

*Trirhabda canadensis* (COLEOPTERA: CHRYSOMELIDAE)  
RESPONSES TO PLANT ODORS

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**Abstract**—The responses of the goldenrod leaf beetle *Trirhabda canadensis* to host and nonhost volatile odors were tested in a Y-tube olfactometer in the laboratory. Beetles preferred host to nonhost odors and were sensitive to concentrations of host odor. Beetles distinguished between host and nonhost volatiles of only one of the two nonhost *Solidago* species, host volatiles were preferred to all nonhost volatiles at the family and order levels. In other words, all nonhosts above the genus level had similar effects on beetle responses. Although the odors of most nonhosts were neutral (i.e., neither attractive nor repellent) to the beetles as tested against air, this neutrality disappeared if the odors of two or more nonhosts were added to the host odor and beetles were given a choice between this mixture and pure host odor. Given this choice, they strongly preferred pure host odor, which suggests that diversity of odors per se is unattractive to the beetles. Beetles walked rather than flew to locate their hosts in the field, and their movements suggest that they used olfactory cues to locate hosts.

**Key Words**—*Trirhabda canadensis*, Coleoptera, Chrysomelidae, *Solidago*, plant volatiles, host finding, olfaction.

INTRODUCTION

Host selection by insect herbivores comprises a number of behavioral responses to various stimuli associated with the host plant: stimuli may be olfactory, gustatory, visual, or mechanical (Visser, 1986). In particular, the orientation of phytophagous insects to chemical stimuli has been most extensively studied in agricultural systems (Finch, 1980; Visser, 1986). In these, it has been shown

that volatile plant odors are important stimuli that aid specialist insects in short- and long-distance discovery of suitable host-plant patches and in selecting individual host plants. Since host-plant patches may vary in size, density, and the diversity of non-host-plant species associated with them, the volatile odors emanating from different patches may also vary. The concentration of host odor and the presence of nonhost odors may affect the ability of insects to find host plants in various ways (Root, 1973; Tahvanainen and Root, 1972; Kareiva, 1983; Stanton, 1983; Visser, 1986). Thiery and Visser (1986), for example, have shown experimentally that mixing nonhost odor with host odor neutralizes the normal response of the Colorado potato beetle, *Leptinotarsa decemlineata*, to host odor. They describe this effect as masking of the host odor by the nonhost odor.

The work described in this paper is part of a larger study that examined the responses of a specialized herbivorous beetle to patches of host plants in the field, and, in particular, how the density of the host and the presence of associated nonhost species influenced beetle responses. Here we present data from field and laboratory experiments on the responses of beetles to odors from host and nonhost species. These plant species are in the same genus or same family as the host or in different orders. All species are naturally cooccurring herbaceous perennials native to the tall grass prairie of North America (Table 1). We tested four hypotheses: (1) beetles prefer host volatiles to nonhost volatiles; (2) beetles detect differences in concentration of volatiles from the host plant; (3) volatiles from plants in the same genus as the host are more acceptable

TABLE 1. ARRAY OF PLANT SPECIES TESTED IN THREE SETS OF OLFACTOMETER EXPERIMENTS, AND THEIR TAXONOMIC AFFILIATIONS

Species	Order	Family	Tribe	Subtribe
<i>Solidago altissima</i> L.	Asterales	Asteraceae	Astereae	
<i>Solidago nemoralis</i> Ait.				
<i>Solidago missouriensis</i> Nutt.				
<i>Solidago rigida</i> L.				
<i>S. altissima</i> L.	Asterales	Asteraceae	Astereae	Solidaginae
<i>Helianthus laetiflorus</i> Pers.	Asterales	Asteraceae	Heliantheae	Helianthinae
<i>Liatris aspersa</i> (Michx.) Greene	Asterales	Asteraceae	Eupatorieae	Adenostylinae
<i>Aster ericoides</i> L.	Asterales	Asteraceae	Astereae	Asterinae
<i>S. altissima</i> L.	Asterales	Asteraceae	Astereae	Solidaginae
<i>Asclepias tuberosa</i> L.	Gentianales	Asclepiadaceae		
<i>Lespedeza capitata</i> Michx.	Fabales	Fabaceae		
<i>Monarda fistulosa</i> L.	Lamiales	Lamiaceae		

to beetles since they are closely related and are therefore expected to have some of the same volatile chemicals, while species that are more distantly related are less acceptable since these produce volatiles that are less similar; and (4) beetles prefer pure host volatiles to volatiles from host + non-host combinations.

