



UvA-DARE (Digital Academic Repository)

Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors

Pallini, A.; Janssen, A.; Sabelis, M.W.

DOI

[10.1007/s004420050147](https://doi.org/10.1007/s004420050147)

Publication date

1997

Published in

Oecologia

[Link to publication](#)

Citation for published version (APA):

Pallini, A., Janssen, A., & Sabelis, M. W. (1997). Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors. *Oecologia*, 110, 179-185. <https://doi.org/10.1007/s004420050147>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

Angelo Pallini · Arne Janssen · Maurice W. Sabelis

Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors

Received: 22 June 1996 / Accepted: 29 September 1996

Abstract Plants under herbivore attack produce volatiles, thus attracting natural enemies of the herbivores. However, in doing so, the plant becomes more conspicuous to other herbivores. Herbivores may use the odours as a cue to refrain from visiting plants that are already infested, thereby avoiding competition for food, or, alternatively, to visit plants with defences weakened by earlier attacks. We investigated the response of one species of herbivore (the spider mite *Tetranychus urticae*) to odours emanating from cucumber plants infested by conspecific or heterospecific (the western flower thrips, *Frankliniella occidentalis*) herbivores. Olfactometer experiments in the laboratory showed that spider mites have a slight, but significant, preference for plants infested with conspecifics, but strongly avoid plants with thrips. These results were substantiated with greenhouse experiments. We released spider mites on the soil in the centre of a circle of six plants, half of which were infested with either conspecifics or heterospecifics (thrips), whereas the other half were uninfested. It was found that 60–70% of the mites were recaptured on the plants within 5 h after release. Results of these experiments were in agreement with results of the olfactometer experiments: (1) significantly fewer spider mites were found on plants infested with thrips than on uninfested plants and (2) more mites were found on plants with conspecifics than on clean plants (although this difference was not significant). From a functional point of view it makes sense that spider mites prefer clean plants over thrips-infested plants, since thrips are not only competitors, but are also known as intraguild predators of spider mites. Possible reasons for the slight attraction of spider mites to plants infested with conspecifics are discussed.

Key words Herbivore · Avoidance · Odour · Competition · Intra-guild predation

Introduction

Plants under attack by herbivores can defend themselves by producing volatile signals that are attractive to natural enemies of the herbivores (for reviews see Tumlinson et al. 1993; Dicke 1994). However, these signals may also be picked up by other herbivores, which may use them in locating new host plants (Dicke et al. 1993). Suppose that a plant under attack by herbivores of species A produces volatiles, and that herbivores of species B are able to perceive these odours. The attack of species A may change the profitability of the plant to species B, through direct competition for the plant, through increased induced resistance of the plant (Karban and Carey 1984), through decreased defence, or through a combination of these factors.

Four scenarios are now possible. First, the presence of species A may decrease the overall profitability of the plant (caused by direct competition, induced resistance, or both), and species B may be better off colonising a host plant that does not carry a population of herbivore A. In this case, species B can be expected to have evolved an avoidance response to plants infested by species A. Second, the reproductive success of herbivore B on plants infested with herbivore A may be increased because the defensive actions of the plant are reduced as a result of the attack of A, and this outweighs the possible negative effects of competition with species A. Now, individuals of species B are expected to be attracted to plants infested by species A. Third, plants with or without herbivore A may be equally profitable for species B, either because competition and defence are unimportant, or because they have opposing, compensatory effects. In this latter case, it can be argued that the production of volatiles by the plants makes it easy for species B to locate the plants. A fourth scenario, which will not be considered further in this paper, is that

A. Pallini (✉)¹ · A. Janssen · M.W. Sabelis
Institute for Systematics and Population Biology,
University of Amsterdam, The Netherlands
fax: (31) 20 5257754; e-mail: pallini@bio.uva.nl

Present address:

¹Department of Animal Biology,
Federal University of Viçosa, Brazil

the reproductive success of species B on plants with herbivore A is decreased as a result of the attraction of a shared predator: the odours perceived by herbivore B can also be used by predators, and these will subsequently attack both herbivore species.

