BEHAVIORAL ECOLOGY

Predator avoidance in phytophagous mites: response to present danger depends on alternative host quality

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Abstract We studied whether volatiles released by putative host plants affect the antipredator response of an herbivorous mite, *Tetranychus urticae*, when the patch was invaded by *Phytoseiulus persimilis*. *Tetranychus urticae* laid a lower number of eggs on tomato leaves than on lima bean leaves, suggesting that lima bean is a preferred host food source for *T. urticae*. In addition, *T. urticae* preferred lima bean plant volatiles to tomato plant volatiles in a Y-tube olfactometer test. To investigate the antipredator response of *T. urticae*, we examined the migration of *T. urticae* from a lima bean leaf disc to a neighbouring leaf disc (either a tomato or lima bean leaf disc) when ten predators were introduced into the original lima bean disc. A Parafilm bridge allowed for migration between the leaf discs. No migrations occurred between leaf discs when there were no predators introduced to the original leaf disc. However, when predators were introduced migrations did occur. When the neighbouring leaf disc was upwind of the original disc, the migration rate of the mite from original lima bean leaf disc to a neighbouring tomato leaf disc was significantly lower than that to a neighbouring lima bean leaf disc. By contrast, when the neighbouring leaf disc was downwind of the original leaf disc, there was no difference in the migration rates between lima bean leaf discs and tomato leaf discs. The number of *T. urticae* killed by *P. persimilis* for each treatment was not different, and this clearly shows that the danger was the same in all treatments regardless of the decision made by *T. urticae*. From these results, we conclude that *T. urticae* change their antipredator response by evaluating the difference in host plant volatiles in the patch they inhabit.

Keywords Antipredator response · *Phytoseiulus persimilis* · Plant volatiles · Predator–prey interaction · *Tetranychus urticae*

Communicated by Stefan Scheu.

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Introduction

In predator–prey interactions, prey alter their morphology (Tollrian 1995; Tollrian and Harvell 1999; Relyea 2003; Kishida and Nishimura 2004), and behaviour (Lima and Dill 1990; Lima 1998, Losey and Denno 1998a, b; Magalhães et al. 2002) to escape from predators. Although these responses would reduce predation risk (Lima 1998; Tollrian and Harvell 1999), several studies have reported that such responses are costly (Abrahams and Dill 1989; Grand and Dill 1997; Matsumoto et al. 2002) and thus it is important for prey to assess their predation risk to minimize the cost of antipredator responses. For example, herbivorous arthropod preys stop feeding and leave a host-plant some time after perceiving the presence of predators. However, several factors have been shown to affect the timing of such a decision (Lima 1998). One exam-

ple is starvation in pea aphids, when the energetic internal stress (i.e., starvation) of the pea aphid *Acyrthosiphon pisum* increases, the predominant antipredator response changes from walking away and dropping to kicking at the parasitoids (Villagra et al. 2002).

Other important aspects of the antipredator response are the relative quality of the host-plant (or patch) used by herbivores and the proximity of available host-plants when predators invade. Specifically, the detectability and/or availability of new host-plants would affect antipredator response of herbivorous arthropods, as they do not always find suitable host-plants near their current food source. Many herbivore species use intact plant volatiles as a cue for host-plant selection (Visser 1986; Bernays and Chapman 1994; Dicke 2000). Thus, plant volatiles are likely to be an important factor for herbivorous arthropods when predators invade and they leave to search for new host-plants. However, it is not known if herbivores change their antipredator responses when plant volatiles released from neighbouring plants indicate that they are less suitable hosts than the host plants where they are feeding. Therefore, the objective of this study is to determine if plant volatiles are critical factors in herbivorous arthropod antipredator responses.

We studied the effect of plant volatiles on the patch-leaving decision of a herbivore when the patch was invaded by its predators. Our predator–prey system consisted of the predatory mite, *Phytoseiulus persimilis*, and herbivorous mite, *Tetranychus urticae*. *Tetranychus urticae* is a polyphagous herbivore, with over 900 host-plant species recorded (Bolland et al. 1998). It has been reported that *T. urticae* avoid plant volatiles emitted by conspecific-infested lima bean plants (Dicke 1986; Horiuchi et al. 2003) and plants with predators (Pallini et al. 1999). However, it is unclear whether they distinguish intact plant volatiles among plant species. To test the effect of intact plant volatiles on the patch-leaving decision by *T. urticae* to escape from *P. persimilis*, we used lima bean plants and tomato plants. Tomato is reported to be an unsuitable host for *T. urticae* due to the presence of toxic phytochemicals in their leaves and glandular trichomes (Aina et al. 1972; Chatzivasileiadis and Sabelis 1997; Chatzivasileiadis et al. 1999). In this study, we address whether or not *T. urticae* change its patch-leaving behaviour to escape from *P. persimilis* (antipredator response) according to volatiles emitted from suitable and unsuitable host plants next to the patch. We also discuss the costs and benefits of the antipredator response of *T. urticae* to *P. persimilis*.

