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Glandular Trichomes on Alfalfa Impede Searching Behavior of the Potato Leafhopper Parasitoid

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New cultivars of alfalfa, *Medicago sativa* L., have been released with glandular trichomes for resistance to potato leafhopper, *Empoasca fabae* (Harris). Yet, the impact of the glandular trichomes on the primary natural enemy of the leafhopper, *Anagrus nigriventris* Girault, is unknown. We compared the host searching behavior of the egg parasitoid on four alfalfa clones varying in trichome characters. Female wasps were videotaped on Ranger, a susceptible clone with relatively sparse trichomes, B14, a resistant clone with dense but nonglandular trichomes, and FG12 and FG18, two resistant clones with glandular trichomes. Although the number of leafhopper eggs per stem exposed to wasps did not significantly differ among the four clones, the frequency of foraging and total foraging time were less on the two clones with glandular trichomes than on the two clones with nonglandular trichomes. In addition, an analysis of covariance demonstrated that, although the number of ovipositional probes increased with egg density on a stem, the number of probes on stems with glandular trichomes was significantly less than that on stems without glandular trichomes. The allocation of time by wasps among drumming, probing, and grooming behaviors was similar among the clones. Wasps tended to fly off of clones with glandular trichomes more often than off of clones with nonglandular trichomes. This study suggests that cultivars with glandular trichomes may interfere with host searching by *A. nigriventris*. © 2000 Academic Press

Key Words: **potato leafhopper; *Empoasca fabae;* egg parasitoid; *Anagrus nigriventris; Medicago sativa;* host plant resistance; foraging behavior; integrated pest management.**

INTRODUCTION

Host plant resistance and biological control have been historically viewed as complementary approaches in pest control. Although host plant resistance may act additively or synergistically with natural enemies to decrease pest survival (van Emden, 1966; Bottrell *et al.*, 1998), specific plant characteristics that confer resistance to herbivores may reduce the effectiveness of their natural enemies. Painter (1951) was one of the first workers in host plant resistance to recognize the potentially negative effects. Hare's (1992) review cited disruption of natural enemies in 6 of 16 cases (37.5%) of resistant crop cultivars. Thus, the development of plant resistance characters to suppress a pest population should be compatible with or, if possible, enhance existing biological control agents (Bergman and Tingey, 1979; Bottrell *et al.*, 1998). The goal of our research was to determine the effect of a new form of host plant resistance in alfalfa, *Medicago sativa* L., using glandular trichomes, on the foraging behavior of the primary natural enemy of potato leafhopper, *Empoasca fabae* (Harris).

Trichomes are hair-like appendages extending from the epidermis of aboveground plant tissues that may confer plant defense to herbivorous insects and that vary in form (Johnson, 1975). Nonglandular trichomes often interfere with the herbivore's spatial requirements by disrupting locomotion, oviposition, and feeding (Levin, 1973). These trichomes may cause death (e.g., Schillinger and Gallun, 1968) but more commonly they have sublethal effects, such as increasing development time, lowering adult weight, and decreasing oviposition of the insects (Price *et al.*, 1980). Glandular trichomes vary widely in structure and secrete many secondary chemicals, such as terpenes, phenols, and alkaloids, to aid plant defenses (Levin, 1973). These chemicals may be toxic to the insect (e.g., Thurston *et al.*, 1966) or they may act sublethally as olfactory or gustatory repellents (Levin, 1973).

