

OLFACTORY RESPONSES OF *PHYTOSEIULUS PERSIMILIS* TO ROSE PLANTS WITH OR WITHOUT PREY OR COMPETITORS

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ABSTRACT — Predators of herbivores use plant volatiles to find patches with prey. Plants benefit from this attraction as predators will reduce herbivore damage. Plants also benefit from arresting predators before prey arrival, as this will minimize future herbivore damage. For predators, however, the benefits of being attracted to clean plants depends on alternative food and on the degree of competition on other plants. Although the interactions between the predatory mite *Phytoseiulus persimilis* and its plant host are well-studied on cucumber or bean, that with other plants remain largely unknown. Here, we studied the olfactory response of *P. persimilis* to volatiles of rose plants that were either clean (*i.e.*, empty), occupied by their prey (*Tetranychus urticae*) or by conspecific competitors, using bean and cucumber as comparisons. We found that, relative to clean air, predators were attracted to clean plants, and also to plants with prey. On cucumber and bean, naïve predators preferred plants with prey over clean plants, but no such discrimination occurred on rose plants. However, after 24 hours of experience with rose plants infested with *T. urticae*, predators preferred those plants to clean roses. Predators avoided plants with prey and conspecifics, even without any previous experience. Our results show that predator attraction to plants hinges on the plant species and on experience. Attracting predators to clean plants may favour biological control, as plants may become better guarded from herbivores, but it may also be detrimental, as predators may starve on those plants.

KEYWORDS — tritrophic interactions; plant volatiles; biological control; mites; experience

INTRODUCTION

Several invertebrates are passive dispersers, hence they do not have control on where they land (Bilton *et al.*, 2001; Kennedy and Smitley, 1985; Moser *et al.*, 2009). To minimize the risk of dispersing in an environment with low availability of profitable patches, dispersers may use volatile cues to infer the quality of patches in the surrounding environment. In the case of predators that feed on herbivores, they

can use volatiles emitted by plants triggered by the feeding of prey (herbivore-induced plant volatiles, HIPV), to locate plants with prey (Agrawal, 2000; Dicke and Sabelis, 1988). These HIPV are beneficial to the predators, as they increase the probability that predators find a patch with prey, but also to plants, which in this way recruit bodyguards to defend them from herbivores (Kessler and Baldwin, 2001; Turlings *et al.*, 1995).

Plants that are free of herbivores are also predicted to produce volatiles to attract predators when they are close to plants infested with herbivores, to prevent a future attack (Kobayashi and Yamamura, 2003). Indeed, there are examples of plants displaying this strategy (Bruin and Sabelis, 2001). In addition, plants may benefit from attracting predators prior to the arrival of prey even when their neighbours are not attacked (Kobayashi *et al.*, 2006). This is because a plant that contains predators before the arrival of herbivores will suffer less from herbivory (Frank, 2010; Gonzalez-Fernandez *et al.*, 2009; Sanchez *et al.*, 2003; Strong and Croft, 1996; Yano, 2006). Mathematical models suggest that this is the case whenever the cost of producing the signal is low relative to the cost of herbivore infestation (Kobayashi *et al.*, 2006). It has been shown that producing volatiles that attract predators involves biochemical (Glawe *et al.*, 2003; Hoballah *et al.*, 2004; Steppuhn *et al.*, 2008) and ecological (Agrawal *et al.*, 2002; Dicke and van Loon, 2000) costs. However, whether such costs outweigh the benefits of being protected is a matter of debate (Dicke *et al.*, 2003).

From the predator perspective, it may be beneficial to land on plants without prey, if the alternative is not landing on a plant at all. Indeed, on plants, predators may gain other resources besides access to prey, such as extrafloral nectar, pollen or leaf contents (Heil *et al.*, 2001; Magalhães and Bakker, 2002; Tompkins *et al.*, 2010; van Rijn and Tanigoshi, 1999a). Moreover, on plants, predators may gain protection from soil antagonists (Losey and Denno, 1999). Alternatively, predators may be attracted to clean plants not because it is beneficial for them, but because they are being lured by plants to do so.

