

Effect of single and mixed diets on the fitness of omnivorous thrips, *Thrips tabaci* (Thys.: Thripidae)

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Abstract

Food choice in omnivorous animals is influenced by the balance of nutritional needs, food availability, and quality of a particular food items. Here, we study whether omnivorous onion thrips, *Thrips tabaci* Lindeman, feed on the eggs of its competitor *Tetranychus urticae* Koch (Acari: Tetranychidae) when an alternative supplemental source is, or is not, available. Thrips were either fed a cucumber leaf alone, or this diet was supplemented with pollen, mite eggs, or both. We demonstrated that the supplemental food sources improved several fitness-determining traits of thrips with pollen, being nutritionally superior to mite eggs. Pollen reduced the development time and increased the population growth of thrips compared to mite eggs. When both pollen and mite eggs were available, thrips fed on both; pollen to improve nutritional status and eggs to eliminate the opponent, despite the latter's consisting lower of nutritional benefit. In all, this study showed that omnivorous thrips benefit from a cucumber leaf diet that is supplemented with other food sources and that pollen and mite eggs increase several fitness traits and positively affect the dynamics of future thrips generations.

Key words: *Tetranychus urticae*, pollen, mite egg, *Cucumis sativus*, competition

چکیده

انتخاب غذا در جانوران همه‌چیزخوار عمدتاً بستگی به کیفیت آن از جمله اندازه و تعادل مواد تشکیل دهنده و همچنین در دسترس بودن غذای مورد نظر دارد. در این پژوهش ما در پی بررسی این موضوع بودیم که در چه حالت و به چه منظور تریپس پیاز، *Thrips tabaci* Lindeman، از تخم رقیب خود، کنه‌ی تارتن دولکه‌ای، *Tetranychus urticae* Koch (Acari: Tetranychidae)، تغذیه می‌کند. آیا هنگامی که غذای کمکی دیگری نیز در دسترس باشد، باز هم تریپس پیاز از تخم‌های کنه‌ی تارتن دولکه‌ای تغذیه خواهد کرد؟ بدین منظور برگ خیار به تنهایی و برگ خیار به اضافه‌ی منابع پروتئینی (گرده‌ی ذرت، تخم کنه، مخلوطی از گرده‌ی ذرت و تخم کنه) به عنوان غذاهای کمکی در اختیار تریپس پیاز قرار داده شد. نتایج نشان داد که منابع پروتئینی اعم از گیاهی و یا جانوری باعث بهبود فاکتورهای زیستی در تریپس پیاز شد؛ ولی در مقام مقایسه، گرده تأثیر بهتری نسبت به تخم کنه‌ی تارتن دولکه‌ای داشت. گرده‌ی ذرت در مقایسه با تخم کنه‌ی تارتن دولکه‌ای طول دوره‌ی رشد را کاهش و جمعیت تریپس پیاز را افزایش داد. زمانی که جیره‌ی غذایی شامل تخم کنه‌ی تارتن دولکه‌ای و گرده به طور توأم بود، تریپس پیاز از هر دو تغذیه کرد. گرچه تخم کنه‌ی تارتن دولکه‌ای نسبت به گرده از ارزش غذایی کمتری برای تریپس پیاز برخوردار است، ولی باز هم در این حالت تریپس از تخم کنه‌ی تارتن دولکه‌ای تغذیه می‌کرد که به نظر می‌رسد این رفتار تغذیه‌ای بیشتر به منظور حذف رقیب باشد. در کل این بررسی نشان می‌دهد برگ خیار همراه با مکمل‌های پروتئینی از ارزش غذایی بالاتری برای تریپس برخوردار است که باعث بهبود بعضی از فاکتورهای زیستی در حشره شده و بنابراین تأثیر مثبتی بر دینامیسم جمعیت آن در نسل‌های بعدی خواهد داشت.