Trichomes may also affect natural enemies (Bergman and Tingey, 1979; Price *et al.*, 1980). Plants with trichomes and their secretions can impede the movement of parasitoids, often affecting searching time and weakening the parasitoid response (Price *et al.*, 1980). For example, the glandular trichome exudate of the resistant wild tomato *Lycopersicon hirsutum glabra-*

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tum C. H. Mull contains 2-tridecanone, a contact toxin repellant that harms the *Manduca* spp. egg parasitoid *Telenomus sphingis* (Ashmead) at high concentrations (Farrar and Kennedy, 1991). These researchers found that the glandular exudates can kill the parasitoid by poisoning or entangling it, repelling it, or reducing its searching efficiency. In another example, the parasitoid *Encarsia formosa* Gahan is hindered by the hairs present on resistant cucumber, but the whitefly host is unaffected (Price *et al.,* 1980). Therefore, the whitefly flourishes on the resistant cucumber in the absence of its natural enemy. Thus, understanding the natural enemy response to host plant resistance characteristics is important for successful integration of tactics used in pest management.

The potato leafhopper, a key pest, injures alfalfa by blocking the vascular tissues when feeding (Ecale and Backus, 1995; Nielsen *et al.,* 1990). The insect's well-known polyphagy, vagility, and multivoltine characteristics contribute to its key pest status (Hogg and Hoffman, 1989). Feeding injury and high densities combine to reduce alfalfa crop quality and yield, thus causing economic loss (Cuperus *et al.,* 1983; Lamp *et al.,* 1991). Eggs deposited in the alfalfa vascular tissue require 7–10 days to hatch (DeLong, 1938). Few mortality factors affect the eggs other than *Anagrus* parasitoids (McGuire, 1989). Management tactics for potato leafhopper in alfalfa are limited, with insecticides being the most commonly used (McGuire, 1989). The enhancement of natural control by *Anagrus* parasitoids could become a key component of integrated management practices for this pest.

New alfalfa cultivars have been developed by private seed companies with glandular trichomes as a trait that confers resistance to the potato leafhopper (Elden and McCaslin, 1997). The new cultivars were derived from perennial tetraploid and diploid *Medicago* spp. (Sorensen *et al.,* 1985, 1986; Shade and Kitch, 1986). Leafhopper density was lower and less damage was observed on field *M. glandulosa sativa* and *M. glutinosa* plots than on *M. sativa* commercial cultivars (Danielson *et al.,* 1991). Field trials conducted in 1996 indicated that resistant germplasm reduced leafhopper injury, but leafhoppers colonized, reproduced, and developed on the resistant plants (E. A. Flora, University of Minnesota and R. M. Sulc, Ohio State University, personal comm.).

Anagrus nigriventris Girault, a mymarid wasp, is the primary natural enemy of potato leafhopper (McGuire, 1989). We found earlier (D. L. Liewehr and W. L. Lamp, unpubl. data) that the first local generation of potato leafhopper escapes parasitization by *A. nigriventris,* but subsequent generations can cause significant egg mortality. The parasitoid killed 68% of the leafhopper eggs infesting alfalfa during July 1994. Little has been published on the biology of this parasitoid in association with potato leafhopper, although the biology of *Anagrus girault i* (=*A. nigriventris;* synonomized by Chiappini *et al.,* 1996) has been described in association with beet leafhopper (e.g., Moratorio, 1990). The female of *A. nigriventris* searches along stems of alfalfa for the completely embedded leafhopper eggs. The females oviposit singly into leafhopper eggs, which are killed by developing parasitoid larvae.

Because of the small size of *A. nigriventris* and known examples of physical interference of small insects by glandular trichomes, we hypothesized that the new alfalfa cultivars would adversely affect *A. nigriventris* searching behavior. To test this hypothesis, we compared host searching behavior of *A. nigriventris* on four alfalfa genotypes that varied in trichome type and resistance to the potato leafhopper.

MATERIALS AND METHODS

To compare the searching behavior of *A. nigriventris* on susceptible and resistant alfalfa, plants were used that were derived from four alfalfa clones: Ranger, a susceptible clone (control treatment); B14, a clone (developed by Tom Elden, USDA-ARS-BARC) with a dense covering of nonglandular trichomes mostly appressed on the stem surface (Elden and Elgin, 1992); and FG12 and FG18, two clones (provided by Forage Genetics Inc.) representative of the new glandular-haired alfalfa cultivars (Elden and McCaslin, 1997). The compositions of the glandular exudates from FG12 and FG18 are currently unknown. Plants were propagated by starting cuttings from a 5- to 10-cm section of the tip of stems, placing them in flats of perlite on a mist bench in the greenhouse and transplanting to 15-cm-diameter plastic pots with a standard potting mixture. Tests were run on vegetative stems.