#### METHODS AND MATERIALS

*Goldenrod Leaf Beetle. Trirhabda canadensis* Kirby (Coleoptera: Chrysomelidae) feeds on a narrow range of goldenrod *Solidago* species (Hogue, 1970). At Cedar Creek Natural History Area in Anoka and Isanti counties, Minnesota, the beetles feed on *S. altissima* L. and *S. missouriensis* Nutt. In May, larvae hatch from eggs that have overwintered in the soil at the base of goldenrod plants. They crawl up host plants to feed, complete three instars by mid-June, and drop to the ground to pupate in the soil. Adults 8–10 mm long emerge in early July and recolonize host plants, sometimes dispersing to new goldenrod clones. Beetles mate repeatedly and feed on the host until the end of the summer, usually early September.

*Experimental Beetles and Plant Material.* Adult beetles were obtained from Cedar Creek at intervals from July 21 to August 26, 1986. They were collected from *Solidago altissima* and *S. missouriensis* in the early morning and air-freighted to Boston the same day. They were maintained at Northeastern University on locally collected *S. canadensis* (which belongs to the *S. canadensis*–*S. altissima* polyploid complex) under controlled conditions (18°:15°C and 16:8 hr light–dark), and used for olfactometer tests within seven days of collection. Beetles were deprived of food for 2 hr before testing and were used only once in 75% of the tests. Because their number was limited, we used some beetles a second time. However, in those tests we ensured that: (1) the plant material in the second test was as different as possible from that used in the first (for example Air vs. *S. altissima* and then Air vs. the mint *Monarda fistulosa* L.); and (2) at least three days elapsed between the first and second tests. A preliminary trial showed that male and female responses did not differ, so beetles of both sexes were used for the tests.

Plant material was also obtained from Cedar Creek, where it was collected in the early morning, stored in a cooler with individual stems in Water-pics, and air-freighted to Boston the same day. Material was refrigerated and used for olfactometer tests within three days; preliminary trials showed that beetles did not respond in a reproducible manner to plant material after three days.

*Experimental Procedures.* The olfactometer was modeled after one described by Ascoli and Albert (1985), with minor modifications (Figure 1). A compressed-air cylinder provided the airstream, and a pipecleaner rather than copper wire was provided for beetles to climb. Plant material was placed in

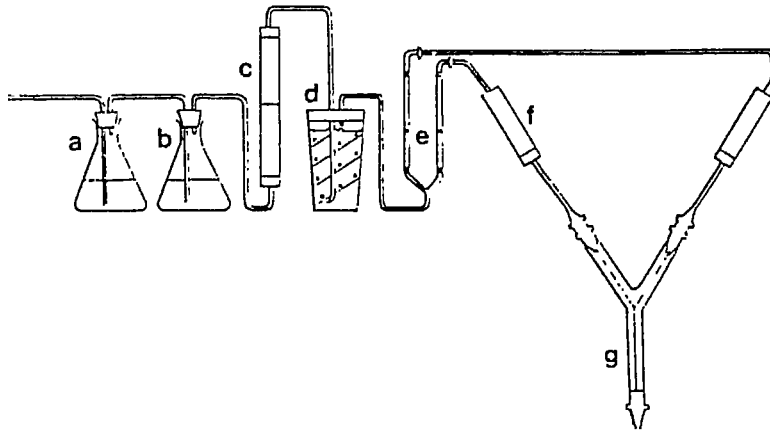


FIG. 1. Schematic diagram of the Y-tube olfactometer apparatus (after Ascoli and Albert, 1985): (a) drierite, (b) charcoal, (c) molecular sieve, (d) water, (e) flowmeters, (f) tube for plant material, and (g) Y tube.

polypropylene sample tubes, connected by polypropylene joints at either end to Tygon tubing, so that the airstream passed over the plant material in the sample tubes at a flow rate of 80 ml/min. We tested air flow in the olfactometer with smoke prior to using it, and determined that flow was smooth, with very little turbulence at the Y junction. The apparatus was positioned in a fume hood in which fluorescent lights provided illumination. Experiments were conducted at room temperature (25°C). The Y tube and pipecleaner were rinsed with acetone after each trial.