واژگان کلیدی: *Tetranychus urticae*، گرده، تخم کنه، *Cucumis sativus*، رقابت

Introduction

Green plants are attacked by various monophagous or polyphagous herbivores (Van Emden, 1990). The co-existence of herbivores on the same host plant produces interactions

such as omnivory, competition, and intra-guild predation (Price *et al.*, 1980; Poppy, 1997). In natural systems, omnivores are common and abundant components of the arthropod fauna and their vertical and horizontal impact in food webs may be influenced by subtle differences in plant quality (Agrawal *et al.*, 1999). The relative dominance of competitive interactions within and among species is a complex issue and considerable interest has focused on such experimental relationships among insect herbivores (Price *et al.*, 1980). Omnivores that feed on plants and prey encounter variation in the quality of both as food sources (Milne & Walter, 1998). If resources at both trophic levels were roughly equivalent and essentially interchangeable, then feeding at more than one trophic level could provide omnivores with ecological flexibility by making them less dependent on a single resource (Polis & Strong, 1996). On the other hand, if resources at different trophic levels are not nutritionally equivalent, then omnivores may depend on a combination of resources and may be forced to simultaneously track resources at multiple trophic levels (Eubanks & Denno, 2000). Foraging theory predicts that omnivores will balance their diet as a result of nutritional need, food quality and availability of alternate food (Agrawal & Klein, 2000).

Thrips are known to be omnivorous and reductions in plant quality cause them to shift from herbivory to predation (Agrawal *et al.*, 1999). However it is unknown whether thrips benefit from sampling different foods and diet mixing (Agrawal & Klein, 2000). Gonzalez & Wilson (1982) observed that late in the growing season of cotton, thrips that inhabited flowers were less effective predators to spider mites. Phytophagous thrips eat mite eggs (Trichilo & Leigh, 1986; Wilson *et al.*, 1996; Milne & Walter, 1998; Agrawal & Klein, 2000) and they are potentially important predators of spider mites in the field (Wilson *et al.*, 1996). Apart from eating mite eggs, *Thrips tabaci* Lindeman and *Frankliniella schultzei* (Trybom) could also affect mite population indirectly by inducing non-specific plant chemical defence that influences mite survival negatively (Karban & Carey, 1984; Karban, 1985). Since thrips and spider mites are pests of the same plant species (Helle & Sabelis, 1985; Lewis, 1997), their simultaneous presence on cucumber leaves in greenhouses will cause a complex interaction. The study reported here will assess the fitness of thrips fed single and mixed diets and has two aims: (1) to determine if onion thrips, *T. tabaci*, will attack two-spotted spider mite, *Tetranychus urticae* Koch, eggs when pollen is available as an alternative supplemental food source, and (2) if this is so, to assess whether thrips eat the mite eggs for nutritional benefit or to eliminate their food competitors.

Materials and methods

Plants

Cucumber (*Cucumis sativus* cultivar Super dominus) was planted in plastic pots (10 cm diameter, 8 cm height) and was cultured in a climate-controlled greenhouse room (25 ± 1 °C, $70 \pm 5\%$ room humidity [RH], L16: D8 photoperiod). Six-week old seedlings leaves were used for experiments. Maize pollen was collected from Indian corn maize in the field (Varamin, Tehran, Iran).

Rearing of onion thrips and two-spotted spider mites

Onion thrips were collected from stored red onions (*Allium haematochiton*; Shiraz, Fars, Iran) and cultured on onion plants in a greenhouse at controlled conditions (L16: D8 hrs and 25 ± 1 °C). Two-spotted spider mites were collected from sugar beet leaves (planted in a greenhouse) and were cultured on cucumber plants also in a greenhouse under the same conditions. The eggs of this mite were used as part of the different diet treatments detailed below.

Treatments and experimental apparatus

To examine the response of onion thrips to varying nutrition, treatments consisted of 4 diets: (1) cucumber leaf (control), (2) cucumber leaf plus corn pollen, (3) cucumber leaf plus mite eggs, and (4) cucumber leaf plus corn pollen and mite eggs. Experimental units were glass clip cages (10×10 cm) with a round open area (diameter 3.5 cm) covered on the top with no thrips™ mesh (~ 150 μm). Between the two glass parts there was a cotton layer, a cucumber leaf and another cotton layer (Ahmadi *et al.*, 2006). Depending on the treatment, pollen, mite eggs or both were added to the cucumber leaf. Females of *T. urticae* were placed in experimental units to lay eggs for 24 h and thereafter the leaf was used as a food source. Each leaf contained between 9-13 mite eggs. Mite eggs were not placed manually on the discs because the silken threads produced by spider mites are removed from the eggs during this process, and this may modify the response of the thrips to the eggs (Trichilo & Leigh, 1986). Pollen was sprinkled onto the leaf surface by a painting brush (No. 04). When pollen and eggs were used together as supplemental diet, thrips could consume them with the equal chance. The whole experiment was conducted under controlled conditions (L16: D8 h, $65 \pm 5\%$ RH and 25 ± 1 °C) in a single growth chamber.

