

Attraction of *Phytoseiulus persimilis* (Acari: Phytoseiidae) towards volatiles from various *Tetranychus urticae*-infested plant species

C.E.M. van den Boom^{1*}, T.A. van Beek¹ and M. Dicke²

¹Laboratory of Organic Chemistry, Phytochemical Section, Wageningen University, Dreijenplein 8, 6703 HB Wageningen, The Netherlands:

²Laboratory of Entomology, Wageningen University, PO Box 8031, 6700 EH Wageningen, The Netherlands

Abstract

Plants infested with the spider mite *Tetranychus urticae* Koch, may indirectly defend themselves by releasing volatiles that attract the predatory mite *Phytoseiulus persimilis* Athias-Henriot. Several plants from different plant families that varied in the level of spider mite acceptance were tested in an olfactometer. The predatory mites were significantly attracted to the spider mite-infested leaves of all test plant species. No differences in attractiveness of the infested plant leaves were found for predatory mites reared on spider mites on the different test plants or on lima bean. Thus, experience with the spider mite-induced plant volatiles did not affect the predatory mites. Jasmonic acid was applied to ginkgo leaves to induce a mimic of a spider mite-induced volatile blend, because the spider mites did not survive when incubated on ginkgo. The volatile blend induced in ginkgo by jasmonic acid was slightly attractive to predatory mites. Plants with a high degree of direct defence were thought to invest less in indirect defence than plants with a low degree of direct defence. However, plants that had a strong direct defence such as ginkgo and sweet pepper, did emit induced volatiles that attracted the predatory mite. This indicates that a combination of direct and indirect defence is to some extent compatible in plant species.

Introduction

Plant species show variation in the direct defence mechanisms that protect them against insect herbivory, such as the composition of toxic secondary metabolites, proteinase inhibitors, spines and glandular hairs (Rhoades & Cates, 1976; Rhoades, 1985; Rosenthal & Berenbaum, 1991). Besides direct defence, plants can also defend themselves indirectly. This is done by promoting the effectiveness of natural enemies of the herbivores, for example by offering alternative food or shelter (Price *et al.*, 1980; Price, 1981; Sabelis *et al.*, 1999; Dicke, 1999a). Another way of indirect defence is to attract predators by the release of herbivore-

induced volatiles, which differ from the volatiles of mechanically damaged leaves in a qualitative and/or quantitative way (Dicke & Sabelis, 1988a; Dicke, 1999a). The volatile infochemicals induced in plants by herbivory that play a role in the attraction of the predators are called synomones (Dicke & Sabelis, 1988b).

The use of these two types of defence, direct and indirect defence, may vary between plant species and plant genotypes. From an evolutionary point of view, plant genotypes that use both types of defence may have an advantage over other plant cultivars, but they may also incur more costs. It is not known to what degree these two different defence mechanisms are compatible. A trade-off between direct and indirect defence has been documented for *Senecio jacobaea* (Asteraceae) (Vrieling *et al.*, 1991). On genotypes with increased levels of pyrrolizidine alkaloids

(direct defence) fewer aphids of *Aphis jacobaeae* Schrank (Hemiptera: Aphididae) were found. As a consequence, fewer ants visited these genotypes to collect aphid-produced honeydew. The ants also attack caterpillars of the specialist herbivore *Tyria jacobaeae* Linnaeus (Lepidoptera: Arctiidae) that is not affected by the alkaloids (indirect defence). Thus, a reduction in aphid and ant presence on plants with a strong direct defence leads to an increase in caterpillar damage because of a reduction in indirect defence. Also, for *Nicotiana attenuata* Torr. Ex. Watson (Solanaceae) a trade-off between direct and indirect defence has been reported (Kahl *et al.*, 2000). When *Manduca sexta* (Johannsen) (Lepidoptera: Sphingidae) larvae feed on *N. attenuata* these plants increase the release of volatile terpenoids, but they do not increase the levels of nicotine, which is the plant's direct defence.

The spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) is a generalist herbivore and a serious pest in many crops. One of its natural enemies is the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), which specializes on spider mites in the genus *Tetranychus* and exterminates spider mite populations (Sabelis, 1981). Behavioural evidence that the predatory mite *P. persimilis* is attracted to *T. urticae*-induced plant volatiles has been presented for lima bean (Fabaceae), tomato (Solanaceae), cucumber (Cucurbitaceae), gerbera (Asteraceae), ground ivy (Lamiaceae), cotton (Malvaceae) and for rose, pear and apple (Rosaceae) (Sabelis & van de Baan, 1983; Dicke & Sabelis, 1988a; Dicke *et al.*, 1990a,b; Bruin *et al.*, 1992; Takabayashi *et al.*, 1994a; Krips *et al.*, 1996). Moreover, it was shown that the predatory mite *P. persimilis* is not attracted to odours from the spider mite *T. urticae* (Sabelis & van de Baan, 1983; Sabelis *et al.*, 1994). This means that the attraction of the predatory mite *P. persimilis* to *T. urticae*-infested plants cannot be explained by herbivore-derived volatiles but is caused by plant-derived volatiles. This has been supported by additional studies. Chemical analysis has resulted in the identification of the spider mite-induced components in the volatile blend of infested lima bean when compared to mechanically damaged leaves (Dicke *et al.*, 1990a). Also, for apple, cucumber, tomato and gerbera plants, differences in odour profiles were found between volatiles emitted in response to spider mite-damage and to mechanical damage (Dicke *et al.*, 1998; Krips *et al.*, 1999; Takabayashi *et al.*, 1991, 1994a). Dicke *et al.* (1990a) showed that individual compounds found in the odour blend of spider mite-infested leaves attracted *P. persimilis*. Besides local induction, also systemic induction of non-infested leaves of the same plant species was found to take place after one leaf of a lima bean plant was infested by *T. urticae* (Dicke *et al.*, 1990b; Dicke, 1994). Finally, treatment of lima bean or gerbera plants with the plant hormone jasmonic acid resulted in (i) the emission of a volatile blend that is qualitatively similar to that induced by spider mite feeding; and (ii) the attraction of the predatory mite *P. persimilis* (Dicke *et al.*, 1999, Gols *et al.*, 1999).

