homogeneity (in our example, $\alpha < 0.98$). The underlying mechanism is that the basal resource is available in two qualities (in our case, leaf and leaf plus pollen) that are spatially separated, and that the predator concentrates more on the higher quality resource, thereby leaving a partial refuge for the prey at the lower quality resource. To prevent the elimination of prey, it is essential that at higher basal productivity levels the prey avoid the higher quality resource ($\beta \rightarrow 0$; Fig. 7a). At the same time, the predator should aggregate at the higher quality resource ($\gamma > \alpha$; Fig. 7b). When, however, the predator aggregates too much on this resource ($\gamma \rightarrow 1$), it no longer controls the prey population and no equilibrium exists (Fig. 7b).

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APPENDIX

Population equilibrium equations are available in ESA's Electronic Data Archive: *Ecological Archives* E083-053-A1.