Experiment procedure and data collection

Development: Thrips larvae (0-12 h) were confined to receive individual prepared diets; 30 replicates were run per treatment. Every third day the thrips were transferred to a fresh leaf to maintain fresh food sources. Thrips prepupae and pupae were not manipulated since they are susceptible to mortality with such treatment. The thrips were observed every 12 h and stage transitions and survival were recorded until adult eclosion.

Reproduction: After development, emerged adults were individually placed into newly prepared arenas. Their supplemental diets and cucumber leaves were replaced in each clip cage every second day. Old leaves were kept in an incubator in order to calculate the number of larvae hatched from cucumber leaves within 7 d. This procedure was followed for the entire life span of each female.

Fertility life table: Adult females from first experiment were individually staged on their respective diet. Age specific fecundity was determined based on the number of larvae that hatched from cucumber leaves within 7 d after their replacement; 30 replicates were run per treatment. Demographic fertility life table parameters, namely, net reproductive rate ($R_0 = \sum l_x m_x$), mean generation time ($T = \sum x l_x m_x / \sum l_x m_x$) and the intrinsic rate of population increase ($r_m = \ln R_0 / T$), were calculated for thrips that had been fed the different diets. The means and standard errors of the life table parameters were estimated by using the Jackknife method (Sokal & Rohlf, 1995).

Statistics

All experiments were arranged in a randomized design with the 4 diets as treatments. We used a Pearson's Chi-square test to detect effects of the diets on thrips' mortality. We used analysis of variance (ANOVA) to determine the effects of diets (4 levels) and to analyze data on thrips' development time r_m , r_0 , generation time and fecundity. When ANOVA results were significant at $p \leq 0.05$, mean separation was completed using the Fisher protected least significant difference (LSD) procedure. All data were analyzed using the statistical software packages of SAS (SAS Institute Inc., 1993).

Results

Duration of development in immature life stages

Development during the immature life stages was accelerated in thrips fed a diet of cucumber leaf and corn maize pollen compared to those fed cucumber leaf alone and

cucumber leaf and mite eggs. As shown in fig. 1, this reduced development time was significant during the larval stages ($F_{3,90} = 9.57$, $P = 0.0001$), but not in pupal stages ($F_{3,71} = 2.06$, $P = 0.113$; fig. 1). The larval stage was shortest when the thrips consumed pollen and longest when mite eggs were available. The diet of pollen and mite eggs increased the duration of larval stages by about 2/3 of a day compared to a diet of pollen and reduced it by approximately 1/3 of a day relative to a diet of mite eggs. The mortality rate of the thrips was not affected by diet as the treatment groups did not differ from each other ($F_{3,115} = 0.12$, $P = 0.95$; table 1).

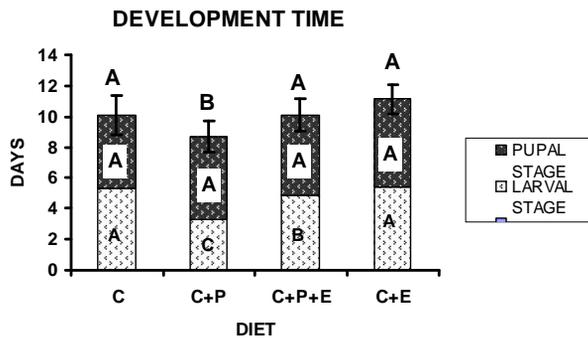


Figure 1. The larval, pupal and total development time of *T. tabaci* feeding on four different diets: cucumber (C), cucumber and pollen (C + P), cucumber and mite egg (C + E), and cucumber and pollen plus mite egg (C + P + E). Each bar represents the mean of 30 replicates. The same letter within a bar for larval and pupal development times, respectively, indicates that the means between the larval and pupal stages do not differ significantly, while different letter specifies significance, at the 5% error rate based on Fisher's PLSD test. Each bar shows duration of premature on four different diets.

