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Trichomes and spider-mite webbing protect predatory mite eggs from intraguild predation

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Abstract Predaceous arthropods are frequently more abundant on plants with leaves that are pubescent or bear domatia than on plants with glabrous leaves. We explored the hypothesis that for some predatory mites this is because pubescence affords protection from intraguild predation. In laboratory experiments, we tested whether apple leaf pubescence protected *Typhlodromus pyri* eggs from predation by western flower thrips, *Frankliniella occidentalis*. To investigate the effect of pubescence further, we added cotton fibers to trichome-free leaves. We also determined whether webbing produced by *Tetranychus urticae* protected *Phytoseiulus persimilis* eggs from predation by *F. occidentalis*. Predation by thrips on *T. pyri* eggs oviposited on field-collected pubescent “Erwin Bauer” apple leaves was significantly less than on glabrous “Crittenden” apple leaves. Phytoseiid eggs oviposited in the cotton fibers were preyed upon significantly less than those on the trichome-free bean disk. Increasing the cotton fiber density from 5 to 20 fibers only slightly further reduced predation by thrips on *T. pyri* eggs. Thrips fed upon significantly fewer *P. persimilis* eggs oviposited in *Te. urticae* webbing than eggs oviposited on a surface that differed only in the absence of *Te. urticae* web. We conclude that a complex leaf topography reduces intensity of intraguild predation in this system.

Key words Intraguild predation · Phytoseiidae · Leaf pubescence · Thrips

Introduction

Plants are known to modulate interactions between arthropod herbivores and their predators (Price et al. 1980; Dicke 1999; Olff et al. 1999). These effects can be attributed to plant characteristics such as the physical structure of the leaves (e.g., Huxley 1986; Walter 1992), nutritional resources provided by the plant and used by natural enemies (e.g., Bentley 1977; Koptur 1989), and allelochemicals produced by the plant (e.g., Vet and Dicke 1992). The influences of these characteristics on herbivore natural enemies have been shown to affect plant fitness (Janzen 1966; Rehr et al. 1973; Agrawal and Karban 1997).

Leaf surface characteristics known to influence predators include pubescence, domatia, surface waxes, and arthropod-produced structures such as spider-mite webbing. Leaves with domatia (tufts of hairs, pits, or pockets on the leaf surface) or pubescence tend to harbor larger numbers of omnivorous phytoseiid mites, thrips, and predaceous hemiptera (Downing and Moilliet 1967; Duso 1992; Walter 1992; Walter and O’Dowd 1992; Agrawal and Karban 1997; Duso and Vettorazzo 1999; Norton et al. 2000). Spider-mite webbing can reduce predation on adult predatory mites (Cloutier and Johnson 1993). However, leaf surface characteristics may also exert a negative influence on natural enemies. For example, the waxy blooms found on species of *Brassica* impede predator search on the leaf surface (Eigenbrode et al. 1995), and highly pubescent leaves and spider-mite webbing have been shown to inhibit predation of herbivores (Rabb and Bradley 1968; Shah 1982; Gerson 1985; Kauffman and Kennedy 1989; van Lenteren and de Ponti 1990; Kleijn et al. 1997; Krips et al. 1999).

While there is good evidence that leaf pubescence and domatia can positively influence predator abundance, the mechanisms are not well known. Leaf domatia are thought to enhance predator numbers by functioning as refugia for breeding and development, and possibly to form barriers to larger predators (Grostal and O’Dowd 1994; Huxley 1986; Walter 1996). Leaf pubescence and

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spider-mite webbing might function in a similar capacity and may serve other roles as well. In fact, there are at least four ways in which leaf surface structures might influence predator abundance: (1) by reducing the chance that animals will be dislodged from the leaf surface, (2) by increasing the capture of pollen or fungal spores which might serve as alternative food sources, (3) by moderating the micro-environment, especially humidity, and (4) by affording protection from intraguild predation.

Omnivorous phytoseiid mites are a group of predators whose abundance can be positively related to leaf pubescence (Downing and Moilliet 1967; Duso and Vettorazzo 1999). Furthermore, in laboratory experiments these predators consistently chose to reside and oviposit on pubescent leaves rather than glabrous leaves (Rasmy and El-Banhawy 1974; Overmeer and van Zon 1984; A. Roda, unpublished work). Similarly, phytoseiid predators specialized to feed on spider mites often oviposit in spider-mite webbing (Sabelis 1985; A. Roda, J.P. Nyrop, Marcel Dicke, and G. English-Loeb, unpublished work). These patterns suggest there is an advantage to phytoseiids residing on leaves with pubescence or in spider-mite webbing. Several authors have speculated on which of the processes described above might lead to these patterns (Overmeer and van Zon 1984; Sabelis 1985; Duso 1992; McMurtry and Croft 1997), but little experimental evidence is available (but see Cloutier and Johnson 1993; Grostal and O'Dowd 1994).

