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**DOI**

[10.1023/B:APPA.0000018885.35044.c6](https://doi.org/10.1023/B:APPA.0000018885.35044.c6)

**Publication date**

1997

**Published in**

Experimental and Applied Acarology

[Link to publication](#)

**Citation for published version (APA):**

Drukker, B., Janssen, A., Ravensberg, W., & Sabelis, M. W. (1997). Improved control capacity of the mite predator *Phytoseiulus persimilis* (Acari: Phytoseiidae) on tomato. *Experimental and Applied Acarology*, 21, 507-518.  
<https://doi.org/10.1023/B:APPA.0000018885.35044.c6>

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## Improved control capacity of the mite predator *Phytoseiulus persimilis* (Acari: Phytoseiidae) on tomato

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### ABSTRACT

The predatory mite *Phytoseiulus persimilis* is frequently reported to perform poorly on greenhouse tomatoes. As the predators are mass-reared on another host plant (bean), we supposed that they are poorly adapted to tomato, a plant densely packed with poisonous and sticky glandular hairs. This hypothesis was tested by comparing the control capacity of a strain of *P. persimilis* directly obtained from a mass rearing with the same strain after four generations on tomato. Both strains were released in a tomato crop in two identical compartments of a greenhouse and the population dynamics of prey (a tomato strain of *Tetranychus urticae*) and predator were recorded at weekly time intervals. It was found that the strain previously exposed to a tomato environment performed better than the unexposed strain: (1) its population increased faster; (2) the prey population declined faster; and (3) the damage to new-grown tomato leaves was considerably lower. To investigate the causes of the difference in performance between the exposed and unexposed strains, oviposition and survival rates were assessed on a diet of two-spotted spider mites on tomato leaf sections. In addition, the unexposed strain was tested on a diet of two-spotted spider mites on bean leaf sections. The difference in oviposition rates of both predator strains was small compared to the overall mean. However, the oviposition rate of the first generation of predators since transfer from bean to tomato dropped to less than half of the original value. Moreover, mortality in the first generation increased from 14% to 89%, whereas it decreased to 0% after four generations. Future research should clarify whether these changes in life history are due to selection or to physiological adaptation.

**Key words:** *Phytoseiulus persimilis*; *Tetranychus urticae*, biological control, selection, adaptation, life-history traits, food quality.

### INTRODUCTION

Mass rearing predatory mites for biological control of spider mites implies a selection process, resulting in predators adapted to the specific environment

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(plants and spider mites, climate) of the mass rearing facilities. The mass-reared individuals are distributed over a wide variety of crops where they will be subjected to the specific environment of each crop. After release it may take some time before the predators are able to cope with the specific environment of the crop. The characteristics of the resulting adapted strains are bound to be lost, as feedback to the mass rearing cultures is usually absent.

Tomato is a good example of a host plant that differs profoundly from that used for mass rearing (bean). Its leaves and especially its stems are densely covered with poisonous and sticky glandular hairs known to entrap and kill phytophagous mites and other arthropods (Stoner *et al.*, 1968; Williams *et al.*, 1980; Farrar and Kennedy, 1987). Also, their natural enemies are affected. Van Haren *et al.* (1987) demonstrated that predatory mites (*P. persimilis*) are entrapped by the glandular hairs on certain tomato cultivars. Another feature that makes tomato a hostile environment is the presence of secondary metabolites in the leaf (alkaloids and phenolic compounds, Roddick, 1974), which may modify prey quality. Finally, the high temperature and low humidity in tomato greenhouses is considered to be optimal for spider mites, but suboptimal for *P. persimilis* (Nihoul and Van Impe, 1992).

That tomato selects for other traits is indicated by the existence of a host race of the two-spotted spider mite on tomato (Gotoh *et al.*, 1993). Behavioural, physiological and genetic differences were found between a green strain obtained from cucumber and a red strain from tomato. The tomato strain prefers tomato over cucumber, its males prefer tomato females, and allozyme analysis (for phospho-gluco isomerase) showed a much lower variation for the tomato strain than for the bean strain (Gotoh *et al.*, 1993). Recently it was shown that the tomato strain is more tolerant to methyl-ketones in the glandular hairs of tomato (Chatzivasileiadis and Sabelis, 1996) than the cucumber strain. These differences suggest that spider mite strains differ in their profitability for *P. persimilis* and may cause the difference in control capacity of the predator.