There is variation in herbivore-induced volatile production between different plant species and cultivars (Takabayashi *et al.*, 1994a; Takabayashi & Dicke, 1996). Some spider mite-infested plant species emit new components that are not emitted when these plants are mechanically damaged. Other spider mite-infested plant species do not emit new components, but their volatile blends differ in a quantitative way from the blend emitted from mechanically damaged plants. Also, different spider mite species feeding

on the same plant species induce qualitatively or quantitatively different odour blends and the predatory mite *P. persimilis* can distinguish between these different induced blends (Sabelis & van de Baan, 1983; Sabelis & Dicke, 1985; Dicke & Sabelis, 1988a; Takabayashi *et al.*, 1991). Moreover, the behavioural response of predatory mites can be affected by experience (Dicke *et al.*, 1990b; Krips *et al.*, 1999; Drukker *et al.*, 2000). *Phytoseiulus persimilis* does not respond to *T. urticae* infested cucumber or gerbera leaves when the predatory mites were reared on *T. urticae* on lima bean. However, after experience with *T. urticae* feeding on cucumber or gerbera, the predator is attracted by the volatiles from these infested plants (Dicke *et al.*, 1990b; Krips *et al.*, 1999). Drukker *et al.* (2000) showed that naive predatory mites responded positively to odours from an unfamiliar environment, after these mites had had a positive experience with prey in combination with the unfamiliar odour.

In this paper, the attraction of *P. persimilis* to *T. urticae*-induced plant volatiles of several plant species from different families is investigated. Furthermore, the effect of two different rearing histories is investigated, to assess whether experience with the volatiles from the spider-mite-infested test plant has an effect on the predatory mite's response. Plant species have been selected that differ in their degree of direct defence (van den Boom *et al.*, 2002). However, indirect defence against spider mites has not been investigated for these plant species yet, although for some of them indirect defence against other herbivore species has been documented. It would be interesting to know to what degree a plant defends itself and to what extent direct and indirect defence mechanisms are interrelated. Special emphasis is placed on plants from the Fabaceae and the Solanaceae. Plant species from the Fabaceae seem to have a less efficient direct defence compared to plant species from the Solanaceae (van den Boom *et al.*, 2002). To defend themselves against herbivory, plants of the Fabaceae are therefore expected to have a relatively stronger indirect defence than plant species from the Solanaceae.

Materials and methods

Plant material

The test plants used in the olfactometer experiments are listed in table 1. These plants, as well as lima bean plants *Phaseolus lunatus* L. (Fabaceae), that were used for rearing the spider mite *T. urticae*, were grown in a greenhouse (20–30°C, r.h. 60–80% and 16L:8D). Leaves were taken from a grapevine *Vitis vinifera* L. (Vitaceae) grown outdoors (height about 0.5–1 m) and ginkgo leaves from a mature ginkgo tree *Ginkgo biloba* L. (Ginkgoaceae) in the Botanical Garden of Wageningen University (height about 15–20 m). The age of the greenhouse-reared plants and the mean leaf area of the leaves used in the experiments are given in table 1. The leaf area was measured with an area meter (Li-Cor LI-3100, CaTeC, the Netherlands) and the average of ten leaves is presented unless mentioned otherwise. Also shown in table 1 is the percentage of *T. urticae* that accepted leaves of the test plant species over leaves of lima bean, which is a measure of the direct defence capacity of that plant species (van den Boom *et al.*, 2002). Hop, *Humulus lupulus* L. (Moraceae), was vegetatively propagated from plants grown outdoors and subsequently reared in the greenhouse. Test

Table 1. Plants used in olfactometer tests.