Evidence for the first two scenarios has been found in bark beetles. Some species of bark beetles use aggregation pheromones of heterospecifics to form mixed-species aggregations (Birch et al. 1980; Poland and Borden 1994). The formation of aggregations is thought to enhance rapid colonisation of the tree, thereby overwhelming the resistance mechanisms. Hence it is advantageous for the bark beetles to attack a tree that is already attacked by other species. Of course, this may not be to the advantage of the species that colonised first (see De Jong and Sabelis 1988 for a discussion on the evolution of bark beetle aggregation pheromone systems). In other species of bark beetles aggregation pheromones of heterospecifics are used to avoid visits to trees attacked by other species (e.g. Birch et al. 1980; Byers and Wood 1980; Byers et al. 1984; Byers 1993). Mixed-species aggregations in these cases are thought to reduce fitness of the bark beetles through interspecific competition. Although these examples concern aggregation pheromones that are produced by the bark beetles themselves, and not by the host trees, it clearly shows that herbivores do use odours associated with heterospecifics when selecting hosts.

In this study we investigated responses of spider mites, *Tetranychus urticae* Koch, to volatiles from cucumber plants infested with conspecific or heterospecific herbivores, i.e. the western flower thrips, *Frankliniella occidentalis* (Pergande). These phytophages are pests on many host plants and co-occur on many crops, such as cucumber in greenhouses. A complicating factor in the interactions between these two herbivores is the occurrence of intraguild predation by thrips on spider mites (Trichilo and Leigh 1986). It is known that cucumber plants produce a blend of volatiles when attacked by spider mites (Takabayashi et al. 1994), but it is not known yet whether cucumber plants infested with thrips also release volatiles. Thrips larvae are shown to produce an alarm pheromone upon disturbance, and this alarm pheromone is used for prey location by its natural enemies, the predatory mite *Amblyseius cucumeris* and the anthocorid bug *Orius tristicolor* (Teerling et al. 1993a,b). Olfactometer experiments in our laboratory showed that two species of predatory mite, *Phytoseiulus persimilis* and *A. cucumeris*, are strongly attracted towards cucumber plants infested with western flower thrips (A. Janssen, unpublished work). In these experiments, the thrips were not disturbed, suggesting that the alarm pheromone is not the cause of the attraction. Dicke and Groeneveld (1986) found that another predatory mite, *Amblyseius potentillae*, was attracted to bean leaves infested with *Frankliniella*.

It is known that *T. urticae* females are able to respond to plant odours (Dicke 1986; Gotoh et al. 1993). We specifically hypothesize that spider mites will not visit

plants infested with thrips, thereby avoiding competition and predation. As a first step, responses of spider mites were studied in the laboratory, using a Y-tube olfactometer (Sabelis and van de Baan 1983). It has been argued that responses of mites in controlled conditions in a Y-tube olfactometer may not be found under more natural conditions, where wind speed and direction, and concentrations of volatiles are variable (Zhang and Sanderson 1992). Moreover, olfactometer experiments are not suitable for study of all steps involved in the selection of suitable host plants. Therefore, we designed greenhouse experiments where spider mites were released in the centre of a circle of clean and infested plants, and were recaptured on the plants. The fractions of spider mites recaptured on clean and infested plants were subsequently compared with results of the olfactometer experiments.

Materials and methods

Spider mites and western flower thrips were collected from cucumber plants (var. Venture RZ, Rijk Zwaan, De Lier, The Netherlands) in a commercial greenhouse in Pijnacker, The Netherlands, in May 1994. Spider mites were reared on cucumber plants of the same variety in a climate room (25°C; l:d = 16:8). Thrips were cultured on cucumber plants in a climate box (27°C; l:d = 16:8). Cucumber plants were grown in a climate room until they were 3 weeks old. Subsequently, some plants were infested with spider mites by putting them in the climate room with the spider mite culture and putting one or two small infested cucumber leaves on the plants. Plants were incubated in this way for c. 3 days. To obtain thrips-infested plants, plants were placed in a thrips rearing unit in a climate box for 1 week. In each experiment, infested and clean plants were of the same age with four fully developed leaves. The number of thrips larvae on a plant ranged from 10 to 30. The number of spider mites on infested plants ranged from a few hundred to over 1000 mites per plant. Infestation with thrips and with spider mites both resulted in visual damage to the plants, but, except in some olfactometer experiments, plants were far from being overexploited.