Reproduction

Fecundity of *T. tabaci* was positively affected by all supplemental diet sources, whether pollen or mite eggs, to similar degrees ($F_{3,35} = 7.91$, $P = 0.0004$). Figure 2 shows that adding pollen, mite eggs, or both caused a 2-3 fold increase in the number of larvae compared to those given cucumber leaf alone. The shape of the fecundity rate curve was similar for all

supplemental diets; fertility peaked 7 to 11 days after adult emergence and then steadily declined (fig. 3).

Table 1. Demographic parameters for *T. tabaci* when fed on different diets.

Diet	$r_m \pm SE$ (female ⁻¹ /day)	$R_0 \pm SE$ (day ⁻¹)	$T \pm SE$ (days)	%Mortality $\pm SE$
Cucumber	0.13 \pm 0.0042 ^c	16.51 \pm 1.72 ^b	21.40 \pm 0.36 ^a	0.53 ^a \pm 0.18
Cucumber + Pollen	0.19 \pm 0.0071 ^a	42.77 \pm 5.033 ^a	19.24 \pm 0.62 ^b	0.48 ^a \pm 0.18
Cucumber + Pollen + Egg	0.18 \pm 0.0077 ^{ab}	39.73 \pm 7.31 ^a	20.55 \pm 0.51 ^{ab}	0.46 ^a \pm 0.18
Cucumber + Egg	0.16 \pm 0.0027 ^b	32.34 \pm 2.14 ^a	20.90 \pm 0.43 ^a	0.46 ^a \pm 0.18

The same letters do not differ significantly at the 5% error rate based on Fisher's PLSD test.

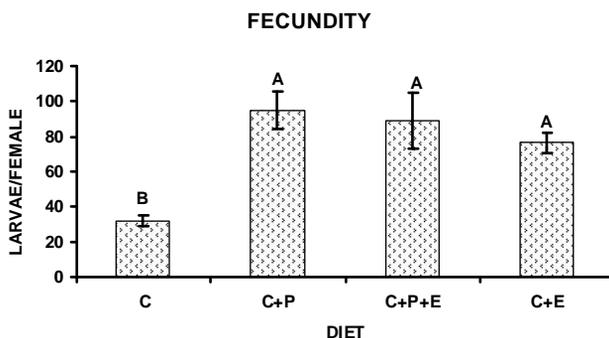


Figure 2. The fecundity of *T. tabaci* administered four different nutritional diets: cucumber (C), cucumber and pollen (C + P), cucumber and mite egg (C + E), and (C + P + E) cucumber and pollen plus mite egg. Each bar represents the means of 10 replicates (one female per replicate). The mean total fecundity of all groups was 72.84 ± 8.91 larvae. The same letter above a bar indicates that the means do not differ significantly, while different letter specifies significance, at the 5% error rate based on Fisher's PLSD test.

Fertility life table

Table 1 shows that the intrinsic rate of population increase (r_m) of *T. tabaci* was significantly affected by nutrition ($F_{3,35} = 21.93$, $P = 0.0001$), with the highest increase rate occurring in thrips fed cucumber + pollen and lowest on cucumber leaves alone (0.19 ± 0.007 and 0.13 ± 0.007 , respectively). The magnitude of population growth increase seen in thrips fed pollen was significantly higher than those given mite eggs ($F_{3,35} = 21.93$, $P = 0.0001$).

The differences between the r_m values mainly reflect differences in the effect of different diets on fecundity.

The net reproductive rate (R_0) of thrips was also significantly affected by diet ($F_{3, 35} = 6.19$, $P = 0.0017$). Although no significant difference was seen among supplemental diets, R_0 was highest when thrips were fed pollen and the lowest when fed mite eggs (42.77 ± 5.03 and 32.34 ± 2.14 , respectively) whereas the diet with both pollen and mite eggs yielded an intermediate R_0 (table 1).

Diet also significantly affected the generation time of *T. tabaci* specifically during immature stages ($F_{3, 63} = 3.21$, $P = 0.0001$; table 1). Thrips fed pollen had significantly reduced generation times especially during larval stages. The shortest and the longest development time were seen in thrips fed pollen (8.64 ± 1.01 days) and mite eggs (10.31 ± 0.94 days), respectively (fig. 1). In contrast, no significant difference was found during adulthood between thrips fed different diets ($F_{3, 35} = 1.13$, $P = 0.95$).