We examined how the leaf surface affects intraguild predation of phytoseiid mite eggs by thrips. Intraguild predation refers to predation between two carnivores that also compete for shared prey (Polis et al. 1989). Although the importance of intraguild predation has been well established (Polis and McCormick 1987; Polis et al. 1989; Batzer and Wissinger 1996; Rosenheim 1998), few studies have examined the mechanisms that modulate the interactions between intraguild predators in terrestrial systems (but see Rosenheim et al. 1995). We hypothesized that a labyrinthine topography on the leaf surface, produced by pubescence or other physical features such as webbing, may reduce encounters between intraguild predators and/or increase the difficulty the predator has in capturing and handling prey. To test this idea, we measured predation by western flower thrips [*Frankliniella occidentalis* (Pergande)] on eggs of two species of predatory mites, *Typhlodromus pyri* Scheuten and *Phytoseiulus persimilis* Athias-Henriot, as influenced by leaf structure. The western flower thrips is omnivorous, feeding on leaf tissue, pollen, and spider mite and predatory mite eggs (Trichilo and Leigh 1986; Lewis 1997; Pallini et al. 1998; A.L. Roda, personal observations). Both species of predatory mites also feed on spider mites but differ dramatically in their feeding habits and life history. *Phytoseiulus persimilis* is a specialist feeding almost exclusively on tetranychid mites, and its numbers depend upon the presence and abundance of spider-mite prey (McMurtry and Croft 1997). In contrast, *T. pyri* is a generalist, surviving on tetranychid mites, pollen and fungal

spores, and persists in a habitat largely independently of prey numbers (Chant 1959; Dicke et al. 1989; Walde et al. 1992; Engel and Ohnesorge 1994; Zemek and Prenerova 1997; Nyrop et al. 1998). Phytoseiid eggs are oviposited on top of leaf hairs, or attached to the web strands produced by spider-mite prey (Sabelis 1985). Eggs may also be found in grooves formed by leaf veins. Females seldom place their eggs on the open leaf surface (Sabelis 1985).

We explored the idea that leaf structures provide protection from intraguild predation as one potential mechanism to explain the greater abundance of predatory mites on plants with pubescence or domatia. Specifically, we asked two questions: (1) Do trichomes and spider-mite webbing found on the leaf surface reduce predation on predatory mite eggs? (2) Does increasing the density of leaf surface structures result in a greater reduction in thrips predation?

Methods

Stock cultures

Western flower thrips, two-spotted spider mites, *T. pyri* and *P. persimilis* used in the experiments were obtained from laboratory colonies (reared at 20–30°C and 50–80% relative humidity, RH). Two-spotted spider mites were reared on lima bean (*Phaseolus lunatus* L.). *Phytoseiulus persimilis* and *T. pyri* were reared on lima bean leaves infested with two-spotted spider mites. *Typhlodromus pyri* colonies also contained either velvet fabric or apple leaves (*Malus domestica* Borkh. "Mcintosh") to encourage oviposition. Thrips were collected from a glasshouse colony maintained on either *Dendranthema grandiflorabean* "Sunny Casa" (bean disk experiments) or *Impatiens wallerana* "Fiesta Lavender Orchid" (apple leaf experiments). Lima bean plants used for colonies and experiments were grown under glasshouse conditions. Apple leaves were collected from a research orchard located at the New York State Agricultural Experiment Station, Geneva, New York, United States. We conducted all experiments in climate chambers held at 23°C, 80% RH with a 16 h light:8 h dark light regime.

Thrips predation on *T. pyri* eggs oviposited on apple leaves

We tested if naturally occurring pubescence affected thrips predation on *T. pyri* eggs oviposited on smooth and pubescent apple leaves. "Crittenden" (smooth) and "Erwin Bauer" (pubescent) apple cultivars were selected from trees maintained at the United States Department of Agriculture, Plant Genetic Resources Unit, Geneva, N.Y. To estimate the pubescence level on each of the varieties, we counted the number of times the trichomes crossed a 3-mm line placed randomly over the inter-vein area of a leaf. The reference line was etched into the ocular of a dissecting microscope. The number of intersecting hairs was counted at three separate locations to give a mean per leaf. Ten leaves were sampled for each variety. The smooth cultivar had 1.3 crossing trichomes mm⁻¹ (SE=0.7) and the pubescent cultivar had 6.0 crossing trichomes mm⁻¹ (SE=1.3).