Materials and methods

Plants and mites

Lima bean plants (*Phaseolus lunatus* cv. Sieva) and tomato plants (*Lycopersicon esculentum* cv. Hausu-Momotaro) were grown in soil in a greenhouse at 25 ± 2°C, 60–70% relative humidity (RH) and a photoperiod of 16L:8D. For the experiments, we used lima bean plants and tomato plants at 10–15 and 15–20 days after germination.

Herbivorous mites (*T. urticae*) were obtained from the Laboratory of Ecological Information, Graduate School of Agriculture, Kyoto University, in 2002, and reared on lima bean plants in an incubator (25 ± 2°C, 60–70% RH, 16L:8D).

Predatory mites (*Phytoseiulus persimilis*) were purchased from Koppert (Berkel and Rodenrijs, The Netherlands). They were reared on detached lima bean leaves, heavily infested with *T. urticae* in an incubator (25 ± 2°C, 60–70% RH, 16L:8D). Fresh *T. urticae*-infested leaves were added every other day.

Oviposition of *T. urticae* on a leaf disc

Using a clean razor blade, we made a 1×1 cm leaf disc from a primary leaf of a lima bean plant and from the fourth leaf from the ground of a tomato plant (*n*=50 for each plant). At that time, the tomato plants had 5–6 leaves. These discs were individually put on water-saturated cotton in a Petri dish (9 cm diameter, 1.4 cm height). For each replicate, an adult female *T. urticae* that had been randomly selected from the rearing colony was placed on a disc. The number of eggs laid by each mite was counted 3 days after the initiation of the experiment. These experiments were conducted in a climate-controlled room (25 ± 2°C, 60–70% RH, 16L:8D). The data were analyzed using a *t*-test.

Response of *T. urticae* to plant odour

A Y-tube olfactometer (see Takabayashi and Dicke 1992 for setup details) was used to test whether *T. urticae* distinguishes between volatiles of intact lima bean and intact tomato plants. We placed a Y-shaped iron wire at the center of the olfactometer. Air that had been cleaned through an activated charcoal filter was pumped (2.5 l/min) to an odour source bottle that was connected to the arm of the olfactometer. For odour sources, we used plants that had been cut with a razor blade just above soil level. The cut area was covered with moist cotton wool. Two plants were

used for an odour source. There was no significant difference in the weight of the lima bean and tomato plants that formed the odour sources (lima bean 7.782 ±1.343 g; tomato 7.579±1.297 g; P=0.8273, Mann–Whitney U-test).

For each assay, a single, randomly selected adult female *T. urticae* was positioned on the start of the iron wire. When the mite reached the end of one arm of the olfactometer, its choice was recorded. The maximum duration of each observation was 5 min. After every five bioassays, the odour sources on each arm were exchanged with that of the other arm to adjust for potential asymmetries in the experimental arena. As *T. urticae* left silken thread when they moved on the iron wire, the iron wire was carefully wiped with dry cotton wool after each bioassay. Individual mites were used only once and a total of 20 spider mites were used in 1 day. Bioassays were replicated 3 experimental days using different odour sources to avoid pseudoreplication. The tests were performed in a climate-controlled room (25±2°C, 60–70% RH, 16L:8D).

Data were analyzed with a binomial test to determine whether the distribution of mites over the two odour sources was significantly different from a 1:1 distribution.

Antipredator response of *T. urticae*

We made a 3.5×2.5 cm leaf disc from a primary leaf of a lima bean plant (hereafter called the original leaf disc), and put it on water-saturated cotton wool in a Petri dish (15 cm diameter, 1 cm height). Then, a 3.5×2.0 cm leaf disc (hereafter called the neighbouring leaf disc), made from either a primary leaf of a lima bean plant or a leaflet (fourth from the ground) of a tomato plant, was put in the same Petri dish, 5 cm from the original disc. Thirty, randomly selected, adult female *T. urticae* were placed on the original disc and allowed to lay eggs for 24 h. We then introduced randomly selected female *P. persimili* onto the original disc (0, 1, or 10 *P. persimilis* per disc). The neighbouring leaf disc was for *T. urticae* to escape from the predators in the original leaf disc (antipredator response). For the control experiments, *P. persimilis* were not introduced. We connected the two leaf discs with a Parafilm bridge (5 cm length, 0.5 cm width), and placed the Petri dishes holding the two discs in a wind tunnel (air flow 10 cm/s, size 40×40×80 cm). We placed three Petri dishes, each of which held a pair of leaf discs with different *P. persimilis* densities (0, 1, 10), as a group in the center of the wind tunnel. The neighbouring leaf discs were positioned upwind of the original leaf disc to expose *T. urticae* to