Family	Genus/species	Common name	Cultivar	Age (weeks)	Mean leaf area \pm SD (cm ²)	% of <i>Tetranychus urticae</i> that accepted the plant \pm SD ⁴
Individual plant species tested in an olfactometer						
Fabaceae	<i>Glycine max</i>	Soybean	Gieso	5	115 \pm 10	99 \pm 1 ⁴
Fabaceae	<i>Vigna unguiculata</i>	Cowpea	Black eye	6	145 \pm 25	65 \pm 6
Ginkgoaceae	<i>Ginkgo biloba</i>	Ginkgo		- ²	40 \pm 5	11 \pm 3
Moraceae	<i>Humulus lupulus</i>	Hop		16 ¹	20 \pm 5 ³	98 \pm 1
Solanaceae	<i>Capsicum annuum</i>	Sweet pepper	Lambada	10	90 \pm 20	25 \pm 5
Solanaceae	<i>Solanum melongena</i>	Eggplant	Black beauty	10	305 \pm 45	74 \pm 6
Vitaceae	<i>Vitis vinifera</i>	Grapevine	Glorie van Boskoop	- ²	165 \pm 20	43 \pm 7
Plants tested for attractiveness by predatory mites on the same day						
Fabaceae	<i>Glycine max</i>	Soybean	Gieso	4	100 \pm 15	
Solanaceae	<i>Solanum melongena</i>	Eggplant	Black beauty	8	260 \pm 25	

¹ Age calculated from the time the plant was vegetatively propagated.

² Age not known.

³ A total of 50 leaves was taken to calculate the average leaf size.

⁴ Plant acceptance by *T. urticae* is based on the percentage of spider mites that accepted a leaf section of the test plant when the alternative was a distant leaf section of a lima bean leaf (see Van den Boom *et al.*, 2002 for details).

plants were infested by placing spider mite-infested lima bean leaves on top of their leaves and were kept in a separate compartment in the greenhouse together with the spider mite-infested lima bean plants. Only fully expanded leaves were used for the experiments. In the case of soybean, *Glycine max* L. (Fabaceae), and cowpea, *Vigna unguiculata* L. (Fabaceae), fully expanded trifoliolate leaves were used.

Rearing of mites

The spider mites, *T. urticae*, were reared on lima bean under the same conditions as the uninfested lima bean plants. The predatory mites, *P. persimilis*, were originally obtained from Entocare cv, Wageningen, the Netherlands. They were reared in the laboratory in Petri dishes sealed with parafilm. The Petri dishes were kept in a temperature controlled room (23 \pm 2 °C, r.h. 60–80 % and 16L:8D). Fresh leaves were added every two to three days. For the experiments only young adult females of *P. persimilis* were used, whose age was 1–7 days since the final moult.

Olfactometer experiment

The attraction of the predatory mites towards the *T. urticae*-infested leaves was investigated with a closed system Y-tube olfactometer described by Takabayashi & Dicke (1992). Two glass jars of 2 l each that contained the odour sources were connected to the Y-tube. Filtered air at 4 l min⁻¹ was led through each of the jars into the olfactometer. The other side was connected to a house vacuum (8 l min⁻¹). Before the start of the experiment, the arms of the olfactometer were flushed with air going through the odour sources for about 10 min. Adult female predatory mites, starved for 1–3 h, were allowed to walk upwind on an iron wire in the Y-tube. At the Y-junction they could make a choice between the two odour streams coming from the two glass jars. When the predatory mite had reached the end of one of the arms her choice was recorded. When she did not reach the end of one of the arms within 5 min, the predatory mite was removed and excluded from the statistical analysis.

Spider mite-infested vs. uninfested leaves of various plant species

In one glass jar of the olfactometer three clean test plant leaves were placed with their petioles in wet cotton wool. For hop, 9–13 test plant leaves were used, because its leaf area was relatively small. In the other glass jar the same amount of plant leaves infested with spider mites for at least three days and at most 14 days was placed. These sets of infested leaves are considered strong odour sources, as two lima bean leaves that have each been infested for one day by 100 spider mites are highly attractive to *P. persimilis* (Janssen *et al.*, 1997). Even much lower degrees of infestation attract the predators (M. Dicke, unpublished data). Ginkgo is not accepted as a host plant by *T. urticae* and thus, it was not possible to rear spider mites on ginkgo. Therefore, ginkgo leaves were treated with jasmonic acid to mimic the volatile induction profile (Boland *et al.*, 1995). For that purpose 20 ginkgo leaves were individually placed with their petioles into a vial with 10 ml of an aqueous jasmonic acid solution (1 mM) for one day or for three days, respectively. The vials were sealed with parafilm. The uptake of the jasmonic acid solution by the ginkgo leaves was 1 ml a day. As a control for the jasmonic acid solution, 20 ginkgo leaves were placed in 10 ml of an diluted acidic solution (1 mM HCl) during the same time period as the jasmonic acid-treated leaves. All olfactometer experiments for each species were carried out on 3–6 different days. On each day ten predatory mites reared on spider mite-infested lima bean leaves and ten predatory mites reared on spider mite-infested test plant leaves tested were alternately introduced into the olfactometer. For the experiments with soybean (Fabaceae) and eggplant, *Solanum melongena* L. (Solanaceae), only predatory mites reared on *T. urticae*-infested lima bean leaves were used. New odour sources were used every day. For each experiment the odour sources were interchanged after five predatory mites had individually made a choice.