Plant material used in the tests was replaced every 30 min. Five to eight leaves were used at a time, except where indicated. In interspecific comparisons, the number of leaves was adjusted so that the amount of leaf material per species was the same.

Between 50 and 80 beetles were used for each test. For each trial, a beetle was placed on the pipecleaner 1 cm from the bottom of the Y tube and allowed to crawl up the pipecleaner. The trial ended when the beetle was within 1 cm of the top of either arm of the Y. A beetle was recorded as not having made a choice if it had not done so in 300 sec. Data were analyzed using chi-square tests for goodness of fit to an even distribution.

To establish whether beetles found a particular plant odor, or combination of odors, attractive, neutral, or repellent, the plant(s) in question were run against air. Then nonhost plants were individually tested against the host, *S. altissima*. Finally, we tested whether beetles distinguished between pure host odor and host odor plus odors from different taxonomic groupings of nonhost species. The nonhost groups were: (1) two species in the same genus, (2) three

species in different tribes or subtribes of the family Asteraceae, or (3) three species in different orders.

*Individual Beetle Movements.* We recorded movements of individually marked female beetles in the field to determine whether they typically move by walking and/or flying and to see whether their paths were directed or random with respect to host and nonhost plants. Eight observers recorded the movements of eight and seven female *T. canadensis* placed 4 m downwind of cut stems of *S. altissima* or *Helianthus* sp. (Asteraceae), respectively. A curved, open "fence" of stems, approximately 40 cm deep, 70 cm high, and 6 m long, was made from cut stems placed in buckets and jars that were dug into a lawn so that stems were at ground level. The *Helianthus* sp. was chosen because its leaves are similar in shape to *S. altissima*. Wind speed varied from 1.8 to 2.7 m/sec during the experiment. We released each beetle onto a 30-cm bamboo skewer and recorded her path across the lawn with numbered skewers.

## RESULTS

*Olfactometer Tests.* In 85% of the olfactometer tests, beetles walked straight up the pipecleaner with their antennae moving as if to test the airstream, and they did not pause before choosing and walking up one of the arms. In 11% of the tests, beetles walked up one branch of the olfactometer for 10–15 mm before returning to the Y junction and walking up the other to make their final choice; these were included in the final sample as having made a choice. Beetles took  $44.3 \pm 9.3$  sec ( $\pm$ SD) to complete a trial. Beetles made no choice in the remaining 4% of the olfactometer tests. These results were included in the calculation of  $\chi^2$  values (Siegel, 1956); they did not alter the significance of any of the tests.

Beetles were attracted (as shown by testing against air) to their host plants *S. altissima* and *S. missouriensis* in significant numbers (Figure 2a). They were not significantly attracted to or repelled by *S. nemoralis* Ait. and *S. rigida* L., two closely related nonhosts, although they showed a slight attraction to *S. nemoralis*. Beetles did not distinguish between their two hosts, *S. altissima* and *S. missouriensis*, when offered a choice (Figure 2b). However, when given a choice between *S. altissima* and the two nonhost goldenrods, the beetles did not distinguish significantly between *S. altissima* and *S. nemoralis*, although they did show a slight preference for *S. altissima*. They did significantly prefer *S. altissima* to *S. rigida* (Figure 2b). In short, *T. canadensis* did not distinguish among the *Solidago* species with the exception of *S. rigida*. *S. nemoralis* has been shown to contain a diterpene which is strongly antifeedant to *T. canadensis* (Cooper-Driver et al., 1986), but the volatile chemicals released by this species were not deterrent to the beetles.

