

SHORT COMMUNICATION

Consequences of thrips-infested plants for attraction of conspecifics and parasitoids

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Introduction

Tri-trophic interactions among plants, herbivores, and natural enemies of herbivores are important in determining the abundance and distribution of organisms in natural and managed ecosystems. Understanding of the complexity of these interactions has grown tremendously since Price *et al.* (1980) wrote a seminal review of the topic. In particular, the role that the plant–herbivore interaction plays in affecting the third trophic level is of growing interest (Takabayashi & Dicke, 1996; Agrawal & Rutter, 1998; Thaler, 1999). Plants infested with herbivores release cues that can provide information to herbivores, predators, and parasitoids in the surrounding community. A growing body of theory and laboratory evidence suggests that herbivores avoid herbivore-infested plants, predators avoid predator-infested plants, and parasitoids are attracted to herbivore-infested plants (Janssen *et al.*, 1995, 1997; Turlings *et al.*, 1995; Karban & Baldwin, 1997; Pallini *et al.*, 1997).

Tri-trophic interactions may be mediated in part by odours or volatiles given off by the plant–herbivore complex. For example, many experiments have demonstrated that herbivore-damaged plants release particular volatile chemicals that attract natural enemies of herbivores (Sabelis & van de Baan, 1983; Takabayashi & Dicke, 1996; De Moraes *et al.*, 1998). Plants alone, herbivores alone, and mechanically damaged plants are often less attractive to natural enemies of herbivores than are herbivore-infested plants. The generality of such interactions and the potential to exploit them in agriculture relies on the fact that they are operative in many systems under field conditions. A few recent field studies have documented that damaged plants attract natural enemies (Drukker *et al.*, 1995; Shimoda *et al.*, 1997; Agrawal, 1998a; De Moraes *et al.*, 1998; Agrawal & Dubin-Thaler, 1999).

A field study was conducted of the tri-trophic interactions among cotton plants *Gossypium hirsutum* var. Acala SJ-2, herbivorous spider mites *Tetranychus urticae*, and omnivorous thrips *Frankliniella occidentalis*. The thrips consume plant material as well as mite eggs, and are thus potentially competitors and predators of spider mites (Trichilo & Leigh, 1986). The goal of the study was to address how plants infested with mites or thrips would affect the colonisation of plants by naturally occurring arthropods.

Materials and methods

A cotton field was established at Davis, California (38°32'N, 121°44'W) by manually seeding five rows. The plot was surrounded by other agricultural fields. One hundred and twenty-one pairs of plants were separated by approximately 2 m, and each pair was covered by a cage. The cages were made of No-Thrips™ mesh ($\approx 150 \mu\text{m}$) (Greentek, Inc., Edgertown, Wisconsin), which prevented visual or tactile cues from being used by arthropods outside the cage. The cages were buried at the bottom and sealed at the top, not allowing immigration or emigration of arthropods.

After the first two true leaves of the plants were fully expanded, the cages were assigned randomly to one of three treatment groups: (1) each plant infested with ≈ 24 spider mites from a laboratory colony maintained on cotton (all stages, mean \pm SE, 23.86 ± 3.4); (2) each plant infested with ≈ 25 adult thrips that were field-collected individually from *Brassica* sp. flowers; (3) each plant infested with ≈ 24 mites and ≈ 25 thrips. There were 40 replicates of each treatment and approximately equal numbers of each treatment in each row. The arthropod introductions were successful and after 2 weeks the populations were as follows: treatment 1, 415.7 ± 78.7 mites; treatment 2, 35.2 ± 5.6 thrips; treatment 3, 264.4 ± 45.42 mites and 76.8 ± 8.4 thrips. At this time, a single sticky card (3×9 cm, Sticky Aphid and Whitefly Trap, Seabright Laboratories, Emeryville, California) was attached to the south-east exterior side (down-wind) of each cage,

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Table 1. Repeated measures ANOVA for the effects of plants infested with mites or thrips on capture of thrips on sticky cards (see Fig. 1a).