The same mites tested on two plant species on the same day

In the previous experiments, all test plant species were investigated on different days and in different weeks. This

may make it difficult to compare the relative degree of attraction measured. To evaluate this, two different test plant species were tested with the same predatory mites on the same day. In this setup, only the relative differences in odour blends could contribute to differences in predatory mite attraction. Two identical olfactometers were used, set-up side by side. In one olfactometer, six infested vs. six uninfested soybean leaves and in the other olfactometer, four infested eggplant vs. four uninfested eggplant leaves were tested. More soybean than eggplant leaves were tested because the soybean leaf area was smaller (table 1). The leaves were infested with *T. urticae* for four to seven days. The experiments were carried out on five different days with 20 predatory mites reared on *T. urticae*-infested lima bean per day. Each individual predatory mite was allowed to make a choice in one olfactometer and subsequently in the other olfactometer. After five mites had made a choice in both olfactometers, the order of initial choice for the predatory mites for one out of two olfactometers was changed. After in total ten predatory mites had made their choice in both olfactometers, the infested and uninfested odour sources of one olfactometer were interchanged with the infested and uninfested odour sources of the other olfactometer. After the arms of the olfactometer had been flushed with air coming from the changed odour sources for 10 min, another ten predatory mites could make their choice in both olfactometers.

Statistics

For the predatory mites with the same rearing history, a χ^2 -test on the total number of predators attracted towards one of the odour sources was performed per test plant. A 2 × 2 contingency table was used to analyse whether the attraction per test plant for the predatory mites with different rearing histories was significantly different. To

evaluate if the response of the predatory mites towards the soybean and the response towards eggplant in the olfactometer setup were significantly different, also a 2 × 2 contingency table was used.

Results

Attraction of predatory mites reared on infested lima bean leaves

Phytoseiulus persimilis females reared on infested lima bean leaves were significantly attracted to *T. urticae*-infested plants of all species tested (fig. 1). They showed the strongest attraction to infested soybean, sweet pepper (*Capsicum annuum* L. (Solanaceae)) and grapevine, with respectively 82, 82 and 72% of the predatory mites moving towards the spider mite-infested test plant leaves (χ^2 -test, $P \leq 0.001$). To cowpea, hop and eggplant, the response of the predatory mites was weaker, with respectively 67, 65 and 62% (χ^2 -test, $0.05 \geq P > 0.01$).

Attraction of predatory mites reared on infested test plant leaves

When the predatory mites were reared on infested leaves of the test plant, the attraction of the predatory mites to the *T. urticae*-infested leaves was also significant for all plant species (fig. 1). Strongest attraction (78, 81 and 76%) was shown by the predatory mites to sweet pepper, grapevine and hop, respectively (χ^2 -test, $P \leq 0.001$). For cowpea 71% (χ^2 -test, $0.01 \geq P > 0.001$) and for eggplant only 68% (χ^2 -test, $0.05 \geq P > 0.01$) of the predatory mites chose the infested leaves. For none of the test plant species was a significant difference in attractiveness found between predatory mites with different rearing histories.

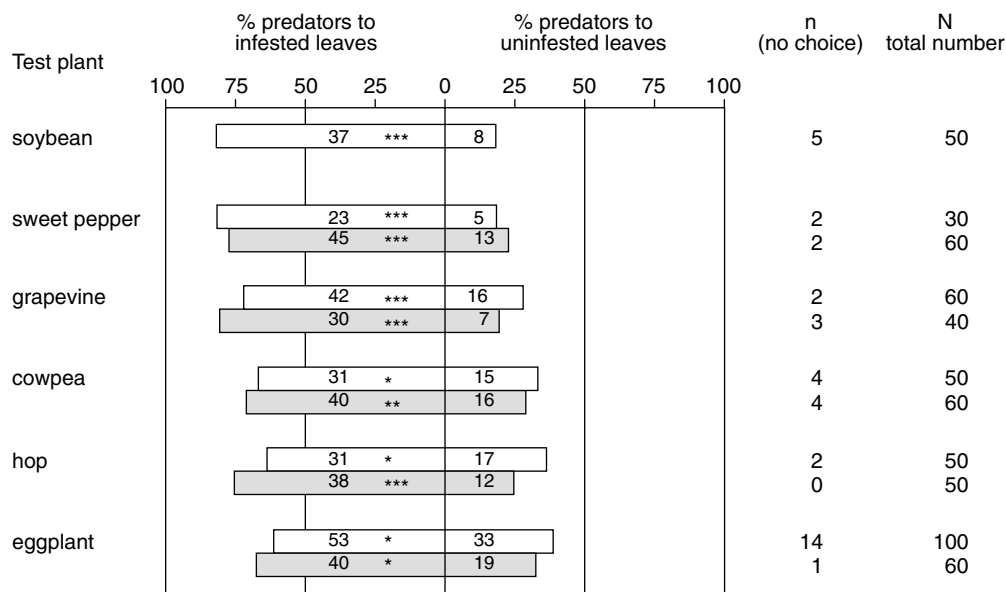


Fig. 1. Response of adult female *Phytoseiulus persimilis* towards *Tetranychus urticae*-infested leaves vs. uninfested leaves of the same plant species in a Y-tube olfactometer. The predatory mites were reared on spider mites feeding on either lima bean (□) or on the test plant (■). The number of predatory mites that made a choice of one of the sides is depicted in the bars. The number of predatory mites that did not make a choice (n) and the total number of predatory mites tested (N) is shown at the right side of the figure. Statistics: χ^2 -test (***) = $P \leq 0.001$; ** = $0.01 \geq P > 0.001$; * = $0.05 \geq P > 0.01$; n.s. = $P > 0.05$).