Olfactometer experiments

In a Y-tube olfactometer, spider mites were offered the choice between the odours of clean plants versus plants infested with conspecifics, or the odours of clean plants versus thrips-infested plants (Sabelis and van de Baan 1983; Gotoh et al. 1993). The olfactometer consists of a glass tube in the form of a Y, with a Y-shaped metal wire, painted white, in the middle to channel the mites. The base of the tube was connected to an air pump that produced an air flow from the arms of the tube to the base. Airflow through both arms of the Y-tube was calibrated with a flow meter with needle valves between the air outlet of the containers of the odour sources and the arms of the olfactometer. When wind speeds in both arms are equal, the odours form two neatly separated fields in the base of the Y-tube with the interface coinciding with the metal wire (Sabelis and van de Baan 1983). The wind speed was c. 0.3 m/s in each arm.

Potted plants—either infested or not—served as odour sources, and were placed in a tray (l × w × h = 46 × 30 × 8 cm) that was placed inside a second, water-containing tray (60 × 40 × 4.5 cm). A plexiglas container (50 × 36 × 43 cm) was put over the plants so that it rested in the water-containing outer tray. In this way a water barrier was created to prevent escape of thrips and spider mites, and the water served as an air tight seal for the container at the same time. The containers had an air inlet and outlet (diameter

4 cm) at opposing walls. The inlet and outlet were covered with mite-proof gauze.

Prior to the experiments adult female spider mites were starved for 3 h. As the experiments lasted 2–2.5 h and the mites were tested individually, the mites tested later in the experiment were starved for a longer period. Mites were introduced one at a time, by disconnecting the pump and putting the female on the metal wire at the base of the Y-tube. After the pump was reconnected, the female started moving upwind to the junction of the wire, where she had to choose for one of the two arms. Each individual was observed until she had reached the end of one of the arms or for a maximum of 8 min and was then removed. After removing each mite, the metal wire in the middle of the tube was cleaned with a piece of cotton wool soaked in alcohol (70%) to remove any possible traces (silken threads, faeces) left by the spider mite. Subsequently, the wire was left to dry before the next mite was tested. In this way, we tried to eliminate any effect of spider mite silk or residues deposited on the metal wire on the behaviour of subsequent spider mites (Gotoh et al. 1993). We tested about 20 spider mites per experiment, and the odour sources were switched to the opposite arm of the olfactometer after each 5 mites tested to correct for any unforeseen asymmetry in the experimental set-up. Differences in fractions of mites choosing any of the odour sources were tested using the binomial test.

Release-recapture experiments

Six cucumber plants *c.* 3.5 weeks old were placed in a circle (diam. 80 cm) in a plastic tray (174 × 100 × 19 cm) filled with soil in a greenhouse compartment. Plants were put into the soil so that the rim of the pot was just below the soil surface. Soil was added to the pot so that soil levels inside and outside the pot were equal. The lowest leaf of each plant touched the soil, and care was taken that the distance of this leaf to the centre of the circle was equal for all plants during one experiment. However, distance of the lowest leaf to the centre varied between experiments (14–34 cm). In each experiment, clean and infested plants were alternated, so that each clean plant had two infested neighbours, and vice versa. About 200 adult female spider mites were collected from infested cucumber leaves, and were put in a petri dish (diam. 8 cm), that was placed inside a larger petri dish filled with wet cotton wool. Spider mites were starved in this way for one hour. Subsequently, the petri dish containing the spider mites was positioned in the centre of the circle of plants, and the spider mites were allowed to disperse. As wind speed in the greenhouse was too low to initiate wind dispersal, they could only disperse by walking over the soil. Starting 1 h after release, the plants were checked for spider mites every hour for 4–6 h, and all spider mites found were removed. Because spider mites spend much more time than 1 hour per plant (A. Janssen, personal observations), the numbers of mites found on the plants are not affected by differential arrestment on plants, but reflect the attractiveness of the plants. The next day, all plants were again checked for spider mites; only a few of the released mites were found on the plants.

Two series of experiments were done. In one series, half of the plants were infested with spider mites, whereas in the other half of the plants were infested with thrips larvae. Six replicate experiments, each with a different set of plants, tested clean plants and plants with spider mites, and four of such experiments tested clean plants and thrips-infested plants. In all cases, care was taken that each plant position was occupied with infested plants in half of the experiments, and with clean plants in the other half. This was done to control any unforeseen directionality in mite searching behaviour. To distinguish between spider mites already present on the plant and the mites that arrived on the plant upon release, the lowest leaf of the infested plants was kept clean by isolating it from the rest of the plant with a ring of glue that was applied to the stem just above the petiole of the lowest leaf. Any mites that were found on this lower leaf before the start of the experiment were removed with a brush. Hence, the spider mites released could enter the

lowest leaf from the soil, but mites that were on the other leaves of the plant could only reach it by dropping from higher leaves. The number of mites that did so was quite low (A. Pallini and A. Janssen, personal observations). Results of the release experiments were analysed with multifactor ANOVA of arcsine transformed percentages of mites recaptured (Sokal and Rohlf 1981), with treatment of the plants and positions within the circle as factors.