We collected 20 leaves from each variety and cut a 2-cm-diameter disk from the inter-vein area. The disks were supported ventral surface up on water saturated cotton and provisioned with c. 0.05 mg cattail (*Typha* spp.) pollen that was placed in a small patch at the edge of the disk to facilitate later removal. Four female *T. pyri* were placed onto each disk and allowed to oviposit. After 48 h, the mites were removed and the cattail pollen carefully brushed off so that no pollen remained on which the thrips might

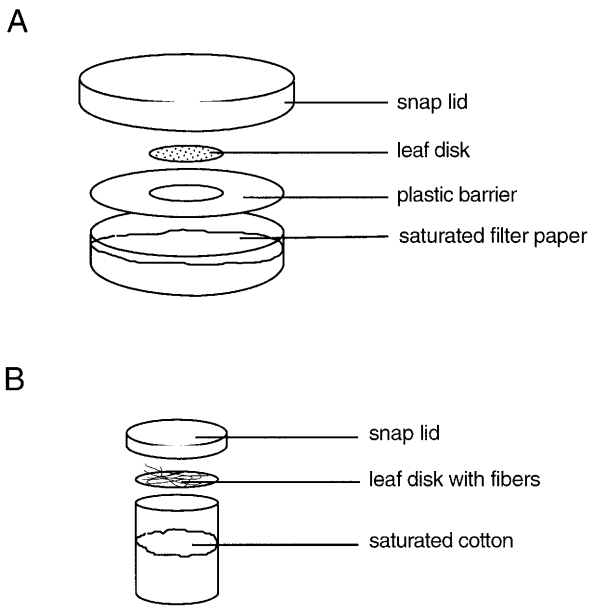


Fig. 1A,B Bioassay arenas used to evaluate thrips predation on predatory mite eggs

feed. We selected disks that had at least four *T. pyri* eggs evenly distributed across the surface. Excess eggs were removed so that four eggs remained on each disk.

The prepared disks were placed on water-saturated filter paper held in snap petri dishes (Fig. 1A). A clear, plastic disk with a 2.5-cm-diameter hole in the center was placed around the leaf to prevent the thrips from becoming trapped on the wet filter paper. Adult, female western flower thrips were aspirated from the colony, provisioned with water, and starved for 24 h at 23°C. A thrips was placed onto each of the 40 disks (20 for each variety). After 24 h, the number of eggs fed upon was recorded along with the status of the thrips (present and alive, present and dead, or absent). Using these methods, 99% of the thrips were present and alive after 24 h. If the thrips was missing or dead, the disk was not included in the analysis. Data were analyzed using logistic regression calculated with a robust variance estimate (StataCorp 1999). The robust variance estimate was used because the observational units, eggs, were clustered within the experimental units, leaf disks. With such a design, the variance among observational units may be greater than if each egg was an experimental unit because survival of eggs on a disk may be correlated. The robust variance estimator accounts for the correlation. Using the asymptotic estimate of variation from the logistic model, 95% prediction intervals were calculated for the estimates of survival.

Thrips predation on *T. pyri* and *P. persimilis* eggs oviposited in fibers

To test whether physical structures influenced thrips predation on predatory mite eggs, we created a hairy surface by adding cotton fibers to a trichome-free bean leaf disk or a black plastic disk, each of which was 2 cm in diameter. Phytoseiids were allowed to oviposit in cotton fibers placed on leaf disks ("maternity disks") and the cotton fibers with the eggs were then transferred to another leaf disk on which predation was allowed to occur. Leaf disks were cut from the inter-vein areas of young, fully expanded bean leaves and supported with the ventral surface upwards on wet cotton. Four *T. pyri* or two *P. persimilis* adult females were placed on the disks with either 5, 10, or 20 cotton wool fibers (each fiber c. 3.5 cm long). The cotton fibers were placed on the leaf disk in a loosely wound mass. Cattail pollen was provided as a food source

for *T. pyri*. To provision *P. persimilis*, the leaf disks were cut from bean leaves infested with two-spotted spider mites (all stages available). After 24 h, the fibers containing the predatory mite eggs were removed from the maternity disk and placed on either a clean bean leaf or black plastic disk (2 cm diameter). This was done to prevent thrips from feeding on the pollen or spider mites on the maternity disk, and so that the plastic and leaf disk treatments would differ only in the substrate used. If more than four eggs were oviposited in the fibers, the excess eggs were removed with a paint brush. For treatments with no fibers, eggs were taken from the maternity disks and placed on a clean bean or plastic disk with a paint brush. Removal and placement of eggs were conducted so that the eggs were evenly distributed in the fibers or on the disks. Each disk was placed in a separate vial on water-saturated cotton (Fig. 1B). The vials were sealed tightly with a cap in order to contain the thrips and minimize air currents. The cap had a c. 1-cm-diameter ventilation hole that was covered with a fine mesh screen.