The same mites tested on two plant species on the same day

For an experiment in which two plant species were compared on the same day, soybean and eggplant were chosen, because they were the two extremes in predatory mite attraction in the separate olfactometer experiments (82 and 62% respectively, fig. 1). Figure 2 shows that there was a significant difference in the response of the predatory mites towards the two plant species (2×2 contingency table, $P = 0.008$). For soybean, 83% of the predatory mites moved towards the spider mite-infested leaves and for eggplant only 64% of the predatory mites went to the spider mite infested leaves. These predatory mite responses to both infested soybean and infested eggplant do not differ significantly from the responses shown in fig. 1.

Attraction of predatory mites by jasmonic acid-induced plant odour

There was no significant attraction of the predatory mites to the jasmonic acid-treated ginkgo leaves (fig. 3) after one day or after three days of incubation. Respectively, 60% and 59% of the predatory mites went to the jasmonic acid-treated

leaves. The responses of the predatory mites towards the jasmonic acid-treated ginkgo leaves with different incubation times were not significantly different, and therefore the data were pooled. The pooled data revealed a significant attraction ($P < 0.05$) of the predatory mites to jasmonic acid-treated ginkgo leaves (fig. 3).

Discussion

Attraction of predatory mites reared on infested lima bean leaves

The *T. urticae*-infested plants of all species tested in the olfactometer produced volatiles that attracted the predatory mite *P. persimilis*. The components that play a role in the attraction of predatory mites to spider mite-induced plants have been investigated for lima bean (Dicke *et al.*, 1990a). The induced components from lima bean that individually attracted the predatory mites were (3E)-4,8-dimethyl-1,3,7-nonatriene, linalool, (E)- β -ocimene and methyl salicylate. It is possible that one or more of these attractive components were also released by the currently investigated plants. It is known that beet armyworm, *Spodoptera exigua* (Hübner)

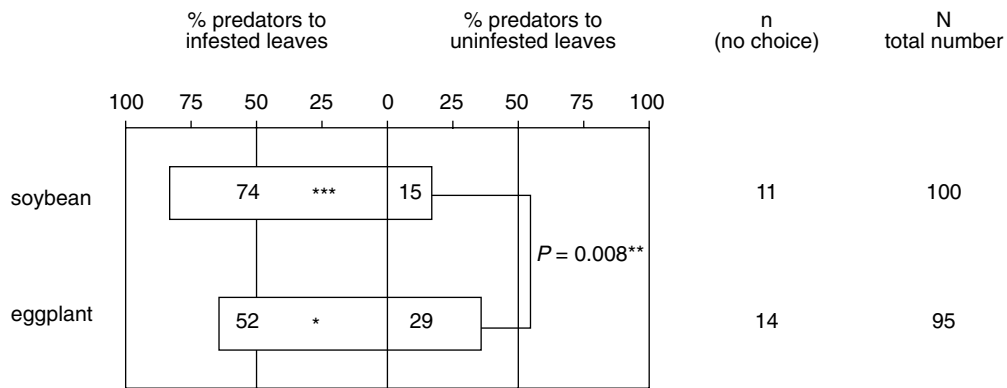


Fig. 2. Response of adult female *Phytoseiulus persimilis* reared on lima bean tested in an olfactometer for both soybean and eggplant on the same day. For each test plant *Tetranychus urticae*-infested leaves were tested versus uninfested leaves. For statistics: a χ^2 -test and a 2×2 contingency table were used (see fig. 1 for an explanation of the asterisks).

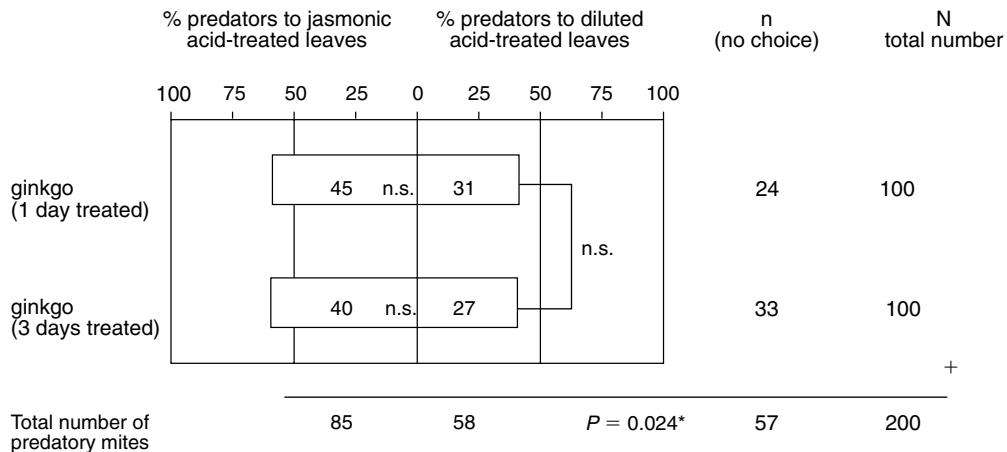


Fig. 3. The attraction of *Phytoseiulus persimilis* towards jasmonic acid-treated ginkgo leaves versus hydrochloric acid-treated ginkgo leaves. The leaf petioles were placed in an aqueous jasmonic acid solution and the control leaf petioles in a diluted acidic solution during one day or during three days. The pooled data with the total number of predatory mites are also depicted. For statistics: see fig. 1.