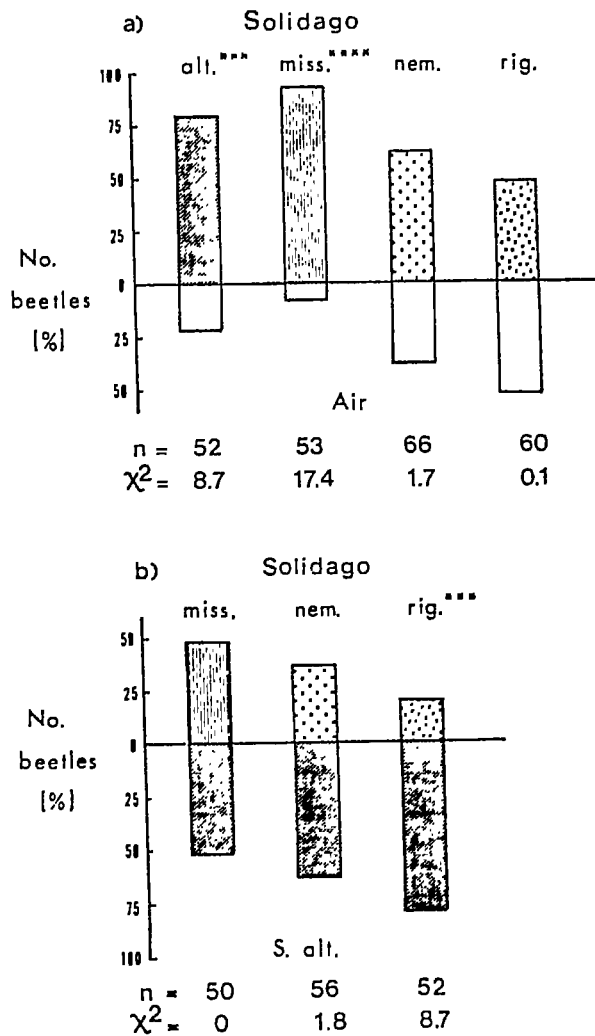


FIG. 2. The choices of adult *Trirhabda canadensis* of plant odors in a Y-tube olfactometer. Choices among plants of the genus *Solidago* were offered against (a) air and (b) the host, *S. altissima*. *S. altissima* = diagonal lines. *S. missouriensis* = vertical lines, *S. nemoralis* = crosses, *S. rigida* = open circles, air = white. \*\*\* $P < 0.01$ , \*\*\*\* $P < 0.001$ .

To test whether beetles responded to differences in odor concentration of the host, they were offered volatiles from one small leaf vs. two small leaves and five leaves vs. 20 leaves of *S. altissima* in two different tests. Beetles did not distinguish between volatiles from five leaves and 20 leaves, but showed a

TABLE 2. RESPONSES OF ADULT *Trirhabda canadensis* TO DIFFERENT CONCENTRATIONS OF HOST PLANT ODOR IN Y-TUBE OLFACTOMETER

Choice offered <sup>a</sup>		Choice made <sup>b</sup>			N	$\chi^2$	P
1 Sa	2 Sa	14	38	0	52	4.00	<0.05
5 Sa	20 Sa	25	40	3	68	1.65	NS
5 Sm	20 Sm	25	27	1	53	0.04	NS

<sup>a</sup>Sa = *S. altissima*, Sm = *S. missouriensis*. Numbers preceding host species refer to the number of leaves offered.

<sup>b</sup>The first two columns indicate the number of beetles choosing each host odor, the third the number of trials in which beetles made no choice.

significant preference for two leaves over one leaf (Table 2). Thus, it appeared that a threshold concentration existed above which the odor was strong enough to elicit a positive response no matter what the concentration.

All three confamilial species tested [*Liatris aspersa* (Michx.) Greene, *Aster ericoides* L. and *Helianthus laetiflorus* Pers.] were neutral to *T. canadensis*, as shown by testing against air, although beetles appeared slightly to prefer air in all three tests (Figure 3a). However, they showed a significant preference for *S. altissima* to all three of these species (Figure 3b). In the orders group, *Monarda fistulosa* was highly repellent to *T. canadensis*, as tested against air, while the other two species were not (Figure 4a), and beetles significantly preferred the host plant to any of the three (Figure 4b). Thus, in the family and orders comparisons, one of the six species tested was repellent to the beetles; the other five appeared to be neutral, although there was a slight (but statistically nonsignificant) tendency for beetles to prefer air in all five tests. Beetles significantly preferred the host, *S. altissima*, to all six species.

Four of the six comparisons of beetle preference given *S. altissima* alone versus *S. altissima* plus one nonhost species showed that the nonhost species was neutral (Figure 5). Of the family group, *Helianthus* was the only species the odor of which caused the beetles to choose *S. altissima* alone over *S. altissima* + nonhost, in spite of being neutral to the beetles on its own; neither the odor of *Liatris* nor of *Aster* had this effect (Figure 5a). Of the three species in the orders group, *Monarda* was the only one that caused the beetles to prefer *S. altissima* on its own to *S. altissima* + nonhost (Figure 5b).

