Abstract  Phytoseiid mites, both in agricultural and natural systems, can play an important role in the regulation of herbivorous mites. Host plant traits, such as leaf pubescence, may influence the dynamics between predator and prey. In this study, we examined the influence of leaf surface characteristics (leaf pubescence and two-spotted spider mite webbing) on the behavior of two species of predatory mites, the generalist *Typhlodromus pyri* and the spider mite specialist *Phytoseiulus persimilis*. In laboratory trials, *T. pyri* females consistently spent more time and deposited more eggs on leaf discs from trichome-rich apple varieties compared to relatively trichome-poor varieties. A similar result was found when the choice involved trichome-rich and trichome-poor apple varieties planted into the same pot where leaves were allowed to touch so that the mites could freely move from leaf to leaf. To further explore the effect of structure created by pubescence and to remove possible confounding effects of chemical cues, we added cotton fibers to trichome-free bean leaves. *T. pyri* females consistently spent more time and deposited more eggs on the side of a glabrous bean leaf with artificial cotton fibers versus the side without added fibers. When given a choice between two densities of cotton fibers, *T. pyri* females consistently selected the highest density of available fibers in which to reside and oviposit. *T. pyri* also preferred cotton fiber configurations in which it could move underneath and access the plant surface. The artificial pubescent leaf was also used to test the effect of leaf hairs and two-spotted spider mite webbing on the behavior of *P. persimilis*. *P. persimilis* females preferred residing and ovipositing on surfaces with cotton fibers or two-spotted spider mite webbing than on bean leaf areas without these structures. When presented a choice between cotton fibers or webbing, the behavior of *P. persimilis* females depended on the cotton fiber density. In a mixed-variety apple orchard, we investigated the relationship between leaf pubescence and phytoseiid density under field conditions. We found a highly significant, positive relationship between density of trichomes on leaves and abundance of *T. pyri*, whereas spider mite prey numbers were uniformly low and unrelated to trichome density. These field results suggest that the behavioral responses found in our laboratory experiments have population consequences.

Keywords  Phytoseiidae · Ovipositional preference · Tritrophic interactions

Introduction  Host plant characteristics can influence the outcome of interactions between arthropod herbivores and their enemies in several ways (Price et al. 1980; Kareiva and Sahakian 1990; Dicke 1999; Olff et al. 1999; Sabelis et al. 1999). Plants may enhance predation or parasitism by making herbivores more vulnerable to natural enemies (Strong et al. 1984), by offering an ameliorated habitat and nutritional “rewards” (Huxley 1986; Juniper and Southwood 1986; Willmer 1986), or by signaling the enemy of a herbivore’s presence (Vet and Dicke 1992). Plants can also reduce predator survival and fitness (Bottrell et al. 1998). For example, predators may ingest harmful plant toxins by feeding on prey or the plant itself (Rothschild et al. 1973; Rice and Wilde 1989). Predators may also become trapped in glandular and non-glandular trichomes (Belcher and Thurston 1982; van Haren et al. 1987). When plants enhance the survival and...
foraging ability of a predator, plant fitness can increase (Janzen 1966; Rehr et al. 1973; Agrawal and Karban 1997).

Because predators often encounter herbivores on plants, the topography of plant surfaces may influence herbivore and natural enemy interactions. Leaf surface characteristics such as pubescence, domatia (tufts of hairs, pits or pockets on the leaf surface), surface waxes, and arthropod-produced structures (e.g., spider mite webbing) have been shown to affect predation and predator survival and fitness. For example, pubescence and webbing can enhance predator survival by decreasing the likelihood that predators will be dislodged from the leaf surface (Juniper and Southwood 1986), by moderating the micro-environment, especially humidity (Grostal and O’Dowd 1994), and by providing protection from predation (Lucas and Brodeur 1999; Norton et al. 2000; Roda et al. 2000). In contrast, highly pubescent leaves, waxy blooms found on species of Brassica, and spider mite webbing have been shown to impede a predator’s ability to search the leaf surface, thereby inhibiting predation of herbivores (Rabb and Bradley 1968; Shah 1982; Kauffman and Kennedy 1989; van Lenteren and de Ponti 1990; Eigenbrode et al. 1995; Kleijn et al. 1997; Krips et al. 1999). The interplay of the positive and negative effects of leaf topography on predator survival and fitness will likely impact herbivore population dynamics. Exploring how leaf topography affects predator behavior offers insight into the importance and possible ways that plant surface structures influence predator abundance and fitness on a plant and, ultimately, their interactions with arthropod herbivores.