(Lepidoptera: Noctuidae), induces (3E)-4,8-dimethyl-1,3,7-nonatriene in cowpea leaves, but in soybean leaves this component is not induced or only in very small concentrations (Turlings *et al.*, 1993). Furthermore, it has been shown that methyl salicylate is induced by spring migrants of the damson-hop aphid, *Phorodon humuli* Schrank (Hemiptera: Aphididae), when they feed on hop leaves (Campbell *et al.*, 1993). When different herbivores feed on the same host plant species, the volatile blends are generally similar in qualitative sense, though quantitative difference in the relative contributions of the blend components occur (see Turlings *et al.*, 1993 and Dicke, 1999b for reviews).

Attraction of predatory mites reared on infested test plant leaves

The predators were attracted to *T. urticae*-induced volatiles of all test plant species independent of rearing history. This has been documented in more cases where predatory mites were attracted to spider mite-infested test plants without experience on these plant species (Dicke & Sabelis, 1988a). However, for gerbera and cucumber the predatory mites were only attracted to the spider mite-infested plant leaves when reared on spider mites on these plants (Dicke *et al.*, 1990b; Krips *et al.*, 1999). Both spider mite-infested gerbera and cucumber induced the compounds (3E)-4,8-dimethyl-1,3,7-nonatriene, (E)- β -ocimene and small amounts of linalool (Takabayashi *et al.*, 1994b; Krips *et al.*, 1999). Methyl salicylate was only induced in minor amounts in gerbera. Associative learning was proven for the predatory mite *P. persimilis* by Drukker *et al.* (2000). They showed that naïve predatory mites responded positively to odour from an unfamiliar environment when a positive experience with prey in combination with the investigated odour source was given to the predatory mites.

The same mites tested on two plant species on the same day

Even though more leaves were used for both soybean and eggplant than in the separate experiments, the predatory mites showed the same percentage of response to each of the plants. Also, the relative response of the predatory mites towards infested eggplant and soybean leaves was not significantly different. Thus, there is no evidence that our data on the relative attraction to different plant species have been affected by a day-effect or by variation in the number of infested leaves.

Attraction of predatory mites by jasmonic acid-induced plant odour

The pooled data of the two jasmonic acid-experiments that differ in incubation time show that the predatory mites were slightly attracted to the jasmonic acid-induced ginkgo leaves. Although jasmonic acid can mimic the spider mite-induced blend, the two blends are not identical. Dicke *et al.* (1999) used lima bean to investigate the differences in the jasmonic acid- and spider mite-induced volatiles and concluded that most of the jasmonic acid-induced components were the same as the spider mite induced components. However, some components were not produced in response to jasmonic acid application or only in smaller quantities. Dicke *et al.* (1999) also found that

predatory mites were attracted to the jasmonic acid-induced lima bean leaves, but the predators preferred the spider mite-induced lima bean leaves in a 2-choice test. Boland *et al.* (1995) determined the components that were induced when 10 mM jasmonic acid was supplied through the petiole of freshly detached ginkgo leaf for 30 h and found that linalool was induced in large quantities and methyl salicylate in low quantities. The components (3E)-4,8-dimethyl-1,3,7-nonatriene and (E)- β -ocimene were not induced at all. A slight but significant predatory mite attraction to the jasmonic acid-treated ginkgo leaves was found, possibly due to the induction of linalool and small amounts of methyl salicylate. Although linalool and methyl salicylate can individually attract predatory mites at certain concentrations (Dicke *et al.*, 1990a), it might be possible that their induction was not sufficient to give a strong predatory mite response.

Direct vs. indirect defence in a plant species

It was hypothesized that plants with a strong direct defence have a less efficient indirect defence than plants that are not characterized by a strong direct defence. Table 1 shows the percentage of *T. urticae* that accepted leaves of the test plant species over leaves of lima bean, which is a measure of the direct defence capacity of that plant species (van den Boom *et al.*, 2002). Ginkgo has a strong direct defence mechanism against spider mites (Dabrowski, 1973). Therefore, it is not really necessary for ginkgo to induce synomones for the attraction of predatory mites. However, a slight but significant attraction of the predatory mites to the jasmonic acid-treated leaves was found. This indicates that indirect defence exists in jasmonic acid-treated ginkgo to a minor extent. This effect may even have been stronger if induction through spider mite-feeding on the leaves had occurred. Soybean and hop were highly susceptible to spider mites in contrast to sweet pepper and grapevine, which were poorly accepted by spider mites (van den Boom *et al.*, 2002). However, spider mite-infested leaves of all these plants were highly attractive to predatory mites. Eggplant and cowpea were less susceptible to spider mites than soybean and hop (van den Boom *et al.*, 2002). Spider mite-infested leaves of these plants showed a less prominent predatory mite attraction, although their leaves were quite heavily infested. It might be interesting to use more than three leaves in the olfactometer experiments, although Janssen *et al.* (1997) showed that predatory mites were already attracted by only two lima bean leaves each infested with one hundred *T. urticae* females.