When both clean and infested plants are present in the environment, predators are expected to be attracted to plants with prey and to avoid clean plants or plants with competitors or with their own predators. Indeed, there are numerous examples of predators being attracted to plants with prey relative to clean plants (Dicke and Sabelis, 1988; Karban *et al.*, 1997; Kessler and Baldwin, 2001; Turlings *et al.*, 1995). Other studies have shown that predators of herbivores are also able to avoid plants with com-

petitors (Janssen *et al.*, 1997; Zahedi-Golpayegani *et al.*, 2007) or with their own predators (Magalhães *et al.*, 2005; Venzon *et al.*, 2000), but this is not always the case (Janssen *et al.*, 1999). In this ecological context (the presence of plants harbouring different species), the interests of predators and plants may be aligned or conflicting. Indeed, plants with prey are expected to benefit more from the presence of predators than clean plants or plants with competitors of such predators. Hence, if signal production is costly enough, only plants with prey are expected to attract predators, and the interests of predators and plants are aligned. However, if the signal cost is low, all plants are expected to produce it, and predators will be equally attracted to plants with prey as well as to plants without prey and/or with competitors. Assuming that other resources are equally distributed among plants with or without prey or competitors, it is clearly disadvantageous for predators not to discriminate among these types of plants. Hence, the ability to discriminate among those types of plants is expected to evolve in predators, provided that signals are available to perform this discrimination. Therefore, whether predators are able to discriminate between clean plants and plants with prey and/or competitors depends on the cost of the plant signal and on the stage of the coevolutionary arms race between predators and plants. The ability to discriminate between signals may also depend on the individual experience of predators (De Boer and Dicke, 2006; Koveos and Broufas, 1999; Maeda *et al.*, 2006; Shimoda and Dicke, 2000; Takabayashi and Dicke, 1992; Uefune *et al.*, 2010).

In this study, we investigate the attraction of predators towards volatiles produced by plants under different ecological contexts, using a system composed of the predatory mite *Phytoseiulus persimilis* (Athias-Henriot), its prey *Tetranychus urticae* (Koch) and rose plants. The responses of *P. persimilis* toward volatiles produced by bean and cucumber plants infested with *T. urticae* have been extensively studied (Agrawal *et al.*, 2002; De Boer and Dicke, 2004; Dicke and Sabelis, 1988; Kappers *et al.*, 2010; Shimoda and Dicke, 2000; Takabayashi *et al.*, 1994b). We will thus use these plants to test whether the

responses of our specific predator population are comparable with those described for other populations of this species. Subsequently, we will test the responses of this predatory mite on rose, as its prey, *T. urticae*, is a major pest of this crop (Gough 1991, Sanderson and Zhang 1995, Nicetic *et al.* 2001, Landeros *et al.* 2004). Specifically, we will ask (1) are predators attracted to clean plants?; (2) can predators discriminate between clean plants and plants infested with prey?; (3) can they discriminate between clean plants and plants with prey and competitors?; (4) are these responses affected by the predators' experience? and (5) are prey also attracted to clean plants?

MATERIALS AND METHODS

Stock cultures

All plants (Rose: *Rosa* L. Hybrids cvar. Black Magic; Cucumber: *Cucumis sativus* L. Hybrids cvar. Negin; Bean: *Phaseolus vulgaris* L. cvar. Alamot), were planted at University of Tehran, Karaj, Iran under controlled conditions (23 ± 2 °C, 60 ± 5 % RH and 16:8 h (L:D) photoperiod) in a greenhouse. They were grown in a mixture of soil and perlite, to which a 20-20-20 NPK master fertilizer was periodically added. For the experiments, we used plants of the same age.

Spider mites (*T. urticae*) were collected from rose greenhouses in Pakdasht, Valamin, Iran in March 2010. They were maintained on bean plants in the laboratory under the same conditions as before. Every 2 or 3 days, clean plants with approximately four leaves were added to the spider mite culture. From this culture, infested leaves were selected, detached from plants, and used to feed the predatory mite culture.