Trichome characteristics were recorded on 10 stems of separate plants for each clone. A section of the stem approximately 2 mm long was excised and viewed under a dissecting microscope. The length and diameter of the section were determined by ocular micrometer at 250×. The number of trichomes/mm^2 was calculated using the formula for surface area of a cylinder (3.14159 · diameter · length). Five trichomes on each section were randomly selected, and their lengths were measured when viewed by an ocular micrometer at 500×.

Wasps were obtained from a wild population in an alfalfa field near Clarksville, Maryland. Uninfested alfalfa plants, greenhouse-grown in plastic pots, were placed in the field for 4–7 days. The time between oviposition and emergence is about 2 weeks; so, the pots were stored in a greenhouse for another 5–7 days after retrieval. This period was based on the developmental threshold and period for *A. nigriventris* of 7°C and 260 centigrade degree-days, respectively (D. L. Liewehr and W. O. Lamp, unpubl. data). After this period, the potted alfalfa stems were excised, placed

into water-filled test tubes (17 by 75 mm), and set into emergence containers (3.8-L circular cardboard cartons wrapped in aluminum foil). A 1-dram glass vial was placed into a hole near the top for the wasps to enter upon emergence. We manipulated incubator conditions to ensure emergence of adults during times when experimental trials could be run. Incubator conditions for emergence containers were photophase: scotophase at 10 ± 2:14 ± 2 h, 25:10°C, respectively. Only females that had emerged within 4 h of the taping session were used. They were transferred into a 1-dram glass vial containing 80% honey solution for at least 10 min before being used in an experiment. The honey was applied directly onto the vial, or it was dripped onto a piece of filter paper.

Alfalfa stems (cut between leaf nodes and within 10 cm of the stem tip) were infested with female potato leafhoppers (1 insect per stem) for 24 h. The leafhoppers were from a field-collected culture maintained on susceptible alfalfa. The leafhoppers were enclosed in a plastic tube (40 × 25 mm) stoppered with foam plugs and confined to 1 cm of the stem. The leafhoppers aspirated through a hole in the side of the tube, which was then stoppered with another foam plug. On average, a potato leafhopper will lay two eggs per 24 h. However, because eggs are completely embedded in the plant tissue, we were uncertain of the presence or location of eggs. Subsequent to each experimental trial, stems were stained with acid fuchsin and boiled in lactophenol to locate and count eggs (Simonet and Pinkowski, 1977).

To begin an experimental trial with an *A. nigriventris* female, the leafhopper and the arena were removed from the stem after the 24-h confinement and the stem was cut and placed into a water-filled vial (25 by 55 mm). The top of the vial was sealed with parafilm to prevent water from entering the viewing arena. A glass arena (20 by 50 mm) was placed onto the stem around the same 1-cm section, with the ends plugged as before. A freshly emerged female wasp was then aspirated through a hole in the side of the arena. The hole was closed by pushing the top foam plug down to cover the hole.

A black and white Sanyo CCD video camera was attached to a Leica MZ APO microscope for videotaping the wasps. We used variable magnifications, generally between 200 and 300. By holding and turning the arena under the microscope, while observing the wasp on the monitor, we were able to record the parasitoid's foraging. Recording began when the wasp walked onto the stem. When the forage sequence was completed, the wasp and the arena were removed from the stem. Wasps were used once and released.