the plant volatiles from the neighbouring leaf disc. The number of *T. urticae* on each neighbouring leaf disc, and the number of *T. urticae* killed by *P. persimilis* on each original leaf disc, were counted 24 h after the introduction of the Petri dishes into the wind tunnel. Care was taken not to expose *T. urticae* to plant volatiles from different Petri dishes. We arranged three dishes in a triangle in the wind tunnel. Under this condition, we confirmed that contamination of volatiles from one leaf disks set to another did not occur by checking the flow of smoke introduced into the wind tunnel. The position of each Petri dish in the wind tunnel was changed for every experiment to adjust for potential asymmetry in the experimental arena. Experiments were conducted in a climate-controlled room (25±2°C, 60–70% RH, 16L:8D).

We then tested whether the migration of *T. urticae* was also triggered by an increase in *T. urticae* density, and how *T. urticae* migrated in response to predators when they were not exposed to plant volatiles from the neighbouring leaf disc. To test the first possibility, 30 additional *T. urticae* adult females were placed on each original leaf disc 24 h after the initial 30 *T. urticae* adults were introduced onto the disc. As for the above experiments, a neighbouring leaf disc was connected to the original with a Parafilm bridge. The Petri dishes were placed in the wind tunnel, with the original leaf disc downwind to the neighbouring leaf disc. To test the second possibility, we used the same experimental design as for the initial experiment. In this experiment, however, the neighbouring leaf disc was positioned downwind in the wind tunnel so that *T. urticae* were not exposed to plant volatiles. The numbers of *T. urticae* adults that migrated to the neighbouring leaf disc were counted 24 h after placing the Petri dishes in the wind tunnel.

We calculated the proportion of migrated mites [i.e., the number of *T. urticae* that migrated to the neighbouring leaf disc/the number of *T. urticae* introduced into the original leaf disc (30)] for each replicate. We repeated the above experiments 18 times per treatment. The proportions of migrated *T. urticae* data were normalized by arcsine square root transformations and compared using a Tukey–Kramer test followed by two-way ANOVA (the effects of predator density and plant species on the migration rate). The numbers of *T. urticae* killed by *P. persimilis* were compared using a Tukey–Kramer test followed by two-way ANOVA (the effects of predator density and plant species on the mortality). The control data were excluded from the statistical analyses, because we focused on the number of spider mites that were preyed upon by the predatory mites.

Results

Performance and olfactory response of *T. urticae* to different plant species

Tetranychus urticae laid on average of about five times more eggs on lima bean leaf discs than on tomato leaf discs (mean±SE number of *T. urticae* eggs on lima bean leaf discs: 30.28±1.38; on tomato leaf discs: 6.50±0.48; *P*<0.0001, *t*-test). When *T. urticae* was offered a choice between lima bean plants and tomato plants in a Y-tube olfactometer, it preferred lima bean plants to tomato plants (number of *T. urticae* attracted to lima bean plant volatiles=40 and to tomato plant volatiles=20; *P*=0.0135, binomial test).

Antipredator response of *T. urticae*

When the neighbouring leaf discs were positioned either upwind or downwind of *T. urticae* in the wind tunnel, the proportions of *T. urticae* adults that migrated to the neighbouring leaf disc (lima bean and tomato) increased with the density of *P. persimilis* that invaded the original leaf disc (*P*<0.0001, two-way ANOVA; Table 1a, b; Fig. 1a, b). When ten *P. persimilis* were introduced on the original leaf disc, the proportions of *T. urticae* adults that migrated to lima bean leaf discs were significantly higher than those that migrated to tomato leaf discs (*P*=0.0033, two-way ANOVA; Table 1a), (*P*<0.05, Tukey–Kramer test; Fig. 1a). There were no significant differences in the proportions of *T. urticae* adults that migrated to the neighbouring leaf disc (lima bean or tomato) between the introduction of one and no *P. persimilis* on the original leaf disc (*P*>0.05, Tukey–Kramer test; Fig. 1a). The interaction between the density of *P. persimilis* and the plant species of the neighbouring leaf disc was significant in the migration from downwind to upwind (*P*=0.0153, two-way ANOVA; Table 1a), and marginally significant in the migration from upwind to downwind (*P*=0.0521, two-way ANOVA, Table 1b).