Equal numbers of beetles chose the odor from a "genus bouquet" (a mixture of *S. altissima*, *S. nemoralis*, *S. missouriensis*, and *S. rigida*) and odor from pure *S. altissima*, that is, beetles did not distinguish between the odor from pure *S. altissima* and that from the bouquet (Figure 6). When a larger amount of pure *S. altissima* (20 leaves) was offered equal to the total amount of leaf material in the genus bouquet, beetles only slightly preferred the odor

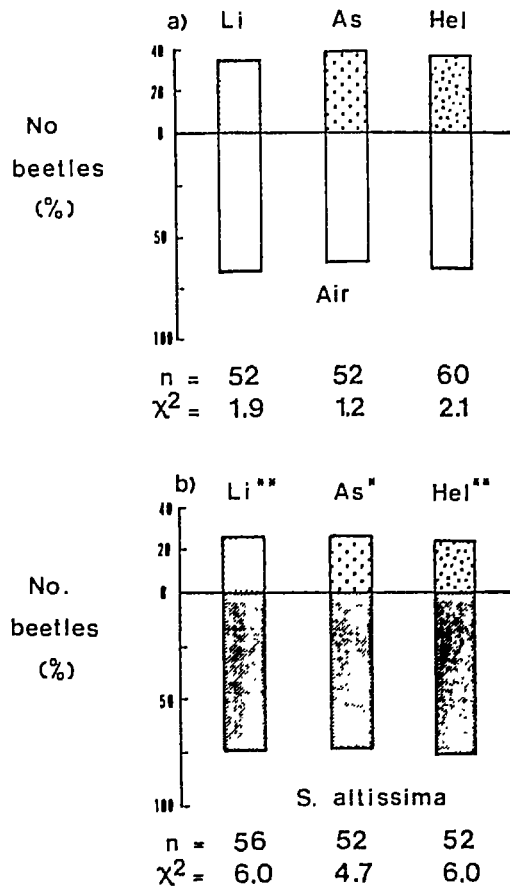


FIG. 3. The choices of adult *Trirhabda canadensis* of plant odors in a Y-tube olfactometer. Choices among different nonhost species in the family Asteraceae were offered against (a) air and (b) the host, *S. altissima*. *S. altissima* = diagonal lines. *Liarris aspersa* = dots, *Aster ericoides* = crosses, *Helianthus laetiflorus* = open circles, air = white. \* $P < 0.05$ , \*\* $P < 0.02$ .

of pure *S. altissima* (32 beetles vs. 19,  $\chi^2 = 1.63$ , 1 *df*, NS), but this result was not statistically significant.

*S. altissima* plus the three species from the family array was neutral to the beetles (as shown by testing against air) (Table 3). Interestingly, when *S. altissima* was removed from the family array, the number of beetles preferring air increased (Table 3), although the preference was not significant. However, beetles significantly preferred pure *S. altissima* to *S. altissima* plus the three non-



