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REPORT

Predators induce interspecific herbivore competition for food in refuge space

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Abstract

Resource competition among herbivorous arthropods has long been viewed as unimportant because herbivore populations are controlled by predators. Although recently resurrected as an organizing force in arthropod communities on plants, there is still general agreement that resource competition among herbivores is reduced by predators. Here we show the reverse: predators induce interspecific resource competition among herbivores. We found that thrips larvae (*Frankliniella occidentalis*) use the web produced and inhabited by the spider mite *Tetranychus urticae* as a refuge from predation by the phytoseiid mite *Neoseiulus cucumeris*. Thrips larvae prefer clean plant parts, but move into the web upon perceiving volatile cues associated with thrips and predators. This behaviour leads to lower predation risk, but also to reduced developmental rate and lower production of thrips larvae due to competition with spider mites. In addition, thrips larvae consume spider-mite eggs. Thus, predators induce interspecific competition and intraguild predation among herbivores within refuge space, even when host plants have an overall green appearance.

Keywords

Antipredator behaviour, biological control, interspecific herbivore competition, odour, refuge.

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INTRODUCTION

There has been intense debate concerning the importance of competition among herbivores, starting with the hypothesis by Hairston *et al.* (1960) that predicts that competition among herbivores would be unimportant in systems consisting of three trophic levels because herbivores are kept in check by predators. Lawton & Strong (1981) reviewed evidence for the importance of competition among folivorous insects, and provided alternative explanations for community patterns that were thought to be caused by competition. Later studies show that competition among herbivores can be substantial (for review, see Sih *et al.* 1985; Denno *et al.* 1995). The differences of opinion concern the importance and occurrence of predation as a factor that reduces competition, but there is general agreement among ecologists that if predation on herbivore populations occurs, it should reduce herbivore competition (Oksanen *et al.* 1981, 1996; Schoener 1983; Strong *et al.* 1984; Cornell *et al.* 1998). Strikingly, all of the studies mentioned above are based on population-level phenomena rather than on the underlying mechanisms, and some of these phenomena may be

caused by indirect interactions other than resource competition (e.g. “apparent” competition; Holt 1977, 1984). It is therefore necessary to study interactions between individuals in detail to reveal competitive interactions. Here, we analyse the behaviour of an herbivorous arthropod (thrips) in response to the presence of a predator (predatory mites) and a competitor (spider mites), and show that the presence of predators causes an increase, rather than a decrease, in competition between two species of herbivores.

THE EXPERIMENTAL SYSTEM

We investigated refuge use of larvae of the western flower thrips, *Frankliniella occidentalis* (Pergande), in response to the threat of predation by the phytoseiid mite *Neoseiulus cucumeris* (Oudemans). The thrips is an important pest in several crops in Europe and North America (Lewis 1997). Natural enemies such as the predatory mite *N. cucumeris* are used for thrips control. The thrips are often found to attack the same plants as another arthropod pest, the two-spotted spider mite, *Tetranychus urticae* Koch, for instance in cotton fields in Australia (Wilson *et al.* 1996), USA

(Trichilo & Leigh 1986), and in greenhouse cucumbers in Western Europe. Besides competing for host plants, these two generalist herbivores can interact in other ways (Janssen *et al.* 1998), such as through intraguild predation by thrips on spider-mite eggs (Trichilo & Leigh 1986).