Results

Olfactometer experiments

T. urticae showed no preference for clean plants or plants infested with conspecifics in 26 out of 33 experiments, whereas we found a significant preference for infested plants in 6 experiments, and a significant preference for clean plants in 1 experiment (Fig. 1). Pooled olfactometer results indicated a slight but significant preference for plants infested with conspecifics (55% of the 850 mites tested chose for infested plants, two-tail binomial test, $P = 0.0082$).

The response of spider mites to plants infested with thrips was much more pronounced (Fig. 2). A significant preference for clean plants was found in three out of five cases, and the trend was in the same direction in the remaining two experiments. Pooled results showed a significant preference for clean plants (28% of the 124 mites tested chose for infested plants, two-tail binomial test, $P = 4.7 \times 10^{-5}$).

Release-recapture experiments

In the release-recapture experiments, the tiny mites had to cross relatively long stretches of barren soil before reaching a plant. Of the released mites 60–70% were recaptured from the plants after 5 h (Fig. 3). A larger fraction of mites was recaptured in experiments with a combination of clean and spider-mite-infested plants than in experiments with clean and thrips-infested plants. This may be due to avoidance of plants infested with thrips, as was observed in the olfactometer.

No significant preference for plants infested with spider mites was found with the release-recapture experiments in the greenhouse (Table 1); infested plants attracted on average 19.3% per plant and clean plants attracted 14.0% of the recaptured mites. There was no significant effect of the position of plants on the fraction of mites recaptured, suggesting that asymmetries in the set-up due to directionality of light or other factors had no effect on choice of the mites (Table 1).

Spider mites showed a significant preference for clean plants compared to thrips-infested plants (Table 2). Clean plants attracted on average 21.6% per plant of all mites recaptured, whereas plants infested with thrips attracted 11.7%, i.e. just over half as many. Again no significant effect of plant position on the fractions of mites recaptured was found.

Fig. 1 Spider mites were offered a choice between the odours of two or three clean cucumber plants and an equal amount of plants infested with conspecifics. Shown are the fractions of spider mites, *T. urticae*, that chose for odours of clean cucumber plants (left) and the fractions that preferred plants infested with conspecifics (right) in a Y-tube olfactometer. Each bar represents one experiment with 20 or more individual mites tested. See text for further explanation. *: $P < 0.05$ (Binomial test). Results are ranked in order of response