A female thrips, starved for 24 h at 23°C, was placed on each disk with phytoseiid eggs. Periodic observations were made to compare feeding behavior on eggs located in the fibers to those on the surface of the bean disk. After 24 h, the number of eggs fed upon and the status of the thrips was recorded as previously described in the apple leaf experiment. We conducted three experiments in which we compared predation in 5 versus 0 fibers, in 10 versus 0 fibers and in 20 versus 0 fibers. Each experiment had three factors: phytoseiid species (*T. pyri* or *P. persimilis*), disk substrate (bean or plastic), and fiber density (2 levels) with each of the eight treatments being replicated 20 times. Data were analyzed using logistic regression calculated with a robust variance estimate, and 95% prediction intervals were calculated for the estimates of survival.

Thrips predation on *T. pyri* eggs oviposited in different densities of cotton fibers

We conducted an experiment to specifically test the effect of increasing cotton fiber density on thrips predation. Four fiber densities were used: 0, 5, 10 and 20. As described above, the fibers were placed on a bean disk with four female *T. pyri*, provisioned with cattail pollen. The mites were allowed to oviposit on the trichome-free bean surface or in the fibers for 48 h. The fibers containing *T. pyri* eggs were then removed and placed on a clean bean disk. On disks where the mites oviposited directly on the bean disk, the cattail pollen was carefully cleaned off with a paint brush.

The prepared disks were placed on water-saturated filter paper held in snap petri dishes (Fig. 1A). As described before, a starved female thrips was placed onto each of the 60 disks (15 for each density). After 24 h, the number of eggs fed upon and the status of each thrips was recorded. The experiment was replicated a second time with another 60 disks and the data analyzed as described for the first experiment with the exception that the two times the experiment was conducted were considered as blocks. Survival of phytoseiid eggs oviposited in the different fiber density was compared using linear contrasts.

Thrips predation on *P. persimilis* eggs oviposited in two-spotted spider-mite web

Phytoseiulus persimilis, as well as other phytoseiids, are frequently observed foraging and ovipositing in webbing produced by two-spotted spider mites. This webbing may protect phytoseiid eggs from predation by thrips. We measured phytoseiid egg predation on leaf surfaces that differed only in the presence or absence of two-spotted spider-mite web. We cut disks (2 cm diameter) from clean lima bean leaves and supported them ventral side up on saturated cotton. Each disk was divided in half by placing a small strip of wet cotton through the middle of the disk. On each half, ten mature female two-spotted spider mites were added. The spider mites

fed, oviposited, and performed other activities that would leave residues and odors to indicate their presence. After 72 h, we removed all motile two-spotted spider mites and the wet cotton divider. With a paint brush, we removed the two-spotted spider-mite web from one half of each disk.

An adult, female *P. persimilis* was added to each prepared disk and allowed to oviposit for 24–30 h. Nearly all *P. persimilis* eggs were found in the spider-mite web. If more than four eggs were oviposited in the web, the excess eggs were removed with a paint brush. We then replaced two-spotted spider-mite eggs from the cleaned side so that each leaf half had approximately 50 spider-mite eggs. We placed four *P. persimilis* eggs evenly distributed on the side of the leaf disks that did not have spider-mite webbing. Each treatment disk was placed in vial and supported on water saturated cotton (Fig. 1B). A western flower thrips adult female, starved for 24 h at 23°C as described in the apple leaf experiment, was placed on each treatment disk.

The experiment consisted of two treatments, each replicated 20 times: disks with *P. persimilis* eggs in the webbing or disks with *P. persimilis* eggs on the web-free side. One half of each leaf disk had two-spotted spider-mite webbing and on the other half the webbing had been removed. This design was used to minimize the chance that the complete absence of webbing on the leaf disk would alter thrips foraging behavior. Phytoseiid eggs were on one half of each leaf disk only. After 24 h, the number of phytoseiid eggs fed upon and the status of the thrips was recorded and analyzed as described in the apple leaf experiment.