When released in cucumber greenhouses to control thrips, *N. cucumeris* predominantly attacks the first instar larvae (Bakker & Sabelis 1989). Although it can also feed on two-spotted spider mites, *N. cucumeris* is not considered an effective predator of these mites, because it is hindered by the dense sticky web produced by this prey (Sabelis & Bakker 1992). The web is thought to be produced as a sort of refuge that protects spider mites against predation: many predator species are hindered by the web, although some species are capable of hunting for spider mites inside the web (Sabelis & Bakker 1992). In greenhouse crops where biological control with *N. cucumeris* is applied, thrips larvae are often found aggregated in spider-mite webs (P.C.J. Rijn and Y.M. van Houten, personal observation). This is somewhat puzzling because we previously found that two-spotted spider mites prefer odours from clean plants over odours from plants infested by thrips (Pallini *et al.* 1997). In this way spider mites avoid resource competition and intraguild predation. Adult thrips, however, do not avoid plants infested with spider mites, but they are also not attracted to them (Janssen *et al.* 1998). It is therefore not clear why thrips larvae in greenhouses aggregate in spider-mite webbing. One reason may be that thrips prey on spider-mite eggs, and the combination of spider-mite eggs and plant tissue is a food source superior to plant tissue only. This is supported by experiments on a closely related thrips species, *F. schultzei* Trybom, which has increased developmental rate and fecundity when reared on a combination of undamaged leaf tissue and spider-mite eggs (Milne & Walter 1997). Another explanation for the observed aggregations of thrips larvae inside spider-mite webbing is that thrips larvae use the refuge produced by their competitors (and intraguild prey) to hide from their own natural enemies. In this paper we test both hypotheses, and we argue that resource competition between two herbivores can be increased by a predator. The optimality of refuge use is also discussed.

METHODS

Stock cultures

Spider mites and western flower thrips were collected from cucumber (var. Ventura RZ[®], RijkZwaan, De Lier, The Netherlands) in a commercial greenhouse 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 Ventura cucumber plants in a climate box (27°C; l:d = 16:8). Clean cucumber plants were grown in a climate room until they were 3 weeks old. Subsequently, plants were infested with thrips by putting them in a climate box containing a thrips culture. Plants were incubated in this way for 1 week.

Preparation of unwebbed and webbed leaf discs

Discs ($\phi = 2.5$ cm) were punched from leaves of 3-week-old pest-free cucumber plants. The discs were placed on sponges (15 × 9 × 4 cm) covered with wet cotton wool and these were kept in trays containing water in a climate room (25°C; l:d = 16:8). Each tray accommodated just one sponge with six leaf discs. Webbed discs were produced by placing 30 adult females of *T. urticae* on each disc for 2 days. Thereafter, the females were carefully removed, leaving the discs with web, spider-mite eggs and faeces. This resulted in discs that were entirely covered with a fine layer of web, and were slightly damaged by feeding spider mites, with the damage scattered over the entire disc. Unwebbed and webbed discs were kept in separated sets of trays in the climate room.

Thrips life history

Developmental time and fecundity were measured after placing individual newly hatched first instar larvae on unwebbed or on webbed leaf discs, one larva per disc, that were then held in a climate room (25°C; l:d = 16:8). Each treatment had 20 replicates, and thrips were transferred to new discs, webbed or unwebbed, every second day to ensure constant disc quality. Survival and developmental stage were scored daily. Females that emerged from these leaf discs were mated once with males from the stock culture. They were allowed to oviposit on webbed or unwebbed leaf discs, whereafter the production of thrips larvae was scored by counting the number of emerged larvae (thrips eggs are inserted in the leaf tissue and could not be counted without damaging the leaf). Data were analysed by a Mann–Whitney *U* test.

Predation rate

Five first-instar thrips larvae were placed on 20 unwebbed and 20 webbed leaf discs. After 1 day, each disc received one female of the predatory mite *N. cucumeris* that was starved for 3 h starting from a well fed state. Predation was recorded 1 day later by counting the number of live larvae and the remains of predated larvae on each disc. Data on the number of thrips consumed were analysed by a Mann–Whitney *U* test.

Two-choice experiments without exposure to odours

Leaf discs were treated so as to obtain one half covered by spider-mite web and one half without. A string of wet cotton wool served as a barrier to confine 30 web-producing spider-mite females on one half of the disc. After 2 days, the spider mites and the barrier were removed, and a bent entomological pin was stuck through the centre of each disc (Dicke & Dijkman 1992). Subsequently, one first instar thrips larva was placed on each pin, allowing access to both halves of the disc. Experiments were repeated three times with 20 replicates each. Leaf discs were kept separately during the trials. The position of thrips larvae was scored after 30 min and 1 day. Differences in fractions of larvae choosing either of the two disc halves were tested using the binomial test.