Predatory mites (*P. persimilis*) were obtained from Koppert in 2009. In the laboratory, they were reared on densely infested bean leaves with spider mites in a growth chamber (75 ± 5 % RH, 25 ± 2 °C, 16:8 h (L:D)). The predators received new infested bean leaves every day and old leaves were removed. Leaves were placed on inverted pots placed on trays with water and covered with a $40 \times 40 \times 60$ cm Plexiglas box to avoid escapes.

Olfactometer experiments

A Y-tube olfactometer was used to test the response of *P. persimilis* to odours of rose, bean and cucumber plants that were either clean or infested with *T. urticae* females, or with *T. urticae* and conspecifics, as well as the response of *T. urticae* to clean plants. The olfactometer consisted of a Y-shaped glass tube (diameter: 4 cm, each arm 25 cm) with a Y-shaped metal wire in the middle of the tube positioned parallel to the tube walls (Sabelis and van de Baan, 1983). The air was first cleaned with activated charcoal, then it was pulled at the base of the tube by a small electrical motor, such that it went through both arms at 0.5 m/s. This speed was confirmed with electronic flowmeters in each arm. Same-aged female (10 days old mated female) predators were starved for 5 hours, by keeping them in a Petri dish (6 cm diameter) with water only. Subsequently, these females were individually introduced at the basal end of the Y-tube with a small brush to initiate upwind movement. Each female was used only once. Plexiglass boxes ($30 \times 30 \times 30$ cm) containing the odour sources were connected to the end of each of the two arms. Each predator (or prey) was observed until it passed the junction and moved into one of the arms of the Y-tube for approximately 15 cm. If it did not reach the junction within 5 min, the experiment was stopped.

For each treatment, tests were performed in three independent replicate experiments, each with *ca* 20 predators (or prey) and each with a new set of odour sources consisting of 3 plants with or without the arthropod species mentioned above. To cancel out any unforeseen asymmetry in environmental factors (*e.g.* light, temperature), odour sources were swapped each time 4-5 mites had been tested. The wire was cleaned between each series. Under the null hypothesis of no preference, we expected 50 % of the individuals tested to enter each of the two arms of the Y-tube. Whenever odour sources consisted of infested plants, infestation was done by introducing 100 spider mites, alone or with 20 *P. persimilis*, on plants in a plexiglass box ($30 \times 30 \times 30$ cm) 24 hours prior to experiments.

We first tested whether *P. persimilis* was attracted to clean plants (rose, cucumber or bean). To this

TABLE 1: Results of replicated G-tests for the olfactory response of *P. persimilis* and *T. urticae* towards different odour sources. For each test, three replicates with 20 individuals each were done. N: number of individuals that responded.

Source of odour	N	Gp	P_{Gp}	Gh	P_{Gh}
Tests with <i>P. persimilis</i>					
Clean air vs clean rose	46	5.6	0.017	0.80	0.66
Clean air vs clean bean	48	14.86	0.0001	0.68	0.71
Clean air vs clean cucumber	49	14.00	0.0001	0.18	0.90
Clean air vs rose with <i>T. urticae</i>	46	7.2	0.007	0.29	0.86
Clean air vs bean with <i>T. urticae</i>	54	36.03	<0.0001	0.82	0.66
Clean air vs cucumber with <i>T. urticae</i>	50	28.81	<0.0001	0.16	0.92
Clean rose vs rose with <i>T. urticae</i>	52	2.79	0.09	1.30	0.52
Clean bean vs bean with <i>T. urticae</i>	56	14.65	0.0001	0.25	0.88
Clean cucumber vs cucumber with <i>T. urticae</i>	51	14.42	0.0001	0.23	0.89
Clean rose vs rose with <i>P. persimilis</i> and <i>T. urticae</i>	53	5.55	0.018	0.35	0.83
Clean bean vs bean with <i>P. persimilis</i> and <i>T. urticae</i>	56	19.43	<0.0001	0.43	0.80
Clean cucumber vs plant with <i>P. persimilis</i> and <i>T. urticae</i>	51	11.50	0.0006	0.01	0.99
Tests with <i>P. persimilis</i> on rose for 24 hours					
Clean air vs clean rose	53	5.55	0.018	0.019	0.99
Clean rose vs rose with <i>T. urticae</i>	49	6.02	0.014	0.75	0.68
Tests with <i>P. persimilis</i> on rose for six months					
Clean air vs clean rose	50	10.01	0.001	1.06	0.58
Clean rose vs rose with <i>T. urticae</i>	56	25.07	<0.0001	1.13	0.56
Tests with <i>T. urticae</i>					
Clean air vs clean bean	53	14.42	0.0001	0.01	0.99
Clean air vs clean cucumber	53	14.42	0.0001	0.05	0.97
Clean air vs clean rose	44	11.51	0.0006	0.55	0.75