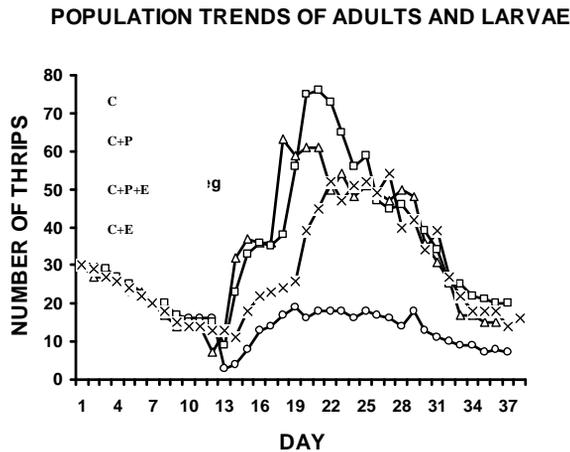


Figure 3. Time series showing population trends of adults and larvae of *T. tabaci* feeding on four different nutritional diets: cucumber (C); cucumber and pollen (C + P), cucumber and mite egg (C + E), and cucumber and pollen plus mite egg (C + P + E).

Discussion

Thrips tabaci fed diets supplemental to cucumber leaves showed marked increases in fecundity, net reproductive rate (r_0), and intrinsic rate of population increase (r_m). They also

exhibited reduced generation time, particularly in immature stages. These effects were greatest with a diet containing pollen whether alone or mixed with mite eggs; diets supplemented with mite eggs alone had the least effect on these measures. Varied diets had different effects on population dynamics of *T. tabaci*. When given a diet comprised of cucumber leaf, pollen, and mite eggs, the number of thrips peaked at ~ 80, the highest of all 4 diets; whereas on a diet of cucumber leaf alone the peak was much lower (~ 20 thrips). Thrips fed a diet of cucumber leaf plus pollen had a shorter immature development time and because of the early emergence of adults, oviposition peak occurred five days before that on a diet of cucumber leaf plus mite eggs. Compared to mite eggs alone, diets supplemented with pollen shortened the duration of larval stages of thrips and caused a significant increase in r_m . These results reflect the influence of developmental rate (*i.e.*, days to first oviposition) on this fitness measure and indicate that pollen provided a better nutritional source for omnivorous thrips.

Arthropod food webs are often complex and the occurrence of omnivory and indirect trophic interactions can make it especially difficult to assign species to distinct trophic levels. An omnivore's diet selection may be influenced by various factors including availability, nutritional quality and defensive strategy of plant and animals (Agrawal & Klein, 2000). Important determinants of food choice in thrips are reduced time spent searching for food over a small spatial or temporal scale and a decreased need for 'resource taking' of highly available or quality foods over longer periods (Agrawal & Klein, 2000).

Previous studies have also investigated the effects of nutrition on thrips' development. Pollen (Hulshof *et al.*, 2003; Trichilo & Leigh, 1988), spider mite eggs (Milne & Walter, 1998) and mite eggs plus turnip weed floral tissue caused a reduction in development time, especially during the larval stages, of thrips *Frankliniella occidentalis* (Pergande) and *T. tabaci*. Our experiments also confirmed that development time of *T. tabaci* was decreased with diets of pollen, but not with mite eggs. Although our study and that of Milne & Walter (1998) used the same species of thrips, the differential effect on larval stages between our data and theirs concerning diets supplemented with mite eggs may be due to differences in the handling of the eggs. Milne & Walter (1998) transferred the mite eggs to cotton leaves in the experimental arena using a moistened bristle brush. This manual transfer will remove the silken threads produced by the spider mite, which may modify the response of thrips to mite eggs (Trichilo & Leigh, 1986). Our previous observations (Ahmadi *et al.*, 2006) indicated that thrips fed less on mite eggs than the thrips in the study of Trichilo & Leigh (1986). In the current study mortality during immature stages did not significantly differ; but was high

which may be due to transferring the larvae or cucurbitacins in cucumber leaf. Mortality was less severe in thrips fed supplemental diets, although this was not a significant effect, suggesting that these added food sources may cause less feeding on leaves which may reduce mortality. Further studies are needed to provide sufficient data to substantiate this idea.