Two-choice experiments with exposure to predator odours

Discs that were half covered with spider-mite web were obtained as described above. They were now placed inside two boxes (Janssen *et al.* 1997), 12 discs in each, and one first instar thrips larva was introduced on the unwebbed side of each disc. Discs were randomly orientated with respect to the position of the webbed halves inside the boxes to avoid, for instance, any unforeseen effect due to anemotaxis. The boxes were then closed with a transparent parafilm-sealed lid. Each box was connected to the odour source via a hose (diameter 6 mm) with a flow meter. Three 3-week-old potted cucumber plants infested with ≈ 60 thrips larvae each served as an odour source, and were placed in a tray ($46 \times 30 \times 8$ cm) that was placed inside a second, water-containing tray ($60 \times 40 \times 4.5$ cm). A plexiglas container ($50 \times 36 \times 43$ 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 the arthropods, 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 covered with mite-proof gauze. Eighty adult female predatory mites were added in one of the two containers on the day before starting the experiment. By connecting the boxes with leaf discs to the vacuum system of the building, air from the containers was pulled through a flow meter over the leaf discs with thrips larvae. Hence, one box with 12 leaf discs with thrips larvae received odours from plants with conspecifics and predators, whereas the other box received odours from plants with conspecifics only. The airflow (0.13 l/s) was regulated with the valves of the flow meter. Observations were done as described in the previous section. Differences in fractions of thrips larvae choosing either of the two disc halves were tested against the null hypothesis of

equal distribution using the two-sided binomial test. The experiment was repeated three times with different thrips larvae, leaf discs, and groups of plants, thereby avoiding pseudoreplication (Hurlbert 1984). Hence, the unit of replication is the set of leaf discs that was exposed to the same odour source.

RESULTS

Thrips life history

We measured thrips life history on dama webbed and undamaged-unwebbed leaf discs, with the damaged leaf discs containing spider-mite eggs. We found that thrips developed slower from first instar larva to pupa on webbed discs (mean $\pm$ SD = 10.57 ± 0.35 days) than on unwebbed discs (7.88 ± 0.33) ($P = 0.000022$; Fig. 1a), despite the fact that the larvae did feed on both spider-mite eggs and leaf tissue inside the web. In addition, the effective production of thrips larvae was significantly lower on webbed discs (0.71 ± 1.47 larvae/female on webbed discs *versus* 10.57 ± 1.47 larvae/female on unwebbed discs, $P < 0.014$; Fig. 1b).

Predation rate

To test whether spider-mite web offers protection to thrips, we measured predation of thrips larvae by *N. cucumeris* on leaf discs that were either clean or covered with web. Predation rate was significantly ($P = 0.028$) lower on webbed leaf discs (0.90 ± 0.27 larvae killed in one day) than on unwebbed discs (1.75 ± 0.27) (Fig. 2), suggesting that thrips larvae benefit from hiding in the refuge created by spider mites, their competitors.

Two-choice experiments without exposure to odour

We carried out two-choice experiments to test whether thrips larvae prefer the unwebbed or webbed side of a leaf disc. Thirty minutes after release, larvae were found on

Figure 1 Developmental time (a) and fecundity (b) of *F. occidentalis* on unwebbed and webbed leaf discs. Averages and standard deviations are from 20 replicates for each treatment. Data were analysed by a Mann-Whitney *U* test. (a) $**P = 0.000022$; (b) $**P < 0.014$. See text for further explanation.

Figure 2 Average predation (plus standard deviation) of *N. cucumeris* on first instar larvae of western flower thrips in the absence (left bar) or presence (right bar) of spider-mite web. Averages and standard deviations are from 20 replicates for each treatment. Difference in predation rate on webbed versus unwebbed leaf discs is significant ($P = 0.028$, Mann–Whitney U test). See text for further explanation.

both the unwebbed and the webbed side, with a slightly (but not significantly) larger fraction of larvae on the unwebbed side in two of the three replicates (top bar graph in Fig. 3). After 1 day, most of the larvae were found on the clean disc half (bottom graph in Fig. 3). Although this effect was not significant in any of the three replicates, the overall fraction of larvae found on the clean half was significantly larger than 0.5 (two-sided binomial test on pooled data, $P = 0.0033$).