Results

Observations on thrips feeding behavior

Thrips were visible on the open (non-fiber) leaf disks as well as in and under the cotton fibers. The thrips embraced exposed eggs with their front legs and positioned their heads over the top of the egg. They used the leaf surface and their front legs to brace the egg as they thrust their mouth parts through the chorion. The thrips repeatedly prodded the egg, driving their heads deeper into the matrix. Feeding time varied depending on whether the egg was completely devoured and how long the thrips had been in the chamber feeding on the leaf surface or on other mite eggs.

To consume eggs in the cotton fibers, the thrips climbed into the mass of fibers and grasped the egg with their forelegs. Because the cotton fiber did not provide a supporting surface, they positioned their front legs underneath the egg in order to brace it, as they thrust their mouth parts through the chorion. The position of thrips in the fibers changed frequently as the thrips lost stability with their other legs and if the egg rolled out of the thrips' grasp.

Thrips predation on *T. pyri* eggs oviposited on apple leaves

Natural pubescence reduced thrips predation of *T. pyri* eggs oviposited on apple leaves (Table 1). Approximately twice as many *T. pyri* eggs oviposited on the pubescent cultivar survived predation compared to eggs oviposited on the glabrous variety ($z=-5.26$; $P<0.001$).

Thrips predation on *T. pyri* and *P. persimilis* eggs oviposited in fibers

The presence of cotton fibers reduced thrips predation on both *T. pyri* and *P. persimilis* eggs compared to thrips predation of phytoseiid eggs on leaf disks lacking fibers (Fig. 2). Survival of eggs oviposited in 10 and 20 fibers was significantly greater than survival of eggs placed on clean leaves ($z=2.51$; $P=0.01$ with 10 fibers; $z=4.55$; $P<0.01$ with 20 fibers; Fig. 2B, C, respectively). Survival of phytoseiid eggs oviposited in 5 fibers was not significantly different from eggs deposited on clean leaves ($z=0.93$; $P=0.35$, Fig. 2A). Survival of *T. pyri* eggs was greater than survival of *P. persimilis* eggs in all three experiments ($z=-2.15$, $P=0.03$ with 5 fibers; $z=-4.24$, $P<0.01$ with 10 fibers; $z=-3.16$, $P<0.01$ with 20 fibers). There was no interaction between phytoseiid species and the presence or absence of cotton fibers.

The type of substrate influenced the level of thrips feeding on eggs of both phytoseiid species. Survival of predatory mite eggs was higher on the bean disks compared to the plastic disks in experiments with 5 and 10 fibers ($z=-3.89$; $P<0.01$ with 5 fibers; $z=-5.52$; $P<0.01$ with 10 fibers). However, in the experiment with 20 fibers there was no difference in predation of eggs on bean and plastic disks ($z=-1.19$; $P=0.23$).

The overall level of thrips predation on disks without fibers varied among the three experiments. In the experiment with 0 and 5 fibers (Fig. 2A), thrips predation was consistently lower (more eggs surviving) on treatments without cotton fibers compared to the same treatment in the other two experiments (0 and 10 fibers and 0 and 20 fibers). This difference was particularly pronounced for thrips feeding on *T. pyri* eggs on the bean disk.

Table 1 Thrips predation on *Typhlodromus pyri* eggs oviposited on pubescent and glabrous apple leaves

Apple variety	Leaf surface type	Proportion of mite eggs surviving ^a	Lower and upper confidence limits ^b
Crittenden	Glabrous	0.38	(0.24, 0.53)
Erwin Bauer	Pubescent	0.88	(0.79, 0.93)

^a Phytoseiid eggs not fed upon by thrips

^b Confidence intervals are 95% prediction intervals that use the estimated standard error from the logistic model