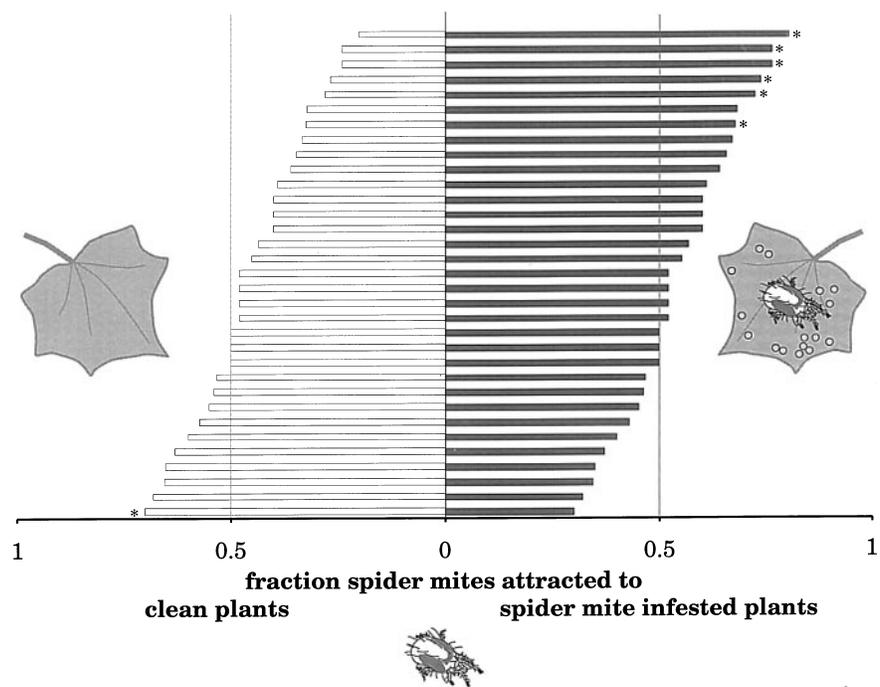


Fig. 2. Spider mites were offered a choice between the odours of two or three clean cucumber plants and an equal amount of plants infested with western flower thrips. Shown are the fractions of spider mites, *T. urticae*, that chose for odours of clean cucumber plants (left) and the fractions that preferred plants infested with thrips (right) in a Y-tube olfactometer. Numbers inside bars indicate number of mites tested. See text for further explanation. *: $P < 0.05$; **: $P < 0.01$ (Binomial test)

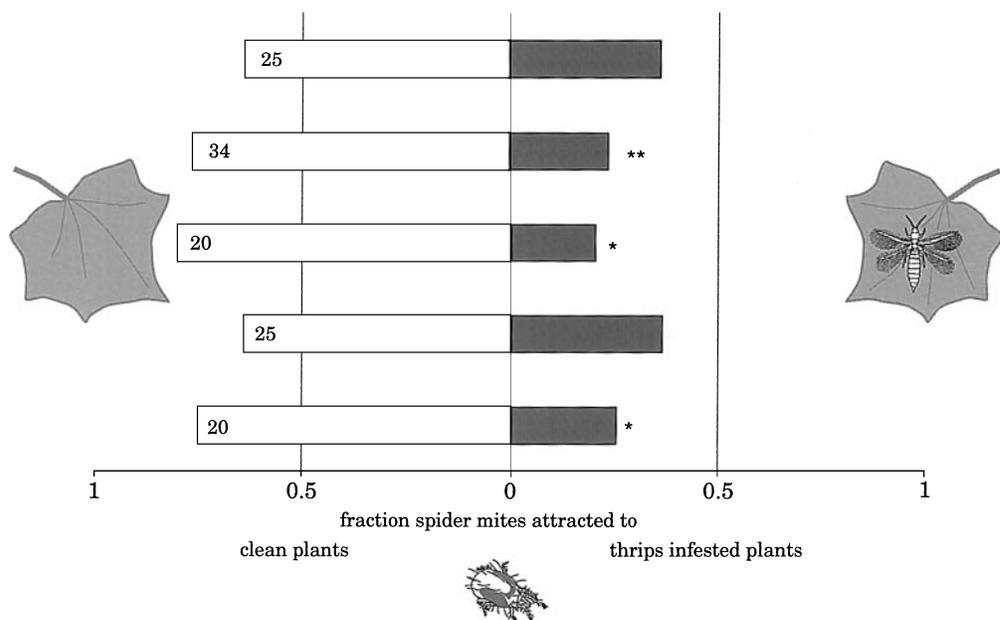


Table 1 Analysis of variance for release-recapture of *Tetranychus urticae* in a circle of clean plants and plants infested with conspecifics. Data are from 6 replicate experiments. Care was taken that each plant position was occupied by infested plants in half of the experiments, and by clean plants in the other half

Source of variation	Sum of squares	df	Mean square	F-ratio	P
Treatment ^a	0.046	1	0.046	3.033	0.0922
Position ^b	0.022	5	0.004	0.287	0.9164
Residual	0.438	29	0.015		
Total	0.506	35			

^a Treatment refers to state of the plants, i.e. clean or infested
^b Position refers to position of the plants in the greenhouse

Table 2 Analysis of Variance for release-recapture of *T. urticae* in a circle of clean plants and plants infested with thrips. Data are from 4 replicate experiments

Source of variation	Sum of squares	df	Mean square	F-ratio	P
Treatment ^a	0.086	1	0.085	4.863	0.0415
Position ^b	0.158	5	0.032	1.814	0.1637
Residual	0.296	17	0.017		
Total	0.539	23			