Two-choice experiments with exposure to predator odours

Larvae that were exposed to odours from plants with conspecific thrips plus predators (*N. cucumeris*) were already mainly found inside the web after 30 min in two of the three replicates (Fig. 4, top-left graph); the overall fraction of larvae found on the webbed half was significantly larger than 0.5 (binomial test on pooled data, $P = 0.02$). After 1 day, the fraction of larvae in the web was significantly larger than the fraction outside the web in two of three experiments, whereas the third replicate showed the same trend (Fig. 4, bottom-left graph); the overall fraction of larvae found in the web again differed significantly from 0.5 (binomial test on pooled data, $P = 0.00001$). As a control, we simultaneously tested the behaviour of larvae that were exposed to odours from thrips-infested plants without predators. After the first 30 min, those larvae were found on both the unwebbed and the webbed side, with an overall slightly but not significant larger fraction of larvae on the unwebbed side (Fig. 4, top-right graph). After 1 day, however, most of the larvae were found on the clean disc half with a significant larger fraction in two of three replicates (Fig. 4, bottom-right graph) (binomial test on

Figure 3 Fraction of thrips larvae found on the unwebbed (white bars) and webbed (black bars) half of a leaf disc. Shown are data from 30 min (top bar graph) and 1 day (bottom) after release of the larvae. Each bar represents an independent experiment with 20 larvae tested individually on a leaf disc. See text for further explanation.

pooled data, $P = 0.0003$). The numbers of thrips larvae found on clean leaf disc halves in the presence of predator odours were compared with those in the absence of predator odours (Fig. 4). Based on the fractions observed on clean leaf disc halves in the absence of predator odours, we calculated the expected numbers of larvae on clean halves in the presence of predator odours. A χ^2 -test revealed that the number of thrips larvae observed on the clean halves in the presence of the predators differed significantly from this expectation after 30 min and 1 day ($\chi^2 = 5.5$, $P < 0.02$; $\chi^2 = 18.89$, $P < 0.0001$, respectively).

DISCUSSION

We hypothesize that thrips optimize the use of webbed leaf areas as refuges from predation (Werner & Gilliam 1984). In the absence of predators, young thrips larvae prefer to feed on clean leaf parts (Figs 3 and 4, right-hand

Figure 4 Thrips larvae were offered a choice to stay on the unwebbed half or to move to the webbed half of a leaf disc while exposed to odours from three plants infested with thrips larvae with (left graphs) or without (right graphs) predators. Each bar represents the fraction of 12 thrips larvae in an independent experiment that chose the unwebbed half (white bars) or the webbed half (black bars) of a leaf disc 30 min and 1 day after release of the larvae. See text for further explanation. ** $P < 0.01$ (binomial test).

side), whereas in the presence of predators they move into the webs produced by their competitor (Fig. 4, left-hand side). By moving into the web, western flower thrips suffer from competition. The lower developmental rate of thrips larvae when maturing inside the web is caused by a lower quality of food present inside the web, due to feeding by spider mites, hence, by competition for food. Adult thrips raised inside the web also show a lower production of offspring than adults raised on clean leaves. This may in turn result from a higher mortality of the eggs due to the diet of the ovipositing adults or because adult females avoid ovipositing on webbed leaves, being an unfavourable microhabitat. Because spider-mite eggs were present on the webbed leaf area and thrips larvae did feed on them, the disadvantages of residing on webbed leaves are not compensated by the increased opportunity to feed on spider-mite eggs, and it is therefore likely that only the reduced risk of predation compensates the negative effects of living inside the web. This is further confirmed by the fact that thrips larvae prefer to remain outside the web when they do not run the risk of being preyed upon; inside the refuge, thrips will compete for food with spider mites. It may be possible to test the role of food competition by repeating the experiments either with leaves or other substrates that are webbed but

experience no feeding damage by the spider mites, or with similar (webbed, but undamaged) leaves with an added resource value achieved by placing spider-mite eggs in the web. That addition of spider-mite eggs increases the resource value follows from experiments by Milne & Walter (1997). They showed that the developmental rate of a closely related thrips species (*F. schultzei* Trybom) increased when offered spider-mite eggs (but no web) in addition to undamaged leaf tissue. Thus, the consumption of intraguild prey seems to promote reproductive success of the thrips and may therefore make webs harbouring spider mites a relatively more attractive place. It is also important to note that older thrips larvae run a lower risk of being eaten by predators because they can defend themselves (Bakker & Sabelis 1986). Hence it would be expected that these second-instar larvae would not move to a webbed leaf area when perceiving the presence of predators (a so-called ontogenetic niche shift; Werner & Hall 1988).