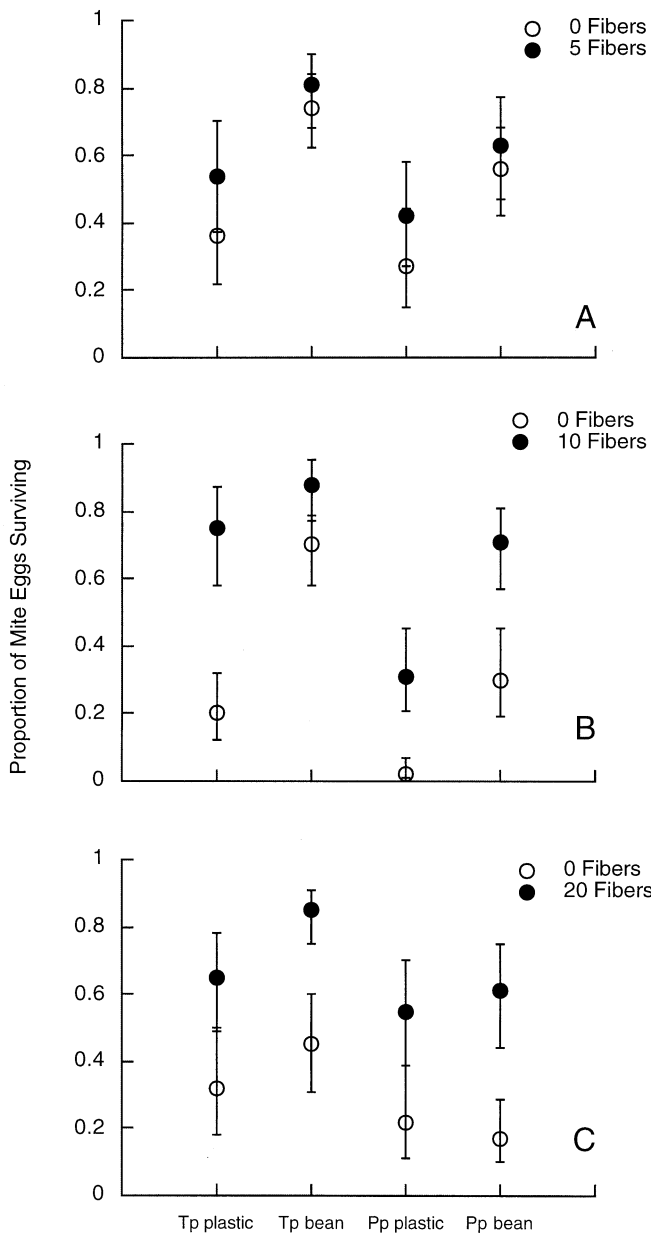


Fig. 2A–C Thrips feeding on *Typhlodromus pyri* (*Tp*) and *Phytoseiulus persimilis* (*Pp*) eggs on plastic and bean leaf disks. Proportion of phytoseiid eggs surviving with **A** 0 and 5 cotton fibers, **B** 0 and 10 cotton fibers, and **C** 0 and 20 cotton fibers. Confidence intervals are 95% prediction intervals that use the estimated standard error for the logistic model

Thrips predation on *T. pyri* eggs oviposited in different densities of cotton fibers

With the three density experiments (Fig. 2) we did not specifically test whether increasing the number of cotton fibers decreased thrips predation on phytoseiid eggs. This prompted the experiment where four levels of fibers were tested simultaneously using only *T. pyri* on bean disks. Thrips fed voraciously on *T. pyri* eggs in the no fiber treatment as seen with the low proportion (<20%) of

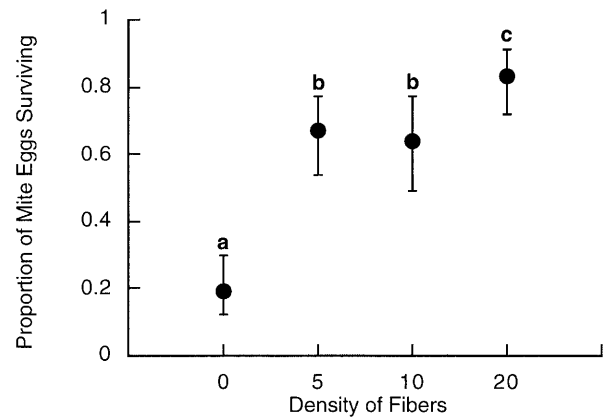


Fig. 3 Thrips predation on *T. pyri* eggs with 0, 5, 10, and 20 cotton fibers. Confidence intervals are 95% prediction intervals that use the estimated standard error for the logistic model. Proportions annotated by different letters differ significantly ($P \leq 0.05$)

Table 2 Thrips predation on *Phytoseiulus persimilis* eggs oviposited in two-spot spider-mite webbing or exposed on a bean disk

Surface type	Proportion mite eggs surviving ^a	Lower and upper confidence limits ^b
No web	0.42	(0.27, 0.58)
Web	0.81	(0.67, 0.89)

^a Phytoseiid eggs not fed upon by thrips

^b Confidence intervals are 95% prediction intervals that use the estimated standard error from the logistic model

eggs surviving (Fig. 3). At all densities, eggs oviposited in the cotton fibers had increased survival compared to eggs on the smooth bean disk. Based on linear contrasts, egg survival with fiber densities of 5 and 10 were equivalent; however survival was greater with a fiber density of 20 compared to a density of 10 ($z = -2.2$; $P < 0.03$). This result may appear incongruous with the prediction intervals shown in Fig. 3 which overlap for fiber densities of 10 and 20. This is because the prediction intervals are based on the information for each fiber density whereas when the contrasts are made, information for two levels of fiber density are used. Overall, the effect of increasing fiber density from 5 to 20 on phytoseiid egg survival was slight.