Source	d.f.	MS	F	P
Mites	1	3.940	0.129	0.720
Thrips	1	51.031	1.672	0.199
Row	4	210.562	6.899	<0.001
Error	102	30.522		
Date	1	0.043	0.002	0.961
Date × mites	1	19.971	1.104	0.296
Date × thrips	1	86.991	4.811	0.031
Date × row	4	12.654	0.700	0.594
Error	102	18.082		

≈ 25 cm above the ground, and left for 1 week. After the cards were removed, a second set of cards was attached to the cages. The attraction of naturally occurring arthropods to plants was measured by their abundance on the sticky cards. The data were analysed using a three-way repeated measures ANOVA with mite inoculation, thrips inoculation, and row as the main effects and two sample dates as the repeated measures.

Results and discussion

Western flower thrips *F. occidentalis* and an undescribed encyrtid parasitoid of pseudococcids, *Rhopus* sp., were abundant on the sticky cards. Infestations of the plants with mites and thrips affected the arthropods found on the sticky cards. Thrips were not affected in the first sample, but in the second sample there were significantly fewer thrips on cards outside cages that contained plants with thrips than plants only infested with mites (see thrips treatment–date interaction in Table 1, Fig. 1a). A univariate ANOVA on the second sample date alone revealed a significant effect ($P < 0.05$) of fewer thrips on cards outside cages that contained plants with thrips than plants only infested with mites. Parasitoids were found marginally more often on sticky cards associated with plants infested with thrips than plants infested with mites alone (Table 2, Fig. 1b). Thus, plants infested with thrips may repel colonising thrips but attract parasitoids.

Herbivore-infested plants provide cues to arthropods in the neighbourhood. Induced resistance is characterised by damage to plants that results in reduced subsequent herbivory (Karban & Baldwin, 1997; Agrawal *et al.*, 1999). Some of these effects may be mediated by direct mechanisms that reduce herbivory (e.g. Agrawal, 1998b, 1999), while others may be indirect and mediated by plant volatiles that affect predators and parasitoids of herbivores (Pare & Tumlinson, 1996; Takabayashi & Dicke, 1996; Thaler, 1999). Cues emanating from infested plants may also mediate other inter- and intra-specific interactions among arthropod species and plants. In these experiments, visual and tactile cues were absent because plants were covered with a fine mesh cage. Thus, the tentative interpretation is that odours emanating from the plant–herbivore complex affected arthropods in the area.

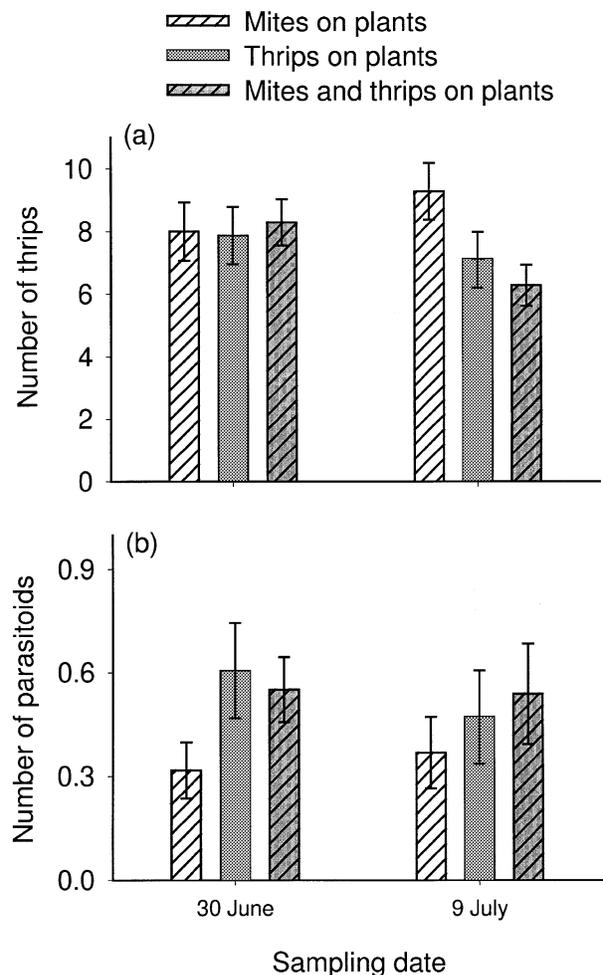


Fig. 1. The effects of plant infestation by mites and/or thrips on (a) the number of thrips and (b) the number of parasitoids found on sticky cards on the outside of each plant. Bars are mean ± SE.