^a Treatment refers to state of the plants, i.e. clean or infested

^b Position refers to position of the plants in the greenhouse

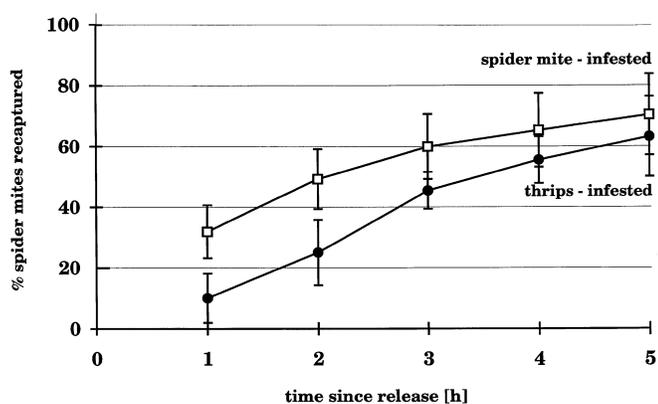


Fig. 3 The cumulative percentage (and standard deviation) of spider mites recaptured as a function of time in greenhouse experiments. Spider mites were released on the soil in the centre of a circle of six cucumber plants, half of which were infested with spider mites (*open squares*) or thrips (*solid circles*). See text for further explanation

Discussion

The olfactometer experiments showed that *T. urticae* is slightly attracted by the odours of plants infested with conspecifics, whereas the odours of plants infested with thrips elicit a – much stronger – avoidance response. Since in olfactometer experiments only a limited part of the behavioural repertoire shown by mites that search for new host plants can be studied, we decided to do release-recapture experiments in the greenhouse. The experiments were designed in such a way that the numbers of mites recaptured were most likely determined by attraction towards the plants, and not by differential arrestment on clean and infested plants. The fraction of mites recaptured on plants infested with spider mites in the greenhouse was 56.7%, remarkably close to that found in the olfactometer experiments (54.5%). Thrips-infested plants in the greenhouse attracted 35.5% of all recaptured mites, and plants with thrips in the olfactometer attracted 28.2%. Note that the time scales of the responses in these two experiments are quite different (10 min vs 24 hours), making comparison difficult. However, our observations suggest that each test ran long enough to reach a stable response fraction. If so, then the similarity in results suggests that the response in the olfactometer is not different from that in the release-recapture experiments. The olfactometer experiments show that spider mites can discriminate between the odours of clean and infested plants, and the

release-recapture experiments show that they use this ability in selecting a host plant under more natural conditions.

Response to plants infested with conspecifics

Spider mites are weakly attracted by plants infested with conspecifics, as shown by the olfactometer and greenhouse experiments. This is a surprising result since Dicke (1986) found that *T. urticae* dispersed away when exposed to the odours of bean leaves infested with conspecifics. This contrast may be due to differences in the volatile signals produced by spider-mite infested bean and cucumber plants. The terpenoid linalool is thought to be responsible for the dispersal behaviour of *T. urticae* (Dicke et al. 1993), and bean plants infested with *T. urticae* produce linalool (Dicke et al. 1990), whereas cucumber plants infested with the same herbivore species do not produce this terpenoid (Takabayashi et al. 1994). Another difference between the two experiments is that the experiments of Dicke (1986) were done in a vertical airflow olfactometer, where the spider mites walk immediately above a static odour gradient, whereas in the experiments described here, especially those in the greenhouse, spider mites were at some distance from the plants. It has been suggested that the dispersal found by Dicke (1986) takes place at a smaller spatial scale, i.e. within a plant (Dicke et al. 1993). Hence, spider mites use odours to localise plants, and subsequently use the odours elicited by parts of the plants that are already occupied by conspecifics to search for empty sites within a plant.

This leaves open the question as to why spider mites would be attracted towards plants infested with conspecifics. This attraction can be understood if so-called positive feedbacks of consumer population densities on resource supply occur (Bianchi et al. 1989). Kennedy (1995) showed that such positive feedbacks occur in mites: the intrinsic growth rate of a phytophagous mite (*Brevipalpus phoenicis*) increased with mite density. If intrinsic growth rates of *T. urticae* also increase with spider mite density, mites would be better off when selecting infested rather than clean plants. However, in some olfactometer experiments, we found significant preference for infested plants even when heavily infested plants with more than 6000 adult spider mites per plant were used as an odour source. The plants died soon after

the end of the experiment as a result of the infestation. It is difficult to envisage that positive feedback would play a role with such high mite densities, resulting in poor quality of the host plant.

An alternative explanation for a preference of spider mites for plants infested with conspecifics may be that infested plants are already covered by the web produced by spider mites. This web may protect the mites against attacks by some species of predator (Sabelis and Bakker 1992). Since it takes some time to produce a web that is sufficiently dense enough to offer such protection, it may be beneficial for spider mites to move to plants where this web is already present. However, other species of predators are not hindered by the webbing, and some of these predators are attracted by odours from plants with spider mites. The fitness consequences of selecting an infested or a clean plant will then depend on the balance between reduced predation by some predators, and increased predation by others.