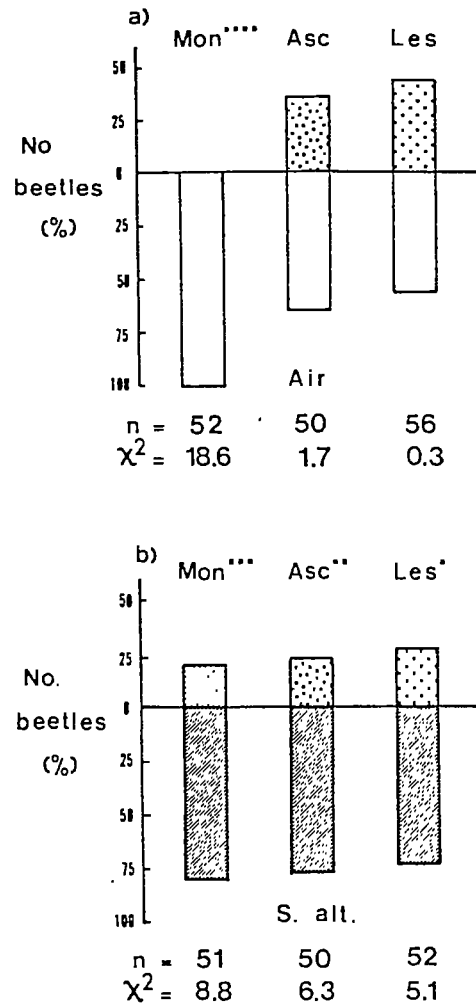


FIG. 4. The choices of adult *Trirhabda canadensis* of plant odors in a Y-tube olfactometer. Choices among different nonhost species in three different orders were offered against (a) air and (b) the host, *S. altissima*. *S. altissima* = diagonal lines. *Monarda fistulosa* = dots. *Asclepias tuberosa* = open circles. *Lespedeza capitata* = crosses. air = white. \* $P < 0.05$ , \*\* $P < 0.02$ , \*\*\* $P < 0.01$ , \*\*\*\* $P < 0.001$ .

host species in the family array (Figure 6). The "order bouquet" was repellent to the beetles when tested against air even though it had *S. altissima* present (Table 3), and this was most likely due to the presence of *Monarda*. Given the repellency of *Monarda* (Figure 4), it was not surprising that the beetles pre-

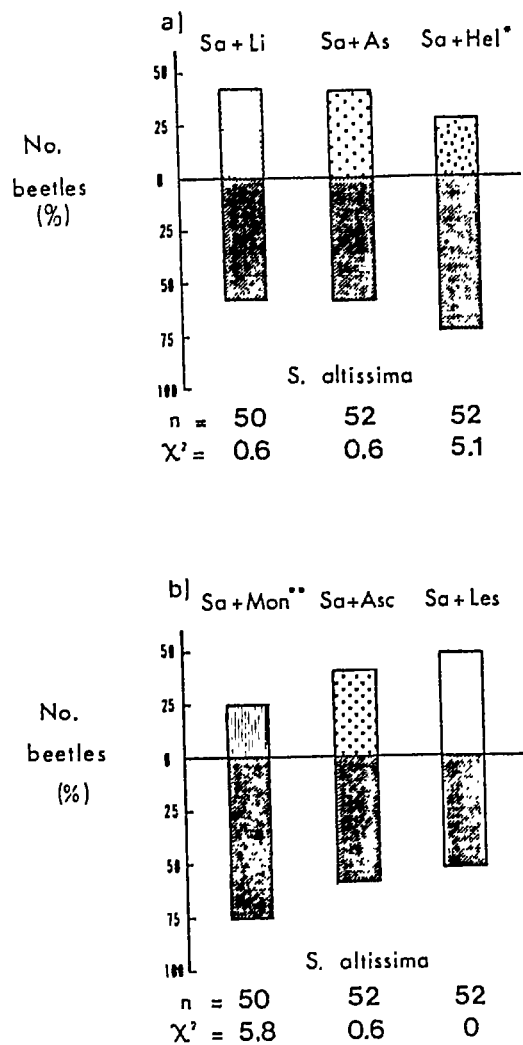


FIG. 5. The choices of adult *Trirhabda canadensis* of plant odors in a Y-tube olfactometer. Choices offered were (a) *S. altissima* (*Sa*) vs. *Sa* + different nonhost species in the family Asteraceae and (b) *Sa* vs. *Sa* + different nonhost species in three different orders. *S. altissima* = diagonal lines, *Sa* + *Liarris aspersa* = dots, *Sa* + *Aster ericoides* = crosses, *Sa* + *Helianthus laetiflorus* = open circles, *Sa* + *Monarda fistulosa* = vertical lines, *Sa* + *Asclepias tuberosa* = inverted triangles, *Sa* + *Lespedeza capitata* = white. \* $P < 0.05$ , \*\* $P < 0.02$ .