Spider-mite control on greenhouse tomato using *P. persimilis* is less effective than on many other greenhouse crops such as cucumber, sweet pepper, melon and bean (French *et al.*, 1976, Nihoul and Van Impe, 1992). We suspect this difference to be due to the hostile environment experienced on tomato. Three testable hypotheses can be formulated: (1) predators are hindered by contact with glandular hairs ("the direct host plant effect" hypothesis; Van Haren *et al.*, 1987); (2) they are directly affected by the quality of the prey independent of the host plant ("the direct prey effect" hypothesis); and (3) they are indirectly affected by reduced nutritional quality of the prey caused by toxins originating from the host plant ("the indirect host plant-prey effect" hypothesis; Drukker and Ravensberg, 1994; Gillespie and Quiring, 1994). Note that these hypotheses are not mutually exclusive.

We now present experiments to test "the indirect effect" hypothesis using the strains obtained from the mass rearing and the release trials. Survival rates and peak oviposition rates of predators retrieved from tomato were compared with

predators from the original stock. Before testing these hypotheses we first present the results of release trials of *P. persimilis* on tomato, showing that predator strains exposed to tomato for four generations were better able to control their prey than strains directly obtained from the mass culture on bean.

#### MATERIALS AND METHODS

##### *Release in commercial greenhouse*

For the release trial a commercial greenhouse compartment ( $\sim 100 \times 50$  m, Houten, The Netherlands) with spontaneous spider mite infestations was selected. Two adjacent rows of plants were found to be entirely infested with spider mites (80 actives per leaf on average), the rest of the greenhouse was infested locally. Predators were released from "spidex plus" bags (small paper bags to be suspended from plants containing ca 30 *P. persimilis* predators each on a medium of vermiculite). The bags were distributed as recommended by the provider (Koppert BV, Berkel en Rodenrijs, The Netherlands). Plants infested with spider mites were provided with three bags whereas the neighbouring plants received two bags. On each plant, up to three leaves (young, medium, old) were inspected once or twice a week until 66 days after release. The same leaves were monitored from the moment they unfolded until they showed the first signs of ageing, then a new leaf was selected on the same plant. From day 2 to 14, 25 spider mite infested plants (26–54 leaves) were monitored, from day 17 to 66, six plants (23–30 leaves). Spider mites and predators were counted and the leaf damage was estimated according to the LDI (Leaf Damage Index) scale proposed by Hussey and Scopes (1985). Adult predators were collected from the greenhouse from two to four weeks after release to start a laboratory culture fed with spider mites (tomato host race) on tomato leaves.

##### *Oviposition and food conversion*

Peak rate of oviposition (at 25°C) of females on a diet of either bean or tomato spider mites was compared. This strain was chosen because it is strongly correlated with predation and the intrinsic rate of increase according to a survey of the literature on life-history traits of the Phytoseiidae (Janssen and Sabelis, 1992; Sabelis and Janssen, 1994). According to the "indirect effect" hypothesis the nutritional value of tomato spider mites is lower than that of bean spider mites. Hence, a change of diet from bean spider mites to tomato may cause problems for the predators that are reflected in life history parameters such as peak oviposition.

Synchronized egg waves were produced by placing an infested bean or tomato leaf for 8–24 hours on a (detached bean leaf-) culture of *P. persimilis*. Subsequently, predator eggs were collected from that leaf and placed on tomato or bean leaves containing an ample supply of spider mite eggs and other stages.

Throughout the experiments the supply of males for mating was ensured. A new generation of adult females is expected to start ovipositing after about 5 days. These females were individually housed in glass tubes containing tomato or bean leaf sections with an abundant supply of eggs from the corresponding host race of spider mites. The number of eggs per female was counted during 5 days and the mean number of eggs per female per day was calculated. The maximum daily rates were used for comparison, following the method of Janssen and Sabelis (1992).