Feeding on a supplemental diet of pollen or mite eggs promoted the intrinsic rate of population increase. Combining these two supplements (*i.e.* pollen + mite eggs) caused intermediate effects on population growth rate. Other studies have shown that adding pollen to cucumber leaves and pollen and mite eggs to cotton leaves causes an increase in intrinsic rate of increase of *F. occidentalis* (Hulshof *et al.*, 2003; Trichilo & Leigh, 1988). Our results are consistent with these data. Furthermore, our results accord with the finding of Trichilo & Leigh (1988) that pollen's influence on population growth is greater than that of mite eggs.

The larval diet is a key factor that affects not only development, but also body size (Gerin *et al.*, 1999; De Kogel *et al.*, 1999). Faster developing, larger insect larvae may be less vulnerable to their natural enemies (Hulshof *et al.*, 2003). Our data show that even though egg feeding extends the larval stages compared to pollen feeding, when both pollen and mite eggs were available thrips ate both of them. This suggests that thrips are attempting to overcome their opponent and eliminate its competitor by eating its eggs.

As shown in previous studies, our data indicate that pollen has more nutritional benefits than mite eggs. These benefits may be attributed to findings that: (1) pollen as a supplemental nutrient source is more suitable than mite eggs (Trichilo & Leigh, 1988); (2) thrips have mouthparts especially adapted for pollen feeding (Wilson *et al.*, 1996; Lewis, 1997); (3) adult thrips raised inside the mite webs showed lower production of thrips larvae than on clean leaves (Pallini, 1998); (4) webs of *T. urticae* are an obstacle for invader thrips (Trichilo & Leigh, 1988); (5) thrips do not prefer to lay eggs in places where mite eggs are present (Pallini, 1998); and (6) thrips need more time to reach the mite eggs placed in webs (Rhoda *et al.*, 2000) than pollen which is on the leaf surface. In a recent study, we showed that *T. urticae* may be aware of thrips' presence and will avoid this omnivorous competitor. The mite does this by increasing the number and location of egg masses within the leaf arena (Ahmadi *et al.*, 2006).

The current study indicates that when thrips were allowed to choose among supplemental diets, specifically pollen or mite eggs, they fed on both of them. Thus, besides satisfying nutritional needs and improving fitness traits (Trichilo & Leigh, 1986; Wilson *et al.*, 1996), feeding on mite eggs will also eliminate the competitor. Milne & Walter (1998)

pronounced that predation by *T. tabaci* on *T. urticae* eggs may be influenced more by conditional presence of two species on a host plant than on such predation being a central aspect of *T. tabaci* ecology. Also when Pallini (1998) observed that adult thrips raised inside the webs showed lower production of thrips larvae compared to clean leaves, he suggested that this might in turn result from a higher mortality of eggs due to diet of ovipositing adults or because adult females avoid ovipositing on webbed leaves, being an unfavorable microhabitat.

When thrips' predators are present, they escape to mite webs to avoid being killed (Venzon *et al.*, 2000). So the presence of spider mites not only provides better nutrition, but also supplies a means by which thrips may escape from their enemies. These circumstances represent a serious difficulty for biological control of thrips. On the other hand, the success of preventive introduction and the subsequent augmentation of omnivorous thrips predators (*e.g.* *Neoseiulus cucumeris* Oudemans, *Iphiseius degenerans* Berlese, and *Orius* spp.) seem to depend on the crops (Hulshof *et al.*, 2003). Both predators and thrips may benefit from pollen (Hulshof *et al.*, 2003). However, Van Rijn *et al.* (2002) indicated that plant parts with pollen were actually spared from thrips destruction. Moreover, they showed that adding pollen locally on cucumber plants, which did not have any pollen, increased the population of predatory mites and caused predation pressure on a population of herbivores. This was not the case when pollen was distributed evenly on all parts of plant. Therefore, it is essential to use pollen locally to improve predators' efficiency.

In summary, this study showed that omnivorous thrips benefit from a cucumber leaf diet that is supplemented with other food sources. Two such supplements, pollen and mite eggs, increase several fitness traits and affected the dynamics of future thrip generations. Mite eggs extended the development time and reduced the population growth of thrips compared to feeding on pollen. While the generation time of spider mites is shorter than thrips, lack of resource could lead to elimination of thrips. To circumvent this by eliminating the competition, thrips resorted to egg feeding.

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