The result that thrips were found less often outside plants infested with thrips on one of the sample dates suggests that thrips may be avoiding intraspecific competition. The lack of an effect on the first sampling date (Fig. 1a) may have been due to the overall low damage on the plants at that stage. The number of thrips found on cards was not affected by the presence or absence of spider mites, suggesting that intraspecific competition was more important for thrips than prey availability or interspecific competition with mites (see also Pallini *et al.*, 1997). The findings of western flower thrips being repelled by thrips-infested plants and unaffected by mite-infested plants are in agreement with more controlled olfactometer experiments conducted with the same organisms (Pallini, 1998). Hairston *et al.* (1960) argued that competition among members of the third trophic level was common, yet trophic chemical cues have only recently been elucidated as a mechanism by which predators and parasitoids avoid competition. For example, parasitoids of *Drosophila* and predators of two-spotted spider mites also appear to avoid competition by

Table 2. Repeated measures ANOVA for the effects of plants infested with mites or thrips on capture of parasitoids on sticky cards (Fig. 1b).

Source	d.f.	MS	F	P
Mites	1	0.064	0.110	0.740
Thrips	1	1.803	30.88	0.082
Row	4	0.995	1.703	0.155
Error	102	0.584		
Date	1	0.066	0.139	0.710
Date × mites	1	0.021	0.044	0.834
Date × thrips	1	0.018	0.038	0.846
Date × row	4	0.584	1.229	0.303
Error	102	0.475		

using odours emanating from the trophic complex (Janssen *et al.*, 1995, 1997).

Thrips-infested plants provided a nonspecific cue that may have attracted a parasitoid to plants. Neither the mites nor the thrips, however, are hosts for this parasitoid, which normally attacks pseudococcids (mealybugs). This is interpreted as parasitoids being attracted to general cues given off by thrips-infested plants. It is possible that thrips-infested cotton plants were producing chemical cues analogous to those produced by plants that are typically infested by pseudococcids. Several recent studies have documented that in some cases different herbivores or types of damage induce the same volatile profile in plants and that parasitoids are equally attracted to these treatments (Geervliet *et al.*, 1996; Takabayashi *et al.*, 1998; Turlings *et al.*, 1998; Vet *et al.*, 1998). For parasitoids of pseudococcids, induced plant attractants appeared to be specific to feeding by pseudococcids in one system (Souissi *et al.*, 1998), while they were more general in a different system (Bertschy *et al.*, 1997). It was unclear what factors were responsible for this lack of specificity in plant responses or lack of discrimination among parasitoids in these cases.

Specificity in tri-trophic interactions is, however, not uncommon and was reported early on by Sabelis and van de Baan (1983). A field experiment by De Moraes *et al.* (1998) with cotton and tobacco found that plants infested with *Heliothis virescens* attracted significantly more parasitoids than plants infested with *Helicoverpa zea* or undamaged controls. In this case, the parasitoid, *Cardiochiles nigriceps*, is only a parasitoid of *H. virescens*. Even finer-scale specificity was found in laboratory experiments by Takabayashi *et al.* (1995), in which corn plants damaged by early vs. late instars of *Pseudaletia separata* produced distinct induced plant responses. Feeding by early instars induced volatiles that attracted parasitoids, while feeding by later instars, which are less susceptible to parasitism, did not induce the production of volatiles. These effects were mediated by changes in the caterpillars' salivary constituents, not by differences in their style of feeding. Although studies of tri-trophic specificity provide fantastic examples of the level to which tri-trophic interactions can be specialised, less specialised interactions may also be common.

The field experiment provided preliminary evidence that plant colonisation by arthropods may depend on the number of competitors on the plant and plant damage associated with non-host herbivores. The cues associated with infested plants used by omnivorous thrips appeared to be specific, while the cues used by parasitoids were general.

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