aim, we connected a clean box to one of the olfactometer arms, and a box with clean plants to the other. Next, we asked whether predators were attracted to plants with prey, by using the same set-up, except that plants were infested with *T. urticae*. We then tested whether predators were able to discriminate between odours from clean plants or from plants infested with prey. Finally, we tested whether predators were able to discriminate between odours from clean plants or from plants infested with conspecific competitors and prey.

Other previous studies have analysed the response of *P. persimilis* towards clean vs infested cucumber and bean plants (Agrawal *et al.*, 2002; De Boer and Dicke, 2004; Dicke and Sabelis, 1988; Kappers *et al.*, 2010; Shimoda and Dicke, 2000; Takabayashi *et al.*, 1994b). However, the olfactory responses of predators toward plant odours vary greatly with the plant species or variety (Kappers *et al.*, 2010; Takabayashi *et al.*, 1994a; van den Boom *et al.*, 2003) and with the genetic composition of the

predator population (Margolies *et al.*, 1997; Sznajder *et al.*, 2010). Therefore, the study of plant-predator interactions cannot be deduced from previous research using other plants and predator populations. Hence, we have repeated these experiments here using our plant and predator populations.

Subsequently, to test whether previous experience with rose plants infested with prey modified the olfactory responses of *P. persimilis* towards clean plants and plants with prey, we exposed *P. persimilis* to such plants for either 24 hours or 6 months, then tested whether those experienced predatory mites could discriminate between (a) clean air vs clean rose and (b) clean rose vs rose infested with *T. urticae*. We used two different periods of exposure to test whether this affected the response of predators.

Finally, we tested whether *T. urticae* were attracted to clean plants. To this aim, same-aged females were given the choice between clean plants and clean air, using the same methodology as

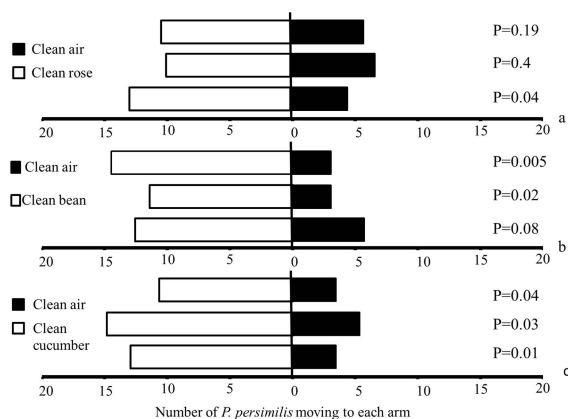


FIGURE 1: In the Y-tube olfactometer, *Phytoseiulus persimilis* were offered a choice between odours from clean air in one arm vs odours from clean plants in the other. a – rose plants; b – bean plants; c – cucumber plants. *P* values of the G test for each replicate are given next to each bar; overall *P* values are given in Table 1.