Two series of tests were performed: in the first series, a group of females reared on bean leaves with spider mites was divided into a group transferred to tomato leaf sections with tomato spider mites and a group that remained on bean leaf sections with bean spider mites. In the second series, a group of females was transferred from bean to tomato leaf sections, and the peak rate of oviposition was compared to that of their daughters who remained to be fed on tomato leaf sections with tomato spider mites. In this way, it was possible to see the long-term effect of feeding on tomato spider mites on individual predators. To find out whether females retrieved from the commercial greenhouse after the first experiment had adapted to the lower food quality, their peak oviposition was measured while being fed on tomato spider mites on tomato leaf sections. In the second series not only the peak rate of oviposition was determined, but also mortality. Mortality was defined as number of dead individuals divided by the sum of dead and alive individuals over the first 10 days of the test.

#### *Pest suppression in the greenhouse by two predator populations*

Predators originating from two cultures were compared with respect to their capacities of pest suppression. One culture originated from Koppert, and was reared on detached bean leaves with bean spider mites. The other culture originated from the mites retrieved from tomato in the greenhouse. Ten tomato plants (1 m high) were placed on a table in each of two identical tents of fine mesh gauze. Equal numbers (25 actives per plant) of spider mites were released in each compartment. Four weeks after release, spider-mite densities had increased to 88 and 138 adult females per leaf, respectively, in the two compartments. These differences were statistically not significant (Student *t*-test). Predators from tomato were released in the compartment with 138 spider mites per leaf and predators from bean in the compartment with 88 spider mites per leaf. As we expected that the control capacity of the tomato-reared predators would be better, we chose to release this strain on the more heavily infested tomato plants. Each plant received ten adult female predators. Numbers of predator and spider mites and the leaf damage index was measured weekly over a period of six weeks. Of each plant one leaf (day 1, 7 and 29) or two leaves (day 14, 21, 35 and 45) of different age was examined. The same leaves were repeatedly examined from the moment they unfolded until they showed the first signs of ageing, then a young leaf was selected on the same plant.

## RESULTS

*Release in commercial greenhouse*

Figure 1a shows predator densities (in mites per leaf) through time after release on plants with heavy spider mite infestation. It is clear that the predator population grows in the first three weeks. The overall density of subsequent generations of predators is lower, probably as a result of the steep decline of spider mite populations from day 12 to day 20 (Fig. 1b).

The spider mite population continued to grow until 12 days after predator release. From day 12 to 20 a rapid decline was observed. The simultaneous prey decline and predator increase suggest that the decline was at least partly caused by predation, but dispersal should also be taken into account. Locally, spider mite and predator populations went extinct, but after 4 weeks prey and/or predators were found in high density on other plants than those on which predators were released. Leaf damage was reduced from day 12 to 20 and remained low until day 40 when a steady increase took place until day 50, followed by a rapid decline (Fig. 1c).

*Peak oviposition and mortality*

The peak rate of oviposition was not significantly reduced when predators were transferred from bean to tomato (Table 1, test 1, 2 and 3). Offspring of transferred females showed a dramatic decline in egg production and a marked reduction in survival (Table 1, test 4 and 5). Their peak oviposition was significantly lower compared to that of females on bean and females transferred from bean to tomato. This was caused by the fact that some females deposited no eggs at all, whereas others produced a normal number of eggs. Offspring mortality was significantly higher than that of their mothers (89% versus 14%,  $\chi^2 = 32.9$ ,  $n = 70$ ,  $df = 1$ ,  $p \ll 0.001$ ).

The females collected in the greenhouse from populations that had spent more than four generations on tomato, had a peak egg production virtually equal to that of predators from bean (Table 1, test 6, 7 and 8). Peak oviposition was significantly higher than the peak oviposition of the next generation of females after transfer from bean to tomato. Mortality was significantly lower than that of the F1 predators ( $n = 75$ ,  $\chi^2 = 50.9$ ,  $n = 75$ ,  $df = 1$ ,  $p \ll 0.001$ ), but not lower than that of predators reared on bean and transferred to tomato ( $\chi^2 = 89$ ,  $n = 38$ ,  $df = 1$ , ns).