When *T. urticae* migrated to tomato leaf discs that were upwind of them in the wind tunnel, there was no
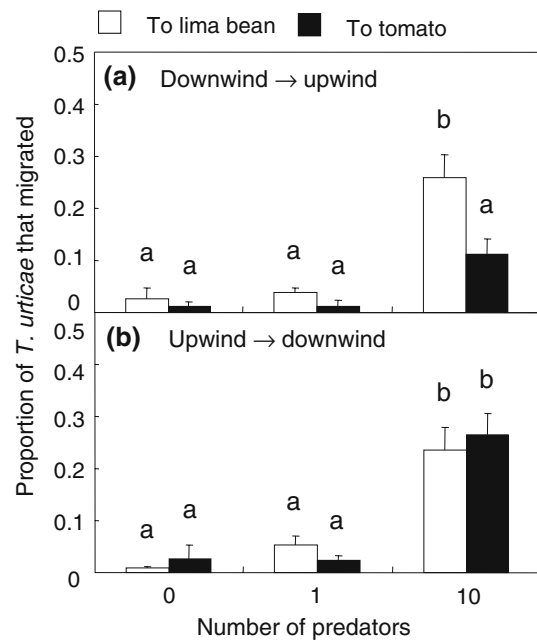

Fig. 1 The proportions of *T. urticae* female adults that migrated from a colony patch to a lima bean leaf disc and a tomato leaf disc (mean±SE). **a** Migration from downwind to upwind. **b** Migration from upwind to downwind. The *letters* above each *bar* indicate significant differences among treatments by Tukey–Kramer test (*P*<0.05)

significant difference in the proportion of migrants with the density of introduced *P. persimilis* (*P*>0.05, Tukey–Kramer test; Fig. 1a), while when *T. urticae* migrated to upwind lima bean leaf discs, there was significant difference (*P*<0.05, Tukey–Kramer test; Fig. 1a). In contrast, when the neighbouring leaf discs were positioned downwind of *T. urticae* in the wind tunnel, we found no significant difference in the proportions of *T. urticae* adults that migrated to the lima bean and tomato leaf discs (*P*=0.0735, two-way ANOVA; Table 1b; Fig. 1b).

To exclude the possibility that the density of the total numbers of *T. urticae* and *P. persimilis* affected the migration rates of *T. urticae*, we introduced 30 additional *T. urticae* onto the original discs to which 30

Table 1 Two-way ANOVA of the proportions of *T. urticae* that migrated from a colony patch to a lima bean leaf disc and a tomato leaf disc. *a* Migration from downwind to upwind. *b* Migration from upwind to downwind

Sources	SS	*df*	MS	*F*	*P*
(a) Proportions of *T. urticae* migrated from downwind to upwind					
Predator	0.678	2	0.339	27.857	< 0.0001
Plant	0.110	1	0.110	9.052	0.0033
Predator × plant	0.106	2	0.053	4.357	0.0153
Error	1.241	102	0.012		
(b) Proportions of *T. urticae* migrated from upwind to downwind					
Predator	0.571	2	0.285	18.130	< 0.0001
Plant	0.051	1	0.051	3.271	0.0735
Predator × plant	0.096	2	0.048	3.041	0.0521
Error	1.605	102	0.016		

T. urticae had previously been introduced. The migration rate was very low, and did not differ significantly between the introduction of 30 and 60 *T. urticae* adults (migration rate for 30 *T. urticae* on the original leaf disc: 0.0278±0.0195, for 60 *T. urticae*: 0.0241±0.0134; *P*=0.870, *t*-test).

When one *P. persimilis* was introduced onto the original leaf disc, few *T. urticae* were killed by *P. persimilis* compared to with no *P. persimilis*. In contrast, the number of killed *T. urticae* increased when 10 *P. persimilis* were introduced onto the original leaf disc (*P*<0.05, Tukey–Kramer test; Fig. 2). The number of killed *T. urticae* increased with increasing density of introduced *P. persimilis* (*P*<0.0001, two-way ANOVA; Table 2; Fig. 2). We found no significant difference in the number of killed *T. urticae* between the two plant species of the neighbouring leaf disc (*P*=0.1458, two-way ANOVA; Table 2; Fig. 2), and the interaction between the density of *P. persimilis* and the plant species of the neighbouring leaf disc was not significant (*P*=0.2495, two-way ANOVA; Table 2).