For each female, the video tape was reviewed and three *A. nigriventris* behaviors were categorized: drumming, grooming, and probing. Drumming behavior was defined by waving their antennae next to the stem (e.g., Conti *et al.*, 1997). Grooming was defined as cleaning of the antennae, wings, legs, and abdomen with its legs (e.g., Cheke, 1977). Probing was defined as the insertion of the ovipositor into stem tissue. In two cases, individuals were observed to stand still for periods of less than 4 s, and this behavior occurred 0.2 and 1.8% of the total search time. Thus, this behavior was ignored in the analysis and the total foraging time was partitioned into one of the three behaviors. In addition, we recorded the number of ovipositional probes. Finally, we observed the behavior of a wasp's departure from a stem at the end of a forage sequence (walking or flying).

While 10 wasp trials were run with Ranger and B14, 11 and 12 trials were run with FG12 and FG18, respectively. We defined the frequency of foraging as the proportion of trials in which the wasp spent at least 10 s on the stem section.

Categorical data analysis was performed to test for association between alfalfa clones and (1) whether foraging occurred on an alfalfa stem and (2) mode of wasp departure from an alfalfa stem. In both cases, a Fisher's exact test was performed to calculate the *P* value (Agresti, 1996). Analysis of variance (ANOVA) was performed to test for differences among the mean total time spent foraging on different clones by wasps. A pairwise comparison of each resistant clone to Ranger as the control clone was performed using two-sided *t* tests. A contrast between the mean total time foraging on clones with simple and that on clones with glandular hairs was also performed. ANOVA was also performed to test for differences in the number of eggs per stem and the number of wasp ovipositional probes on the four clones. Eggs per stem and probes per trial were log(x + 1) transformed to homogenize variance. To further analyze the number of ovipositional probes as a function of host egg density (as a covariable) and the presence/absence of glandular trichomes (as a classification variable), we used Proc Genmod (SAS, 1997), specifying a Poisson distribution and a log link function. Finally, ANOVA was performed to test differences between the proportions of time spent probing and that spent grooming on the four clones. In this case, heterogeneous variance was detected among the residuals, thus violating one of the ANOVA assumptions. As an alternative to transforming the data, the error variance was partitioned into groups of similar variance (Littell *et al.*, 1996).

RESULTS

As expected, trichome characteristics differed among clones (Table 1). While Ranger and B14 had nonglandular trichomes, FG12 and FG18 had glandular trichomes. Density of trichomes on B14, FG12, and FG18 averaged 2.25, 4.19, and 2.13 times greater, respectively, than the trichome density on Ranger stems.

TABLE 1

Plant Characteristics of the Tested Alfalfa Clones

Clone	Type of trichome	Density on stem (trichomes/mm^2)	Trichome length (mm)	Known effect on potato leafhopper
Ranger	Nonglandular	1.6 ± 0.4	0.49 ± 0.05	Susceptible check
B14	Nonglandular, appressed	3.6 ± 0.2	0.77 ± 0.08	Feeding and oviposition nonpreference, nymphal antibiosis (Elden and Elgin, 1992)
FG12	Glandular, erect	6.7 ± 0.5	0.45 ± 0.05	Nonpreference and antibiosis (Elden and McCaslin, 1997)
FG18	Glandular, erect	3.4 ± 0.3	0.34 ± 0.04	Nonpreference and antibiosis (Elden and McCaslin, 1997)

Trichome lengths were similar among Ranger, FG12, and FG18, but trichomes on B14 averaged 1.79 times longer than on the other three clones.

The number of leafhopper eggs per stem did not differ significantly between clones ($F = 1.77$; $df = 3, 40$; $P = 0.17$). The mean number of eggs within stem sections exposed to wasps was 1.40, 1.22, 2.20, and 0.47 eggs for Ranger, B14, FG12, and FG18, respectively.

In all trials with Ranger and B14, wasps always spent at least 10 s on the stem. In contrast, only 55 and 58% of the wasps foraged on FG12 and FG18, respectively. The difference between wasps in frequency of foraging on glandular and nonglandular clones was significant using Fisher's exact test.