*Comparison of pest suppression*

A striking difference in numbers was found between the predators from bean and those from tomato, from the first sampling day on (Fig. 2a). The tomato-reared predators showed a steep increase in density during the first week followed by a slow but steady decrease in the five weeks thereafter; the bean-reared predators on the other hand showed a slower increase in the first four

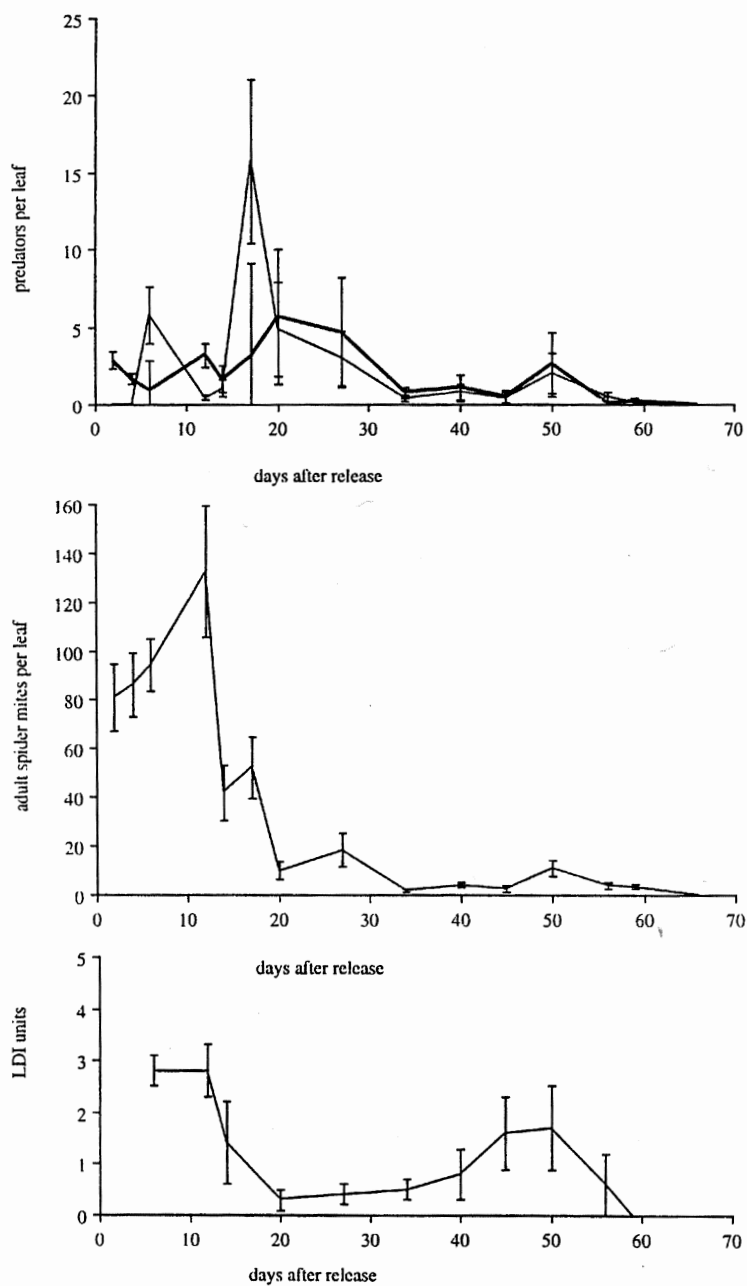


Fig. 1. Density of predatory mites and their prey in a commercial tomato greenhouse in Houten, The Netherlands after predator release on day 1. (a) Mean density of predatory mites, bold line: adults, thin line juveniles. (b) Mean density of spider mites, (c) Leaf damage of young leaves expressed in LDI units according to Hussey and Scopes (1985). Vertical bars indicate SE.

TABLE 1.