In the study reported here, we conducted experiments to determine how a labyrinth environment created by physical structures on the leaf surface affected the behavior of phytoseiid mites. Phytoseiid mites are an economically important group of arthropod predators commonly used in the biological control of spider mites. Their abundance and ability to control pest populations has been found to vary on different plant varieties (Downing and Moilliet 1967; Duso 1992; Duso and Vettorazzo 1999; Krips et al. 1999). This variation may result from different types and prevalence of plant surface structures (Downing and Moilliet 1967; Walter 1996; Duso and Vettorazzo 1999). Several authors have proposed that plant morphological traits such as non-glandular trichomes, large veins, rough fruit spurs, and bark may affect survival and foraging of phytoseiids (Downing and Moilliet 1967; Walter 1996; Duso and Vettorazzo 1999). Smooth, simple surfaces that lack physical complexity may expose phytoseiids to unfavorable abiotic conditions and to predators, whereas more structurally complex surfaces may protect phytoseiids from these dangers (e.g., Norton et al. 2000; Roda et al. 2000). However, surface structures can also inhibit phytoseiid movement and thereby increase searching time and reduce encounters with prey (Krips et al. 1999). Studying how plant surface characteristics affect phytoseiid behavior may reveal which processes, if any, influence their abundance on a plant.

Laboratory studies support the hypothesis that leaf pubescence influences phytoseiid behavior. In experiments comparing different plant species, the predatory mite Amblyseius potentillae (Garman) was found to reside more often on leaves from plant species with relatively high numbers of leaf trichomes compared to other plant species with smoother leaves (Overmeer and van Zon 1984). Although these studies suggest a preference for leaves with trichomes, the results are confounded because chemical and/or other factors inherent to different plant species were not separated from leaf pubescence. Volatiles (allelochemicals) produced by plants may have acted to attract or repel predators. Furthermore, the preference for leaf hairs was not absolute. In comparisons between species with highly pubescent leaf surfaces and those with smoother surfaces, A. potentillae selected the smoother species. In another comparison, a species with domatia was not selected over a glabrous species. Further study is needed to clarify how leaf pubescence influences phytoseiid behavior.

Phytoseiids specializing on tetranychid spider mites may have a preference for the physical structure created by spider mite webbing much like other phytoseiids species have for trichomes (Schmidt 1976). These specialist predators often deposit their eggs in their prey’s web, possibly to enhance the foraging profitability of emerging larvae (Gerson 1985). However, the predators may select web because the physical structure has indirect benefits such as creating a more favorable microclimate (Gerson 1985) or decreasing predation (Cloutier and Johnson 1993; Roda et al. 2000). Whether predatory mites prefer the physical structure created by spider mite web still needs to be determined.

We investigated whether two species of phytoseiid mites, Typhlodromus pyri and Phytoseiulus persimilis, had higher residence times and oviposited more on leaf surfaces with structural complexity compared to smooth leaf surfaces. These predatory mites differ dramatically in their feeding habits and life history. P. 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 that can feed on tetranychid mites, pollen, and fungal spores, and persists in a habitat largely independent 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). Both species are important biological control agents in agricultural systems.

To study the response of these phytoseiids to structural complexity, we separated the effects of leaf topography from other possible influences by comparing behavior on sets of apple leaves, one of which had abundant trichomes while the other had greatly reduced trichome numbers. We also constructed an artificially pubescent leaf to further disassociate chemical and other possible factors from the effects of physical structure. By using artificial pubescence, we were able to manipulate fiber density and arrangement and assess the influence on