Discussion

The proportion of *T. urticae* that migrated to the neighbouring leaf disc increased when ten *P. persimilis* were
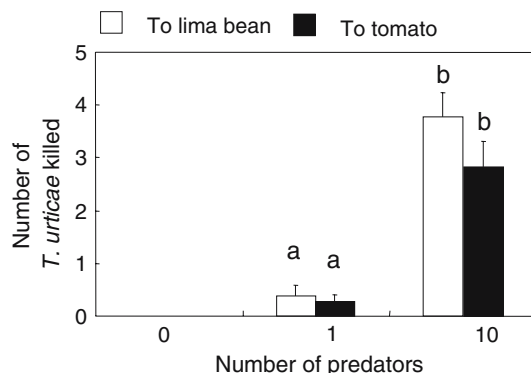

Fig. 2 The number of *T. urticae* female adults killed by *P. persimilis* in a colony patch when *T. urticae* migrated to a lima bean leaf disc and a tomato leaf disc. The *letters* above each *bar* indicate significant differences among treatments by Tukey–Kramer test (*P*<0.05)

Table 2 Two-way ANOVA of the number of *T. urticae* killed by *P. persimilis* in a colony patch when *T. urticae* migrate to a lima bean leaf disc and a tomato leaf disc

Sources	SS	df	MS	F	P
Predator	159.014	1	159.014	68.654	< 0.0001
Plant	5.014	1	5.014	2.165	0.1458
Predator × plant	3.125	1	3.125	1.349	0.2495
Error	157.500	68	2.316		

placed onto each original leaf disc (Fig. 1a, b). This increase could be explained simply by the increased density of arthropods (both spider mites and predatory mites) per colony patch. However, this explanation is unlikely because *T. urticae* did not migrate to the neighbouring leaf disc when 30 additional *T. urticae* were introduced onto the original leaf disc that had already been harbouring 30 *T. urticae*. Our data indicate that *T. urticae* migrated from the original to the neighbouring leaf disc as an antipredator response against 10 *P. persimilis* (Fig. 1a, b; Table 1a, b). The predation risk in a patch harbouring 10 *P. persimilis* was significantly higher than that in a patch harbouring one *P. persimilis* (Table 2; Fig. 2). In this study, we did not investigate the cues that triggered the migration of *T. urticae* in response to *P. persimilis*. However, it is reported that *T. urticae* avoids *P. persimilis*-exposed leaf discs, as well as pierced eggs (Grostal and Dicke 1999). It may be that *T. urticae* decides when to leave a predator-invaded patch using such cues.

The migration of *T. urticae* to a tomato leaf disc was significantly lower than to a lima bean leaf disc when the neighbouring disc was positioned upwind of the original disc in the wind tunnel (Fig. 1a; Table 1a). However, when the neighbouring leaf disc was positioned downwind of the original disc in the wind tunnel, there was no significant difference in the proportions of *T. urticae* that migrated to the two plant species of the neighbouring leaf discs (Fig. 1b). The predation risk on the original leaf disk did not differ with the species of the neighbouring leaf disc (Table 2), and yet more *T. urticae* were attracted to lima bean plants than to tomato plants in a Y-tube olfactometer. This attraction correlates with previous research that has shown that tomato plants are less suitable host-plants for *T. urticae* than lima bean plants (Aina et al. 1972; Chatzivasileiadis and Sabelis 1997; Chatzivasileiadis et al. 1999). These results suggest that *T. urticae* may changes its patch-leaving behaviour not only because of the potential predation risk but also in response to plant volatiles upwind. Further study is needed to clarify if changes in patch-leaving decisions lead to enhanced reproductive success.

Tetranychus urticae may migrate among their host-plants to escape from predators not only by walking, but also by wind (Kondo and Takafuji 1985; Li and Margolies 1993) and by phoresy (Athias-Binche 1993; Holte et al. 2001; Yano 2004). When they migrate by wind and phoresy, they have little to no control over their landing site and, under these circumstances, it is unlikely that plant volatiles in the patch play any role.

Although there are many plant species that can host *T. urticae*, their suitability as a food source varies. In this study, we showed that *T. urticae* changes its patch-leaving

behaviour in response to plant volatiles around their feeding site, even with increased potential predation risk. It is risky for herbivores to leave their food source since they might not find a suitable alternative host plant nearby and this behaviour therefore entails a potential cost. Under such conditions, they need to decide whether to leave the host-plants by estimating both the predation risk in the patch and the availability of finding suitable host-plants nearby. Plant volatiles provide information that organisms can use from a distance in order to make critical antipredator responses. In conclusion, we showed that plant volatiles play an important role in the decision-making of antipredator responses by herbivores.

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