In the two-choice test with exposure to predator odours, on average 68.3% of the larvae were found inside the web (from 30 min after the start of the exposure), whereas only 31.1% of the larvae that were exposed to odours without predators were found in the web. If these percentages are an indication for the average time expenditure of individual larvae, it is clear that each larva spends a considerable amount of time inside the web when only the odour of predators is present. Probably, they will even spend more time inside the web when predators themselves are actually present in the vicinity. Given the large differences in rate of development and production of thrips larvae on leaves with and without web, this will inevitably lead to a reduction in growth and reproduction.

Testing the hypothesis on optimal refuge use is not straightforward, however, because the risk of predation may vary with the number and type of predators, and the intensity of food competition depends on the number of spider mites as well as on the number of conspecific larvae. Thus, optimal refuge use depends on population variables and their distribution over the two microhabitats (webbed or unwebbed leaves).

These considerations have interesting implications for future research because one may wonder where the information on predators, competitors, and refuge space is coming from and how reliable the information is. It is not known whether the odours stimulating the thrips to move into the web are produced by the thrips larvae on the plants in the odour source, by the predators, or by thrips and predators together. We do not expect the predators to betray themselves; thrips are more likely candidates for information release. Indeed, when attacked by predators (Bakker & Sabelis 1989) they are known to produce a droplet of rectal fluid, which contains volatile compounds

that function as alarm pheromones (Teerling *et al.* 1993). The primary function of the alarm pheromone is probably to warn related thrips larvae nearby, but upon releasing this information the larvae cannot prevent other non-related thrips larvae from exploiting the information as well. Possibly, in our experiments, these pheromones stimulated the downwind thrips larvae to seek refuge in the web. Whether these alarm pheromones contain information on the type of predator, their abundance, and hence the exact risk of predation, is an open question for further investigation.

In conclusion, thrips do less well in webbed refuges but prefer these safer microhabitats when predators are around. On plants with spider mites, thrips larvae therefore face a conflict between their demand for higher food quality and their higher risk of being eaten by predators. Because of the costs associated with residing in the refuge, thrips should avoid the web when not threatened by predators. Indeed, in the absence of cues associated with predators, thrips larvae prefer to stay outside the webbed area, but when facing predation risk thrips larvae seek protection in the refuge constructed by its heterospecific competitor. In general, anti-predator behaviour incurs costs such as a reduction of consumption rate and changes to a lower quality diet leading to a decrease in survival, growth rate, and developmental rate (Heads 1986; Dixon & Baker 1988; Lima & Dill 1990; Stamp & Bowers 1993). For thrips, there are additional costs involved because they move into refuges that are already occupied by heterospecific competitors; however, they are able to minimize costs by assessing predation risk (mediated by volatiles), by deciding when and where to escape from predators, and by feeding on their inter-specific competitors. Hence, thrips may well benefit from a flexible response to changes in predation risk and the degree of competition in the web.

The consequences of predator-induced refuge use at the population level are not easy to predict. First, it reduces the rate of thrips population growth due to interspecific and intraspecific food competition within the refuge. Second, it increases reproductive success of the thrips by avoiding predation. Third, predators may move to other areas when their prey hide in refuges. The overall impact on the population level of the herbivore may therefore be positive as well as negative. Assessing the population consequences will be a major task for ecologists and biological control workers. In any case, one consequence will be increased competition among herbivores within refuge space. This is an important message because it provides a clear-cut behavioural mechanism explaining why there is substantial indirect evidence for direct interspecific competition among plant arthropods (Denno *et al.* 1995), even when densities of herbivorous arthropods are kept low by

natural enemies (Strong *et al.* 1984) and plants retain an overall green appearance (Hairston *et al.* 1960).

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BIOSKETCH

Angelo Pallini's research interests are arthropod ecology and biological control, focusing on behaviour and its effects on population dynamics of food webs of plant-inhabiting arthropods.

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