Peak oviposition rate (eggs/female/day) and mortality of *P. persimilis* on prey originating from bean or tomato. The predators received various pretreatment with respect to host plant, its associated line of the two-spotted spider mites and the number of generations on the host plant.

Test	Treatment of predators	Origin of prey in juvenile/adult phase of predators	<i>n</i>	Peak oviposition $\pm$ SD*	Mortality %*
1	Bean	Bean	21	5.60 $\pm$ 1.6 <sup>a</sup>	–
2	Bean	Bean/tomato	27	5.08 $\pm$ 0.9 <sup>ab</sup>	–
3	Bean (mothers of F1 test 4 and 5)	Bean/tomato	10	5.17 $\pm$ 1.8 <sup>ab</sup>	14 <sup>a</sup>
4	Tomato (F1 from test 3, 1st cohort)	Tomato/tomato	12	2.17 $\pm$ 1.9	–
5	Tomato (F1 from test 3, 2nd cohort)	Tomato/tomato	6	1.30 $\pm$ 2.0	89 <sup>b</sup>
6	Tomato (more than 3 generations)	Tomato/tomato	15	5.14 $\pm$ 1.3	–
7	Tomato (more than 3 generations)	Tomato/tomato	4	5.04 $\pm$ 1.6	0 <sup>a</sup>
8	Tomato (more than 3 generations)	Tomato/tomato	6	4.36 $\pm$ 2.3	–

\*Values marked with different characters are significantly different. Peak oviposition data were compared by means of Kolmogorov–Smirnov-2 sample tests using the Dunn–Sidak method (see Sokal and Rohlf, 1995) to adjust the individual levels of significant to produce an experiment-wise error rate of 5%. Mortality data were compared by means of  $\chi^2$ -tests.

weeks and a decline in the sixth week after release. Many eggs and juveniles were observed in the compartment with the tomato-reared predators until 3–4 weeks after release (Fig. 2b). In the compartment with bean-reared predators few juveniles and eggs were found until the fourth week after release (Fig. 2c). After the fourth week the number of adults, juveniles and eggs were comparable to those of the tomato-reared predators in the first week. The initial difference in densities can be explained by a higher juvenile mortality in the first generation of predatory mites from bean, which corroborates the findings of the oviposition/mortality experiment.

The effect of predation on spider mite populations is shown in Fig. 2d: the reduction by the tomato-reared predators is more rapid and leads to a very low density of the prey after four weeks, although there was no overall extinction. Bean-reared predators hardly reduced the prey population until after the fifth week. This had its consequences for the level of leaf damage (Fig. 2e) and even for tomato yield; the compartment with tomato-reared predators had a 77% higher tomato yield (3257 g) than that with bean-reared predators (1845g).

## DISCUSSION

When predators are reared on bean and released on tomato they experience higher juvenile mortality and show lower oviposition rates during the first generation after release. The effects are not significant when transfer to tomato occurs in the adult phase (see also Gillespie and Quiring, 1994), but our results show significant effects on juveniles of the subsequent generation. After at least