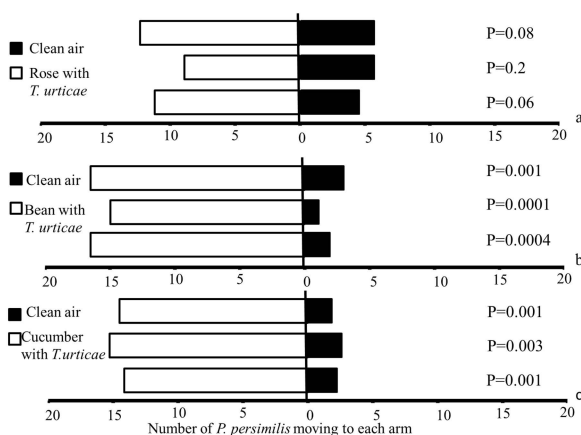


FIGURE 2: In the Y-tube olfactometer, *Phytoseiulus persimilis* were offered a choice between odours from clean air in one arm vs odours from plants infested with *Tetranychus urticae* in the other. a – rose plants; b – bean plants; c – cucumber plants. *P* values of the G test for each replicate are given next to each bar; overall *P* values are given in Table 1.

above.

Statistical analysis was done using a replicated G-test, which includes a test for heterogeneity among replicate experiments (Sokal and Rohlf, 1995).

RESULTS

The three replicates performed for each test were never significantly different from one another (cf. Gh in Table 1).

When *P. persimilis* received clean air from one arm of the olfactometer and odours of clean plants from another, they moved significantly more into the arms with clean plants, irrespective of the plant species (Figure 1, Table 1). Predators also significantly preferred spider mite infested plants over clean air (Figure 2, Table 1). When given the choice between odours from clean rose plants and odours from rose plants infested with prey (*T. urticae*), predators did not discriminate between these plants (Figure 3a, Table 1). This was not the case when cucumber and bean plants were used as odour

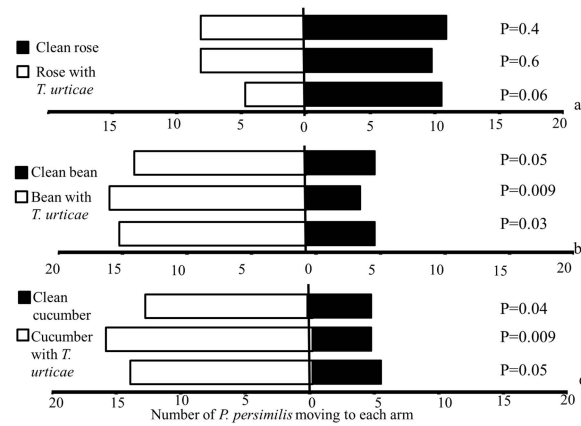


FIGURE 3: In the Y-tube olfactometer, *Phytoseiulus persimilis* were offered a choice between odours from clean plants in one arm vs odours from plants infested with *Tetranychus urticae* in the other. a – rose plants; b – bean plants; c – cucumber plants. *P* values of the G test for each replicate are given next to each bar; overall *P* values are given in Table 1.

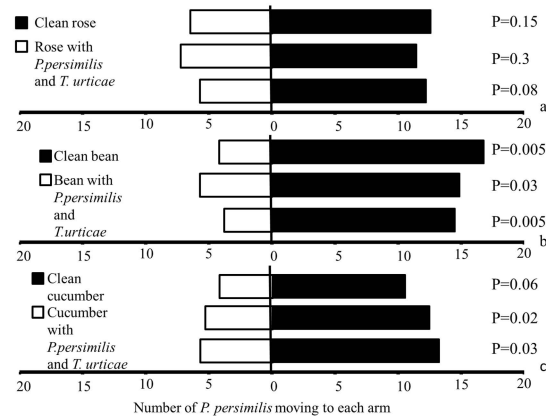


FIGURE 4: In the Y-tube olfactometer, *Phytoseiulus persimilis* were offered a choice between odours from clean rose plants in one arm vs odours from both *Phytoseiulus persimilis* and *Tetranychus urticae* in the other. a – rose plants; b – bean plants; c – cucumber plants. *P* values of the G test for each replicate are given next to each bar; overall *P* values are given in Table 1.