Thrips predation of *P. persimilis* eggs oviposited in two-spotted spider-mite web

Two-spotted spider-mite webbing acted much like the cotton fibers in that the webbing decreased thrips predation of *P. persimilis* eggs (Table 2). Approximately twice as many *P. persimilis* eggs oviposited in the webbing survived predation compared to eggs oviposited on the bean leaf disk ($z = 3.52$; $P < 0.01$).

Discussion

The topography of the leaf surface strongly influences thrips predation of phytoseiid eggs. The presence of leaf structures, including natural pubescence on apple leaves, spider-mite webbing, and cotton fibers, resulted in lower predation by thrips compared to simple surfaces without these structures. When pubescence increased the complexity of the leaf surface, western flower thrips fed upon fewer *T. pyri* eggs compared to when the eggs were oviposited on a glabrous apple cultivar. Adding "hairiness" to the leaf by placing cotton fibers on a bean disk also reduced thrips predation on both *T. pyri* and *P. persimilis* eggs. Similarly, when the leaf surface was altered by the presence of spider-mite webbing, thrips predation was lower on *P. persimilis* eggs oviposited in webbing compared to bean leaf areas where the webbing had been removed. Because similar results were obtained with all of these manipulations, these experiments indicate that the reduction in egg predation is due to the structures created by the trichomes or web rather than other aspects of apple cultivar or spider-mite webbing. Few other studies have demonstrated that leaf morphology or arthropod-mediated changes to leaf topography affect intraguild predation (but see Lucas and Brodeur 1999; A.P. Norton, G. English-Loeb, and E. Belden, unpublished work).

Through the addition of cotton fibers to glabrous bean leaves, we were able to test the effects of increasing "hairiness" on thrips predation. With the densities of cotton fibers selected, phytoseiid egg survival was not greatly increased as the density of fibers increased. Further work is required to determine whether protection from intraguild predation increases with increasing natural pubescence or whether the effect is decidedly nonlinear with most of the effect attributable to modest levels of pubescence.

The level of thrips predation varied considerably in our experiments and this variability caused the results from two experiments that used five fibers to appear inconsistent. In the experiment with 0 and 5 fibers, a low level of thrips predation may explain why there was no difference in survival of eggs deposited in the fibers and on the bean leaf. When thrips readily preyed upon *T. pyri* eggs, as in the experiment where different densities of fibers were compared simultaneously, the presence of 5 fibers significantly reduced predation. In this simultaneous experiment, increasing the density of fibers from 5 to 20 only slightly reduced thrips predation of *T. pyri* eggs, showing that the presence of at least some fibers was more important than the actual density of fibers.

The substrate that the fibers were placed on (plastic or bean leaf) strongly influenced thrips predation. Thrips fed on the bean disks. As a result, thrips predation of phytoseiid eggs was generally lower on the bean disks compared to the plastic disks.

How might pubescence and webbing reduce intraguild predation? The decrease in thrips predation could be due to the greater complexity created by entangled

trichomes or web. This added complexity may reduce the thrips ability to locate the mite eggs amidst the intertwined filaments and thereby reduce their encounters with prey. Studies with parasitoids, *P. persimilis* and other arthropod predators have shown that a greater pubescence decreased predation on herbivores (Rabb and Bradley 1968; Kauffman and Kennedy 1989; van Lenteren and de Ponti 1990; Kleijn et al. 1997; Krips et al. 1999). The authors showed that pubescence affected the walking behavior of the predators and resulted in a reduced rate of encounter with prey.

Another classic example of structures used as a means to avoid predation can be found with lacewing (Chrysopidae) oviposition. Some lacewings place their eggs at the end of a long slender pedicel, up off the surface of the leaf, possibly to protect their eggs from predation and cannibalism (Borror et al. 1989). Some species of tydeid mites (Knop and Hoy 1983) and *T. pyri* demonstrate a similar behavior by ovipositing on the tips of trichomes. Our study suggests that phytoseiid mites may exploit the trichomes and web to limit encounters between foraging thrips or other predators and their eggs.