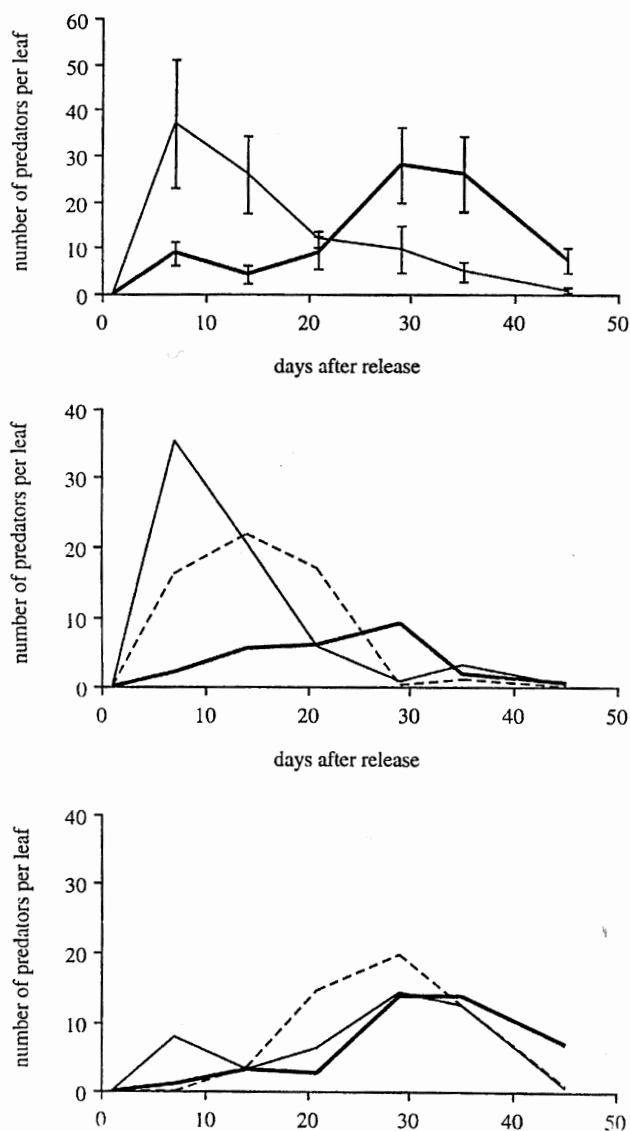


Fig. 2. Release of bean-reared and tomato-reared predatory mites in two greenhouse compartments containing 10 infested tomato plants. All 10 plants (10–20 leaves per plant) were monitored. (a) Mean density of predatory mites (adults and juveniles), bold line: bean reared mites in compartment 1, thin line: tomato reared mites in compartment 2. (b) Mean density of tomato-reared predatory mites, bold line: adults, thin line: juveniles, dotted line: eggs. (c) Mean density of bean-reared predatory mites, bold line: adults, thin line: juveniles, dotted line: eggs. (d) Mean density of spider mites, bold line: with bean reared predators in compartment 1, thin line: with tomato reared predators in compartment 2. (e) Leaf damage of young leaves expressed in LDI units according to Hussey and Scopes (1985), bold line: with bean reared mites in compartment 1, thin line: with tomato reared mites in compartment 2. Vertical bars indicate SE.

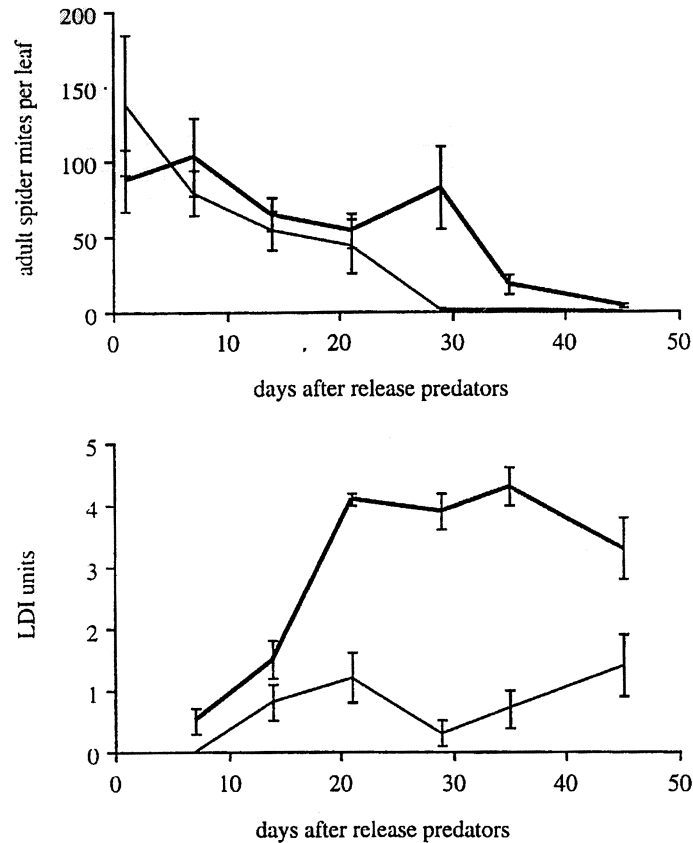


Fig. 2 (Continued)

four generations on tomato, predators exhibit neither a reduction in survival nor in reproduction.