Response to plants infested with heterospecifics

The olfactometer experiments and the release-recapture experiments show that spider mites are able to recognise thrips-infested plants from a distance through the odours emitted by the plant-herbivore complex. These odours should then be different from the odours produced by plants infested with spider mites, either qualitatively or quantitatively, because spider mites respond differently to plants infested with spider mites compared to thrips-infested plants. Chemical analyses of the space around cucumber plants infested with thrips may elucidate the identity of the volatiles, and subsequently, these can be compared to the volatiles identified by Takabayashi et al. (1994) for cucumber infested with spider mites.

As already mentioned, western flower thrips are not only competitors, but can also act as predators of spider mites (Trichilo and Leigh 1986). By avoiding plants with thrips, spider mites avoid not only competition for the host plant, but also intraguild predation by thrips. Intraguild predation in a simple system consisting of three species may lead to all sorts of population dynamical patterns such as exclusion of one of the herbivores, coexistence of both species, increases in resource (= plant) levels, and others (Pimm and Lawton 1978; Polis et al. 1989; Polis and Holt 1992). Therefore, this kind of complex trophic interaction can also influence the pest status and the success of biological control of spider mites and thrips in crops where they co-occur. The reduced attractivity of thrips-infested plants to spider mites partly precludes these complex interactions, but obviously it is of equal importance to determine the response of adult thrips to the odours of spider-mite-infested and clean plants. If adult thrips actually prefer plants infested with spider mites to clean plants, competition and intraguild predation will still occur, but its effect on overall population dynamics may be less pro-

nounced because one of the two herbivores avoids places where the other is present. The response of adult thrips to the odours of clean and infested plants is presently under study.

Odour-mediated avoidance

Odour-mediated avoidance is not a feature of herbivores alone, but has also been found in members of the third trophic level. For example, a parasitoid of *Drosophila* larvae, *Leptopilina heterotoma*, uses odours associated with the presence of conspecific and heterospecific parasitoids to discriminate from a distance between patches, and avoids visiting patches with competitors using this volatile information only (Janssen et al. 1995a,b). It was found that the odour of heterospecific or conspecific parasitoids alone was not sufficient to induce this avoidance behaviour in downwind parasitoids, but that avoidance occurred only when competitors were actively searching and ovipositing (Janssen et al. 1995b). Another example of odour-mediated interactions within the third trophic level is that of a predatory mite, *Phytoseiulus persimilis*, that discriminates between odours from spider mite patches with and without conspecific predators. This predator also avoids visiting patches with conspecifics (Janssen et al. 1997).

It can be concluded that both members of the second and third trophic level can use odours to avoid inter- and/or intraspecific competition. Odour-mediated avoidance can affect the structure of insect communities and the occurrence and severity of competition and intraguild predation (Polis and Holt 1992). Therefore, it is important to study the occurrence of avoidance in natural communities, and in the artificial communities that arise in crops invaded by several species of herbivores whose natural enemies are subsequently released by man.

Acknowledgements We would like to thank Ludek Tikovský and Jaap Fontijn for arranging greenhouse space and for their patience with the climate control system, and Rijk Zwaan B.V., De Lier, for providing cucumber seeds. J. Bazuin, Pijnacker, kindly allowed us to collect spider mites and thrips in his greenhouse. Comments by Hans Breeuwer, Jan Bruin, Marcel Dicke, and an anonymous reviewer improved the manuscript. Robert Lingeman gave statistical advice. A.P. was supported by CNPq/Brasilia/Brazil. A.J. was supported by the Life Sciences Foundation (SLW), which is subsidised by the Netherlands Organisation for Scientific Research (NWO).