The number of wasp ovipositional probes during trials significantly differed among clones ($F = 8.72$; $df = 3, 39$; $P = 0.0001$). The wasps performed a mean of 11.8, 7.2, 0.8, and 1.7 probes on Ranger, B14, FG12, and FG18, respectively. In addition, an analysis of covariance of the number of ovipositional probes as affected by both the presence/absence of glandular trichomes and the number of host eggs per stem demonstrated that both factors were significant. The number of probes per stem increased with the number of eggs per stem ($P = 0.006$). Also, the number of probes was greater on stems without glandular trichomes than on stems with glandular trichomes ($P = 0.0001$). The interaction term between egg density and trichome presence/absence was not significant ($P = 0.18$).

Total foraging time significantly differed between glandular and nonglandular clones (Fig. 1). For those wasps that spent at least 10 s on the stem, 87 and 63% less time was spent on FG12 and FG18, respectively, in comparison to time on Ranger ($P = 0.0001$ and 0.01, respectively; Fisher's least significant difference test). The average time spent foraging on B14 did not differ from time on Ranger ($P = 0.47$).

The percentage of time that wasps spent drumming was similar across all the clones, but a trade-off was observed in grooming and probing behaviors (Fig. 2). On the clones with glandular trichomes, *A. nigriventris* spent 4.5 times more relative time grooming but 0.77 times less time probing than on Ranger. However, no significant differences were found among the proportion of time spent probing or grooming among clones (ANOVA $P = 0.28$ and 0.15, respectively).

We did not observe any wasp mortality because of entanglement in the trichome secretions. The wasps that became entangled always walked or flew away apparently unharmed.

Finally, a significant difference between the glandular and the nonglandular clones in the mode of wasp departure was also observed. On Ranger, 80% of the wasps walked off the stems onto the foam plugs at the end of their foraging sequence, while 20% flew off the stems. For B14, 60% of the wasps walked, while 40% flew. In contrast, 14 and 33% of the wasps walked off the glandular-haired clones, FG12 and FG18, respectively, with 86 and 67% flying off the stems, respectively. The difference between mode of departure on nonglandular clones and that on glandular clones was significant ($P = 0.04$, Fisher's exact test).

DISCUSSION

Differences among clones in host egg density may impact *A. nigriventris* behavior despite trichome characteristics. Although the four clones varied in trichome characteristics and purported levels of resistance to potato leafhopper, we found no difference in the number of leafhopper eggs laid in the stems prior to experimental trials. The no-choice confinement of female leafhoppers on the stem sections may explain this result. In addition, the analysis of covariance of oviposi-

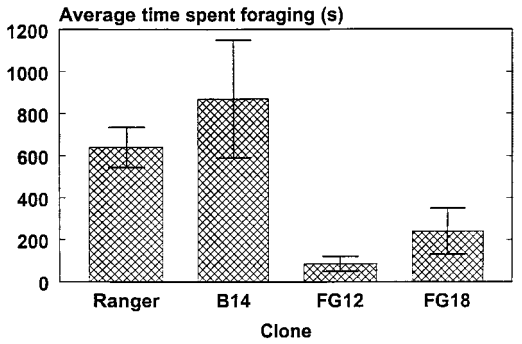

FIG. 1. Mean total time of wasp foraging during trials on each alfalfa clone.