Arthropods living on the leaf surface can also produce structures that influence intraguild predation. Webbing of two-spotted spider mites can entangle predators not adapted morphologically to walk through the webbing (Sabelis and Bakker 1992; McMurtry and Croft 1997). *Tetranychus* spider mites are assumed to produce web as a protection against their predators (Gerson 1985). By hindering arthropods not adapted to search this area, the web may provide a refuge for spider mites and their progeny. Predatory mites specialized to feed on web-producing spider mites, such as *P. persimilis*, have tarsi and long dorsal bristles suggested to help the predator maneuver through spider-mite web and therefore increase access to spider-mite prey (Sabelis and Bakker 1992). Our data suggest that *P. persimilis* may exploit the spider-mite webbing as a refuge to protect their own eggs from predation.

Reduced rate of encounter has been posited as one mechanism whereby thrips predation on phytoseiid eggs is reduced when eggs are deposited in a complex leaf topography. Another mechanism may be that thrips have a more difficult time feeding on mite eggs located in the fibers, trichomes, and webbing than those on the leaf surface. We observed that feeding in the fibers appeared more awkward than feeding on a planar surface. To feed, thrips punch a hole with specialized mouth parts, then suck the plant or prey contents (Lewis 1997). In the fibers, the thrips had more difficulty grasping and bracing the egg as they punctured the egg chorion than when they used the leaf surface to support the force of their punch and subsequent probe.

Thrips preyed upon a greater proportion of *P. persimilis* eggs compared to *T. pyri* eggs. *Phytoseiulus persimilis* eggs may be more apparent to thrips because of their larger size (Sabelis 1985) and bright orange coloring. Adult thrips are known to use color, shape, and size to locate their hosts (Terry 1997). Another possible reason

may be that *P. persimilis* eggs do not have as durable a chorion as *T. pyri* eggs. A third possible reason may be traced to frequent, natural interactions between western flower thrips and *P. persimilis*. Western flower thrips are often present on plants with *Tetranychus* spider mites, the prey *P. persimilis* specializes on (Trichilo and Leigh 1986; Wilson et al. 1991; Pallini et al. 1998). In our experiments, western flower thrips were taken from the glasshouse and may have had an association with *P. persimilis*. As a result, the thrips may have better recognized *P. persimilis* eggs as a food source.

Prey often exhibit escape and avoidance behaviors in response to intraguild predators (Polis and McCormick 1987; Polis et al. 1989; Wissinger and McGrady 1993). In addition, maternal behavior may decrease intraguild predation on their progeny (Polis et al. 1989). In laboratory choice tests, phytoseiids were found to consistently select pubescent leaves on which to oviposit eggs compared to glabrous varieties (Overmeer and van Zon 1984; A. Roda, J.P. Nyrop, Marcel Dicke, and G. English-Loeb, unpublished work). We have also found that *P. persimilis* can be lured away from ovipositing in two-spotted spider-mite web when a high density of cotton fibers is also present (A. Roda, J.P. Nyrop, Marcel Dicke, and G. English-Loeb, unpublished work). This study suggests these behaviors may, in part, be an attempt to protect eggs from predation.

Reduction in intraguild predation may be one factor explaining higher phytoseiid predator populations on plant varieties with pubescence or domatia. The greater number of predatory mites may also result from the ability of trichomes to mitigate the negative effects of the low humidity on egg development and eclosion (Grostal and O'Dowd 1994) or trap alternative food such as pollen important in sustaining phytoseiid mite populations in the absence of prey (Duso 1992; McMurtry and Croft 1997).

Predatory mites can effectively keep spider-mite populations below damaging levels and thereby decrease the need for pesticides to control pest mites (McMurtry and Croft 1997). Selecting cultivars with pubescence or domatia may offer a simple means to maintain higher populations of predatory mites in commercial production systems once any potential benefits to herbivores are excluded. Also, understanding the role of leaf structure in regulating intraguild predation may aid in devising variety-specific management strategies to establish and conserve predatory mites, especially in systems where the cultivars vary greatly in the level of pubescence and presence of domatia.

We conclude that structures found on the leaf surface affect intraguild predation in this system. In our laboratory experiments, trichomes and spider-mite webbing both provided protection for phytoseiid eggs against predation by western flower thrips. Finding similar results with two predatory mite species with very different life histories suggests that the role of the leaf structures in mediating intraguild predation of phytoseiids may be widespread. Further research is needed to explore wheth-

er leaf structures influence intraguild predation under larger and more complex field conditions and if these interactions affect the structure of the predator community.

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