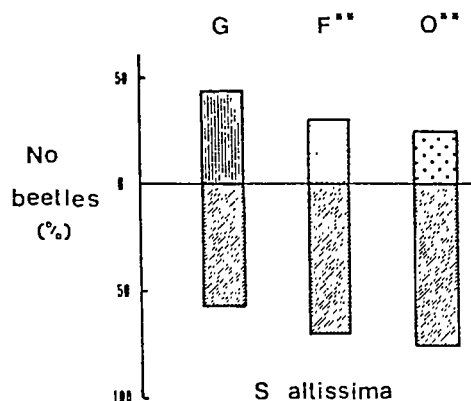


FIG. 6. The choices of adult *Trirhabda canadensis* between plant odors in a Y-tube olfactometer. Choices offered were between the host, *S. altissima* and a "bouquet" of plant species. G = genus bouquet comprising *S. altissima*, *S. missouriensis*, *S. nemoralis* and *S. rigida*. F = family bouquet comprising *S. altissima*, *Liatriis aspersa*, *Aster ericoides* and *Helianthus laetiflorus*. O = orders bouquet comprising *S. altissima*, *Monarda fistulosa*, *Asclepias tuberosa* and *Lespedeza capitata*. \*\* $P < 0.02$ .

ferred *S. altissima* to the order bouquet (Figure 6). However, even when *Monarda* was removed from the order bouquet, the remaining two species caused the beetles still to prefer *S. altissima* on its own to *S. altissima* plus these two species (44 beetles vs. 21,  $\chi^2 = 4.01$ , 1 *df*,  $P < 0.05$ ).

*Individual Beetle Movements.* Beetles stayed on their release sticks for 5-120 min before walking across the lawn, and they climbed up grass blades frequently while walking. They moved their antennae as if to test the air in the

TABLE 3. ADULT *Trirhabda canadensis* CHOICES BETWEEN PLANT ODORS AND AIR IN Y-TUBE OLFACTOMETER, TESTING WHETHER ODORS ARE ATTRACTIVE, NEUTRAL, OR REPELLENT TO BEETLES

Choice offered <sup>a</sup>		Choice made <sup>b</sup>		<i>N</i>	$\chi^2$	<i>P</i>	
Air	F	36	30	2	68	0.26	NS
Air	F-Sa	42	20	6	68	3.56	NS
Air	O	47	20	2	69	5.28	<0.05

<sup>a</sup>F = "Family bouquet" comprising *Solidago altissima* (Sa) + *Liatriis aspersa* + *Aster ericoides* + *Helianthus laetiflorus*; F-Sa = family bouquet minus Sa; O = "order bouquet" comprising *Solidago altissima* + *Monarda fistulosa* + *Asclepias tuberosa* + *Lespedeza capitata*.

<sup>b</sup>The first two columns indicate the number of beetles choosing between air and plant material, the third the number of trials in which beetles made no choice.

same way as they did in the olfactometer tests. One beetle flew after walking for 58 min. On average, beetles moved  $5.5 \pm 2.0$  m/hr ( $\pm$ SD) and walked 4–12.9 m before finding a goldenrod stem (Figure 7). Of the eight beetles released downwind of *S. altissima*, seven moved upwind and six of these found a goldenrod stem. Of the seven beetles released downwind of *Helianthus*, two went downwind from their starting points and both eventually found *S. altissima* stems. The other five initially moved upwind; two reversed direction and one