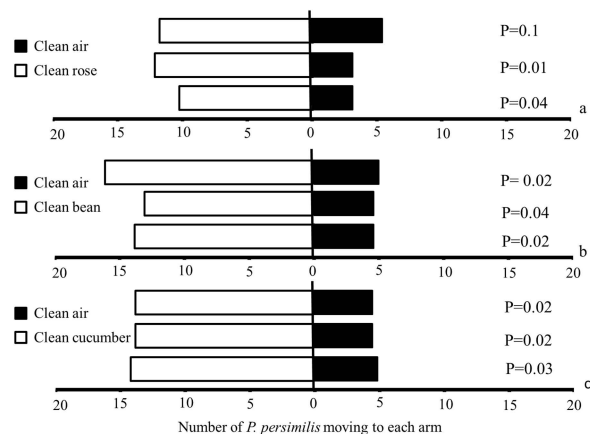


FIGURE 5: In the Y-tube olfactometer, *Tetranychus urticae* were offered a choice between odours from clean air in one arm vs odours from clean plants in the other. a – rose plants; b – bean plants; c – cucumber plants. *P* values of the G test for each replicate are given next to each bar; overall *P* values are given in Table 1.

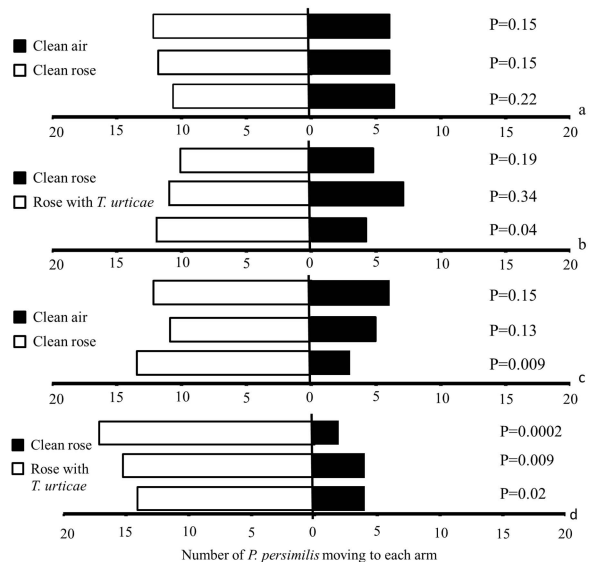


FIGURE 6: In the Y-tube olfactometer, *Phytoseiulus persimilis* were offered a choice between odours from clean air in one arm vs odours from clean rose plants in the other (a,c) and between clean rose plants in one arm vs odours from both *Phytoseiulus persimilis* and *Tetranychus urticae* in the other (b, d). The population of *Phytoseiulus persimilis* used had been exposed to rose plants with *T. urticae* for 24h (a – b) or during 6 months (c – d). *P* values of the G test for each replicate are given next to each bar; overall *P* values are given in Table 1.

sources, as predators significantly preferred cucumber and bean plants with prey over clean plants of the same species (Figure 3b,c, Table 1). However, when given the choice between clean plants and plants with conspecifics and prey, they avoided plants with conspecifics and prey, irrespective of the plant species used (Figure 4, Table 1).

When given the experience of rose plants for 24 hours, *P. persimilis* discriminated between clean rose plants and clean air, and between clean rose plants and rose plants infested with *T. urticae* (Figures 5a,b, Table 1). The same results were obtained when *P. persimilis* were reared on rose for 6 months (Figures 5c,d, Table 1).

To investigate whether clean plants are also attractive to prey, we gave *T. urticae* the choice between clean plants and clean air. *T. urticae* moved significantly into the arm with odours from clean plants, irrespective of the plant species (Figure 6, Table 1).