References

- Bianchi TS, Jones CG, Shachak M (1989) Positive feedback of consumer population density on resource supply. *Trends Ecol Evol* 4:234–238
- Birch MC, Svirha P, Paine TD, Miller JC (1980) Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. *J Chem Ecol* 6:395–414
- Byers JA (1993) Avoidance of competition by bark beetle species, *Ips typographus* and *Pityogenes chalcographus*. *Experientia* 49:272–275

- Byers JA, Wood DL (1980) Interspecific inhibition of the response of the bark beetles *Dendroctonus brevicomis* and *Ips paraconfusus* to their pheromones in the field. *J Chem Ecol* 6:149–164
- Byers JA, Wood DL, Craig J, Hendry LB (1984) Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. *J Chem Ecol* 10:861–877
- De Jong MCM, Sabelis MW (1988) How bark beetles avoid interference with squatters: an ESS for colonization by *Ips typografus*. *Oikos* 51:88–96
- Dicke M (1986) Volatile spider-mite pheromone and host-plant kairomone, involved in spaced-out gregariousness in the spider mite *Tetranychus urticae*. *Physiol Entomol* 11:251–262
- Dicke M (1994) Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. *J Plant Physiol* 143:465–472
- Dicke M, Groeneveld A (1986) Hierarchical structure in kairomone preference of the predatory mite *Amblyseius potentillae*: dietary component indispensable for diapause induction affects prey location behaviour. *Ecol Entomol* 11:131–138
- Dicke M, Beek TA van, Posthumus MA, Ben Dom N, Bokhoven H van, Groot AE de (1990) Isolation and identification of volatile kairomone that affects acarine predator-prey interactions. *J Chem Ecol* 16:381–396
- Dicke M, Bruin J, Sabelis MW (1993) Herbivore-induced plant volatiles mediate plant-carnivore, plant-herbivore and plant-plant interactions; talking plants revisited. In: Schultz J, Raskin I (eds) *Plant signals in interactions with other plants*. American Society of Plant Physiologists, Rockville, Maryland, USA, pp 182–196
- Gotoh T, Bruin J, Sabelis MW, Menken SBJ (1993) Host race formation in *Tetranychus urticae*: genetic differentiation, host plant preference, and mate choice in a tomato and a cucumber strain. *Entomol Exp Appl* 68:171–178
- Janssen A, Alphen JJM van, Sabelis MW, Bakker K (1995a) Odour-mediated avoidance of competition in *Drosophila* parasitoids: the ghost of competition. *Oikos* 73:356–366
- Janssen A, Alphen JJM van, Sabelis MW, Bakker K (1995b) Specificity of odour-mediated avoidance of competition in *Drosophila* parasitoids. *Behav Ecol Sociobiol* 36:229–235
- Janssen A, Bruin J, Jacobs G, Schraag R, Sabelis MW (1997) Predators use volatiles to avoid prey patches with conspecifics. *J Anim Ecol* 66 (in press)
- Karban R, Carey JR (1984) Induced resistance of cotton seedlings to mites. *Science* 225:53–54
- Kennedy JS (1995) Functional ecology of the false spider mite, *Brevipalpus phoenicis* (Geijskes). PhD thesis, Université Catholique de Louvain
- Pimm S, Lawton J (1978) On feeding on more than one trophic level. *Nature* 275:542–544
- Poland TM, Borden JH (1994) Semiochemical-based communication in interspecific interactions between *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Coleoptera: Scolytidae) in lodgepole pine. *Can Entomol* 126:269–276
- Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol Evol* 7:151–154
- Polis GA, Myers CA, Holt R (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330.
- Sabelis MW, Baan HE van de (1983) Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomol Exp Appl* 33:303–314
- Sabelis MW, Bakker FM (1992) How predatory mites cope with the web of their tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp Appl Acarol* 16:203–225
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edn. Freeman, New York
- Takabayashi J, Dicke M, Takahashi S, Posthumus MA, Beek TA van (1994) Leaf age affects composition of herbivore-induced synomones and attraction of predatory mites. *J Chem Ecol* 20:373–386
- Teerling CR, Gillespie DR, Borden JH (1993a) Utilization of western flower thrips alarm pheromone as a prey-finding kairomone by predators. *Can Entomol* 125:431–437
- Teerling CR, Pierce HD, Borden JH, Gillespie DR (1993b) Identification and bioactivity of alarm pheromone in the western flower thrips, *Frankliniella occidentalis*. *J Chem Ecol* 19:681–697
- Trichilo PJ, Leigh TF (1986) Predation on spider mite eggs by the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem *Environ Entomol* 15:821–825
- Tumlinson JH, Turlings TCJ, Lewis WJ (1993) Semiochemically mediated foraging behavior in beneficial parasitic insects. *Arch Insect Biochem Physiol* 22:385–391
- Zhang Z-Q, Sanderson JP (1992) Short-distance location of spider mite colonies by three predatory mites (Acari: Tetranychidae, Phytoseiidae): predator responses to prey- and predator-associated stimuli. *Environ Entomol* 21:799–807