In conclusion, *T. urticae*-infested plants of all species tested emitted induced synomones that attracted the predatory mites. Even jasmonic acid-treated ginkgo leaves that possess a strong direct defence were slightly attractive to predatory mites. Furthermore, both among the Fabaceae (soybean and cowpea) and among the Solanaceae (sweet pepper and eggplant), plant species use indirect defence to defend themselves. However, it remains to be investigated whether all these plant species have a similar mechanism of indirect defence. For instance, plants may produce novel compounds in response to herbivory, which results in a specific blend composition or they may emit a qualitatively similar blend that differs in ratios among blend components (Dicke, 1999b). The emission of novel compounds represents the induction of novel biosynthetic pathways (Paré & Tumlinson, 1997; Dicke, 1999b) and may be seen as a more sophisticated form of

indirect defence than the emission of volatiles through pathways that are also induced by mechanical damage. The type of induced odour production of the plant species tested is currently being examined. The relationship between the specificity of indirect defence and the degree of a plant's direct defence is currently being investigated.

Acknowledgements

The authors would like to thank Herman Dijkman for the supply of spider mites. Henk Smid took care of the plants in the greenhouse. Furthermore we thank the PhD discussion group of the laboratory of Entomology for their comments on a previous version of the manuscript.

References

- Boland, W., Hopke, J., Donath, J., Nüske, J. & Bublitz, F. (1995) Jasmonic acid and coronatin induce odor production in plants. *Angewandte Chemie: International Edition in English* **34**, 1600–1602.
- Boom, C.E.M. van den, van Beek, T.A. & Dicke, M. (2002) Differences among plant species in acceptance by the spider mite *Tetranychus urticae* Koch. *Journal of Applied Entomology*, in press.
- Bruin, J., Dicke, M. & Sabelis, M.W. (1992) Plants are better protected against spider-mites after exposure to volatiles from infested conspecifics. *Experientia* **48**, 525–529.
- Campbell, C.A.M., Pettersson, J., Pickett, J.A., Wadhams, L.J. & Woodcock, C.M. (1993) Spring migration of damson-hop aphid, *Phorodon humuli* (Homoptera, Aphididae), and summer host plant-derived semiochemicals released on feeding. *Journal of Chemical Ecology* **19**, 1569–1576.
- Dabrowski, Z.T. (1973) Studies on the relationships of *Tetranychus urticae* Koch and host plants. II. Gustatory effect of some plant extracts. *Bulletin Entomologique de Pologne* **43**, 127–138.
- Dicke, M. (1994) Local and systemic production of volatile herbivore-induced terpenoids: their role in plant–carnivore mutualism. *Journal of Plant Physiology* **143**, 465–472.
- Dicke, M. (1999a) Direct and indirect effects of plants on performance of beneficial organisms. pp. 105–153 in Ruberson, J.R. (Ed.) *Handbook of pest management*. New York, Marcel Dekker, Inc.
- Dicke, M. (1999b) Evolution of induced indirect defense of plants. pp. 62–88 in Tollrian, R. & Harvell, E.D. (Eds) *The ecology and evolution of inducible defenses*. Princeton, New Jersey, Princeton University Press.
- Dicke, M. & Sabelis, M.W. (1988a) How plants obtain predatory mites as body guards. *Netherlands Journal of Zoology* **38**, 148–165.
- Dicke, M. & Sabelis, M.W. (1988b) Infochemical terminology: based on cost-benefit analysis rather than origin of compounds? *Functional Ecology* **2**, 131–139.
- Dicke, M., van Beek, T.A., Posthumus, M.A., Ben Dom, N., van Bokhoven H. & de Groot, A. (1990a) Isolation and identification of volatile kairomone that affects acarine predator–prey interactions. *Journal of Chemical Ecology* **16**, 381–396.
- Dicke, M., Sabelis, M.W., Takabayashi, J., Bruin J. & Posthumus, M.A. (1990b) Plant strategies of manipulating predator–prey interactions through allelochemicals: prospects for application in pest control. *Journal of Chemical Ecology* **16**, 3091–3118.
- Dicke, M., Takabayashi, J., Posthumus, M.A., Schütte C. & Krips, O.E. (1998) Plant-phytoseiid interactions mediated by herbivore-induced plant volatiles: variation in production of cues and in response of predatory mites. *Experimental and Applied Acarology* **22**, 311–333.
- Dicke, M., Gols, R., Ludeking, D. & Posthumus, M.A. (1999) Jasmonic acid and herbivory differentially induce carnivore-attracting plant volatiles in lima bean plants. *Journal of Chemical Ecology* **25**, 1907–1922.
- Drukker, B., Bruin, J., Jacobs, G., Kroon A. & Sabelis, M.W. (2000) How predatory mites learn to cope with variability in volatile plant signals in the environment of their herbivorous prey. *Experimental and Applied Acarology* **24**, 881–895.
- Gols, R., Posthumus, M.A. & Dicke, M. (1999) Jasmonic acid induces the production of gerbera volatiles that attract the biological control agent *Phytoseiulus persimilis*. *Entomologia Experimentalis et Applicata* **93**, 77–86.
- Janssen, A., Bruin, J., Jacobs, G., Schraag R. & Sabelis, M.W. (1997) Predators use volatiles to avoid prey patches with conspecifics. *Journal of Animal Ecology* **66**, 223–232.
- Kahl, J., Siemens, D.H., Aerts, R.J., Gäbler, R., Kühnemann, F., Preston C.A. & Baldwin, I.T. (2000) Herbivore-induced ethylene suppresses a direct defense but not a putative indirect defense against an adapted herbivore. *Planta* **210**, 336–342.
- Krips, O.E., Willems, P.E.L. & Dicke, M. (1996) Suitability of the ornamental crop *Gerbera jamesonii* for spider mites and the attraction of predators in response to spider mite damage. *Bulletin IOBC/WPRS* **19**, 81–87.
- Krips, O.E., Willems, P.E.L., Gols, R., Posthumus M.A. & Dicke, M. (1999) The response of *Phytoseiulus persimilis* to spider mite-induced volatiles from gerbera: influence of starvation and experience. *Journal of Chemical Ecology* **12**, 2623–2641.
- Paré, P.W. & Tumlinson, J.H. (1997) Induced synthesis of plant volatiles. *Nature* **385**, 30–31.
- Price, P.W. (1981) Semiochemicals in evolutionary time. pp. 251–271 in Nordlund, D.A., Jones, R.L. & Lewis, W.J. (Eds) *Semiochemicals, their role in pest control*. New York, Wiley.
- Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* **11**, 41–65.
- Rhoades, D.F. (1985) Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist* **125**, 205–238.
- Rhoades, D.F. & Cates, R.G. (1976) Toward a general theory of plant antiherbivore chemistry. pp. 168–213 in Wallace, J.W. & Mansell, R.L. (Eds) *Recent advances in phytochemistry, 10: Biochemical interaction between plants and insects*. New York, Plenum.
- Rosenthal, G.A. & Berenbaum, M.R. (1991) *Herbivores, their interaction with secondary plant metabolites*. 2nd edn, vol. 1. New York, Academic Press.
- Sabelis, M.W. (1981) *Biological control of two-spotted spider mites using phytoseiid predators*, PhD thesis, Wageningen University, The Netherlands.
- Sabelis, M.W. & Dicke, M. (1985) Long-range dispersal and searching behaviour. pp. 141–160 in Helle, W. & Sabelis, M.W. (Eds) *Spider mites. Their biology, natural enemies and control*. Amsterdam, Elsevier.