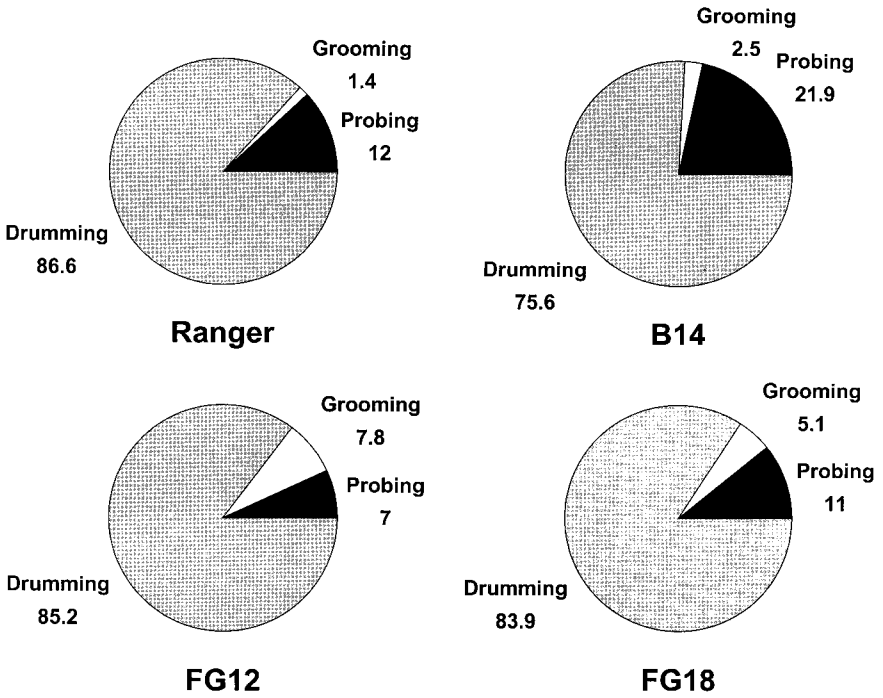

FIG. 2. Mean allocation of time (%) by wasps for each recorded behavior during foraging trials on each alfalfa clone.

tional probes by *A. nigriventris* demonstrated that, although the number of probes increased with host egg density, the wasps also probed fewer times on stems with glandular trichomes than on stems without glandular trichomes. This analysis provides evidence that trichome characteristics, in addition to host egg density, alter *A. nigriventris* behavior.

The results from the experimental trials support our primary hypothesis that *A. nigriventris* egg searching behavior may be adversely affected by glandular trichomes. Wasps were less likely to forage and they spent less time foraging on alfalfa with glandular trichomes than on alfalfa without glandular trichomes. In addition, wasps performed fewer ovipositional probes during an experimental trial on stems with glandular trichomes than on stems with nonglandular trichomes. Furthermore, wasps tended to fly off the stems with glandular trichomes more often than off the stems with nonglandular trichomes. There were no fatalities caused by entanglement on glandular trichomes, but, by increasing the number of dispersive flights and shortening the foraging time, alfalfa stems with glandular trichomes may seriously reduce the effectiveness of *A. nigriventris* on leafhopper egg parasitism.

Nonglandular trichomes that provide only spatial interference are not as likely to affect natural enemies as glandular trichomes (Bergman and Tingey, 1979). The wasp behavior on B14 suggests a form of spatial interference. *A. nigriventris* foraging time on B14 did not differ significantly from that time on Ranger, the susceptible control with no natural defenses. The amounts of time spent probing, grooming, and drumming on B14 were all comparable to the corresponding times spent on Ranger. Thus, nonglandular trichomes may provide a natural defense mechanism compatible with mortality caused by *A. nigriventris.*

Because the potato leafhopper will successfully oviposit in alfalfa clones with the glandular trichomes, our results suggest that alfalfa with this trait may protect the pest from parasitization by *A. nigriventris.* Thus, the use of glandular trichomes for leafhopper resistance may prohibit exploitation of this potentially beneficial natural control. However, laboratory results such as these may not translate to natural enemy interference under field conditions (e.g., Obrycki and Tauber, 1984). Thus, field studies are needed to test for *A. nigriventris* interference. If such interference is corroborated, then future breeding research should aim toward finding alfalfa germplasm with resistance to potato leafhopper that does not hinder the performance of its primary natural enemy.

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