DISCUSSION

When given a choice between clean plants (bean, cucumber or rose) and clean air, predatory mites (*P. persimilis*) were attracted to clean plants. They were also attracted to plants with prey, when these were offered as an alternative to clean air. On bean and on cucumber, predators were able to discriminate between clean plants and plants with prey, being attracted to the latter, and confirming earlier results (De Boer and Dicke, 2004; Dicke and Sabelis, 1988; Sabelis and van der Weel, 1993). However, on rose, this was not the case: predators did not prefer plants with prey over clean plants. Therefore, rose plants emit volatiles that attract predators even when prey is not available and these volatiles hamper their discrimination between profitable and non-profitable patches. However, predators avoided plants with conspecific competitors and prey, irrespective of the plant species used. Hence, they probably are able to use the alarm pheromone of prey to avoid conspecifics on rose, as well as on cucumber and bean, as suggested by a previous study (Janssen *et al.*, 1997). After 24 hours of experience with rose volatiles, *P. persim-*

ilis were able to discriminate between clean and infested plants, and they maintained this ability to discriminate after being reared on rose for 6 months. Finally, we found that *T. urticae* was attracted to clean plants of all species.

Plants attacked by herbivores can produce herbivore-induced plant volatiles that attract predators of these herbivores. The predators then feed on those herbivores, leading to lower herbivore numbers (potentially eradicating the population), hence reducing plant damage (Olf *et al.*, 1999). However, before the arrival of predators, there is a time lag in which herbivores may cause severe damage to plants. This time lag can be eliminated if predators are already present on plants. Hence, plants are expected to benefit from the presence of predators before the arrival of prey. A few studies have shown that this is indeed the case (Frank, 2010; Gonzalez-Fernandez *et al.*, 2009; Sanchez *et al.*, 2003; Strong and Croft, 1996; Yano, 2006). Therefore, plants are expected to produce volatiles to attract predators even when they are not being attacked by herbivores. Indeed, theoretical models predict that this may be the case (Kobayashi *et al.*, 2006). However, there is mixed evidence concerning the fact that predators are attracted to clean plants (Elzen *et al.*, 1983; Khan *et al.*, 1997; Le Ru and Makosso, 2001; Ozawa *et al.*, 2000; Takabayashi and Dicke, 1992).

Another requisite for the strategy of producing signals to attract predators in the absence of herbivore attack to be profitable is that the signal cost must be low (Kobayashi *et al.*, 2006). We showed that clean plants are also attractive to the prey of *P. persimilis* (*T. urticae*). Although we cannot determine whether predators and prey use the same cue to find clean plants, it is clear that plants pay an ecological cost of being conspicuous. Whereas this is clearly detrimental to the plant, it may contribute to explain the strategy displayed by the predators. Indeed, by remaining on those plants, predators are on patches that are attractive to prey.

On cucumber and bean, predators were able to discriminate between clean and infested plants, confirming earlier results (De Boer and Dicke, 2004; Dicke and Sabelis, 1988; Sabelis and van der Weel, 1993). This was not the case on rose. It seems

reasonable to assume that infested plants are more profitable to predators than clean plants. Therefore, the strategy displayed by rose plants may be dishonest. However, predators did avoid plants with conspecifics and prey, irrespective of the plant species. Hence they may use the prey alarm pheromone to avoid competition, as suggested by an earlier study performed on bean (Janssen *et al.*, 1997), and not rely on plant volatiles to take this decision.

There are two possible explanations for the fact that predators do not discriminate between clean and infested rose: (a) the volatiles produced by infested and clean rose do not differ or (b) these volatiles differ but predators are not able to discriminate between them. Given the ample evidence that predators can learn (or evolve) to discriminate between these odours (De Boer and Dicke, 2006; Koveos and Broufas, 1999; Maeda *et al.*, 2006; Shimoda and Dicke, 2000; Takabayashi and Dicke, 1992; Uefune *et al.*, 2010), we gave the *P. persimilis* population the experience of rose volatiles by placing predators on rose plants with prey. When given the experience of rose volatiles, predators discriminated between clean and infested rose plants. Therefore, we can rule out the possibility that clean and infested rose plants emit the same volatile blend.

We have thus shown that clean plants can attract predators mites in the absence of prey and that this can have strong consequences for the discrimination of profitable and non-profitable patches by these predators in some plants. Therefore, as predicted by Kobayashi *et al.* (2006), plants produce volatiles to attract bodyguards even when uninfested. Whether this strategy is honest on all plants remains to be elucidated.

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