- Sabelis M.W. & van de Baan, H.E.** (1983) Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomologia Experimentalis et Applicata* **33**, 303–314.
- Sabelis, M.W., Afman, B.P. & Slim, P.J.** (1984) Location of distant spider mite colonies by *Phytoseiulus persimilis*: localization and extraction of a kairomone. *Acarology VI* **1**, 431–440.
- Sabelis, M.W., Janssen, A., Pallini, A., Venzon, M., Bruin, J., Drukker, B. & Scutareanu, P.** (1999) Behavioral responses of predatory and herbivorous arthropods to induced plant volatiles: from evolutionary ecology to agricultural applications. pp. 269–296 in Agrawal, A.A., Tuzun, S. & Bent, E. (Eds) *Induced plant defenses against pathogens and herbivores: biochemistry, ecology, and agriculture.*, St Paul, Minnesota, APS Press.
- Takabayashi, J. & Dicke, M.** (1992) Response of predatory mites with different rearing histories to volatiles of uninfested plants. *Entomologia Experimentalis et Applicata* **64**, 187–193.
- Takabayashi, J. & Dicke, M.** (1996) Plant-carnivore mutualism through herbivore-induced carnivore attractants. *Trends in Plant Science* **1**, 109–113.
- Takabayashi, J., Dicke, M. & Posthumus, M.A.** (1991) Variation in composition of predator-attracting allelochemicals emitted by herbivore-infested plants: relative influence of plant and herbivore. *Chemoecology* **2**, 1–6.
- Takabayashi, J., Dicke, M. & Posthumus, M.A.** (1994a) Volatile herbivore-induced terpenoids in plant–mite interactions: variation caused by biotic and abiotic factors. *Journal of Chemical Ecology* **20**, 1329–1354.
- Takabayashi, J., Dicke, M., Takahashi, S., Posthumus, M.A. & van Beek, T.A.** (1994b) Leaf age affects composition of herbivore-induced synomones and attraction of predatory mites. *Journal of Chemical Ecology* **20**, 373–386.
- Turlings, T.C.J., Wäckers, F.L., Vet, L.E.M., Lewis, W.J. & Tumlinson, J.H.** (1993) Learning of host-finding cues by hymenopterous parasitoids. pp. 51–78 in Papaj, D.R. & Lewis, A.C. (Eds) *Insect learning*. New York, Chapman and Hall.
- Vrieling, K., Smit, W. & van der Meijden, E.** (1991) Tritrophic interactions between aphids (*Aphis jacobaeae* Schrank), ant species, *Tyria jacobaeae* L., and *Senecio jacobaea* L. lead to maintenance of genetic variation in pyrrolizidine alkaloid concentration. *Oecologia* **86**, 177–182.

(Accepted 7 July 2002)

© CAB International, 2002