There are three possibilities to explain the reduction in population growth rate of the predators: (1) a direct effect of the host plant (glandular hair exudates); (2) a direct effect of the strain of spider mites (independent of the host plant); and (3) an indirect effect of the host plant via the spider mites (possibly related to the strain of spider mites). We suspect that the first possibility is not likely to be the only explanation: in the oviposition experiments females had plenty of opportunity to avoid contact with glandular hairs and the leaf strips used were much less densely occupied with hairs than the stems (at least on the varieties under test). Moreover, the juvenile predators in the mortality tests were not very active, hence the likelihood of contact with the hair tips was much lower.

The second possibility has recently been tested by Gillespie and Quiring (1994). They found no evidence for a direct effect of the strain of spider mite on

adult life span and oviposition rate of the predators, but their experimental set-up does not allow for conclusions on developmental time, because they did not separate host plant effects from spider mite strain effects (see their Table 4). Their results are also incomplete in that they do not provide information on the most crucial features determining the intrinsic rate of population increase, i.e. egg-to-egg developmental time, juvenile mortality, and peak oviposition rate.

Both our and Gillespie and Quiring's results are inadequate to validate the third possibility, i.e. a role of the host plant via the spider mites. This would require an elaborate set of experiments where the effects on life history parameters are related to the time spent by the spider mite on the alternate host plant, thereby taking into account that plant toxins may have accumulated in the prey.

That accumulation of plant toxins in spider mites may well play an important role is illustrated by experiments of Chatzivasileiades, Boon and Sabelis (1996). They found that a tomato strain reared on tomato and a cucumber strain reared on cucumber were equally susceptible to methyl-ketones from glandular hairs. However, when both strains were reared on cucumber, the tomato strain was much more resistant to the methyl-ketones. A similar explanation may also apply to the absence of an effect on the oviposition rates of predatory mites transferred in the adult stage, as opposed to the juvenile stage. Adults transferred as juveniles may have accumulated more of the toxins than adults transferred as adults.

Comparing the initial population peaks in the pest suppression experiments shows that the bean reared predators reach a lower egg peak than the tomato-reared predators. This seems to contradict the finding in the oviposition-mortality experiment where oviposition rates were hardly affected when the females were transferred from bean to tomato. However, it should be noted that extrapolation of the oviposition experiment to the period of initial population growth has its limitation. First, the oviposition experiment lasted only four days whereas the population densities were measured after 7 days. During this period the effects of accumulation of tomato toxins on oviposition and survival may have become manifest in the released predators. Second, the oviposition experiment was carried out on leaf sections, thus omitting the effect of the stems with their dense cover of glandular hairs. As shown by Van Haren *et al.* (1987) this may cause an additional mortality among the adult females.

Two possible mechanisms may underlie the observed improvement of the predators coping with their novel host plant: (1) intrageneration adjustment through immediate behavioural and physiological changes; (2) adaptation through intergeneration selection for genotypes with higher fitness on tomato.

The results of pest suppression experiments show that adaptation takes place on a time scale exceeding one generation, suggesting that intrageneration adjustment cannot be the only mechanism. Hence, selection on genotypes should also play a role. This is further supported by the fact that there is a large variance in oviposition rate and survival in the F1 females (Table 1, test 4 and 5)

so that there is a basis for selection to act upon. Future experiments will be designed to investigate the nature of the differences between the two strains of predatory mites.

#### ACKNOWLEDGEMENTS

Thanks are due to Dr G. van Impe, Gösta Nachman and Leo van der Geest for valuable comments on the manuscript. Technical assistance was provided by Sandra Mulder; her employer, Koppert Biological Systems, Berkel en Rodenrijs. The Netherlands is gratefully acknowledged for funding this project and providing predatory mites. Long term continuation of this project is made possible by financial support of the Netherlands Technology Foundations (STW).

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