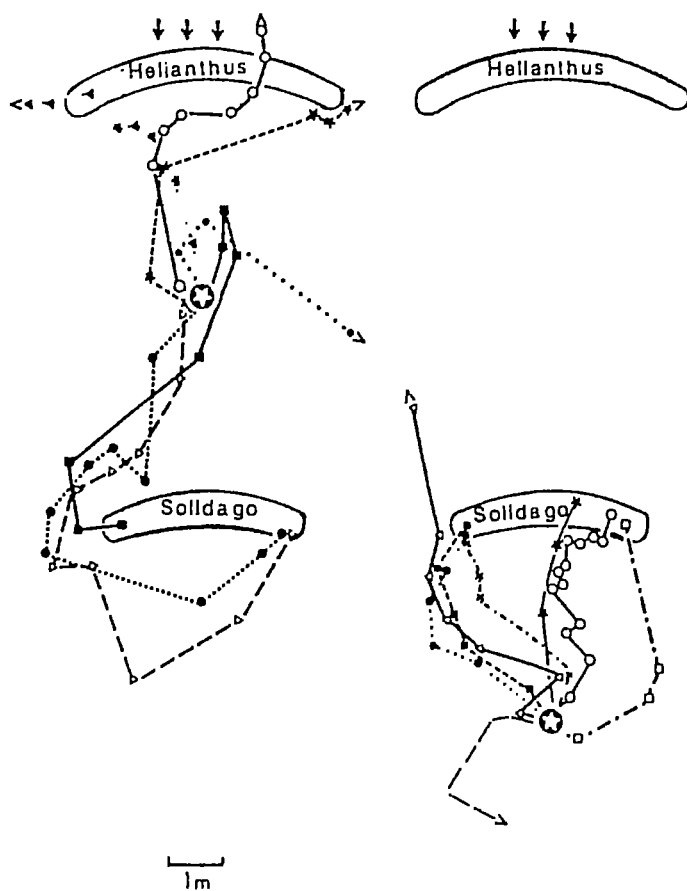


FIG. 7. Paths walked by 15 *Trirhabda canadensis* placed downwind of *Helianthus* sp. (left) or downwind of *S. altissima* (right). White stars indicate release points. Paths ending in  $\vee$  indicate beetles that did not find *S. altissima*. Both groups of beetles were followed simultaneously on the same grid but are shown separately for clarity. Arrows at top indicate wind direction.

of these located an *S. altissima* stem, while the other three passed around or through the *Helianthus*. The circuitous paths walked by the beetles suggested that they found goldenrod stems using olfactory rather than visual cues (Figure 7).

#### DISCUSSION

The behavior of goldenrod leaf beetles in the laboratory showed that beetles responded to olfactory cues from host and nonhost plants and preferred host to nonhost odors. In addition, beetles were sensitive to concentrations of host odor. Beetles distinguished between host and nonhost volatiles of only one of the two nonhost *Solidago* species; host volatiles were preferred to all nonhost volatiles at the family and order levels. In other words, all nonhosts above the genus level had similar effects on beetle responses. Although the odors of most nonhosts at the family or order levels were neutral (i.e., neither attractive nor repellent) to the beetles as tested against air, this neutrality disappeared if the odors of two or more nonhosts were added to the host odor and beetles were given a choice between this mixture and pure host odor. Given this choice, they strongly preferred pure host odor, which suggested that diversity of odors per se (or odors emanating from a diversity of species) was unattractive to the beetles. Beetles walked rather than flew to locate their hosts in the field, and their movements suggested that they used olfactory cues to locate hosts.

Beetle preference in these experiments largely supported the results of several experiments conducted in the field at Cedar Creek, testing the responses of goldenrod leaf beetles to the same set of host and nonhost species. In colonization experiments, beetles preferred monospecific plots to plots with *S. altissima* interplanted either with three species in the same genus or with three species in the same family or with three species in different orders (Morrow, Tonkyn, and Goldberg, unpublished data). It is likely that the final distribution of beetles in the colonization experiments was the result of beetle response to the different volatile "profiles" of the different plots.

The movements of individual beetles in the field experiment (Figure 7) also suggested that beetles were responding to host-plant odor. The likely mechanism was by means of odor-conditioned positive anemotaxis (Kennedy, 1977; Visser and Nielsen 1977; Visser, 1986). The general orientation of insects to chemical stimuli has been studied extensively (Shorey and McElvey, 1977; Visser, 1986, and references therein). Orientation may occur by means of chemotaxis, which comprises a response directed towards or away from a chemical stimulus and depends on a steep odor gradient. Therefore, chemotaxis can occur only at short distances from an odor source. The effective distance for chemotaxis in insect larvae ranges from 0.5 to 4 cm (Visser, 1986), while chemotaxis

occurs over slightly longer distances than this in adult insects since adults are more sensitive to odors than larvae (Baker, 1985). For longer distances, insects are thought to orient by means of odor-conditioned positive anemotaxis. This taxis comprises mechanical stimulation by wind which primes the insect; when it then perceives an attractive odor, it turns upwind (Visser, 1986). The concentration of the odor needs to be only just above the threshold of detection to bring this taxis into operation. Thus, it is thought to be effective over long distances, although the exact distance has not been determined experimentally (Baker, 1985).

The hypothesis that beetles would show a graded response to volatiles from plants that were closely to distantly related to the host (hypothesis 3 above), was only partly supported by our results, since we found that all nonhosts above the genus level had similar effects on beetle responses. This suggests that beetles recognize specific volatile components or profiles associated with *Solidago* species. Visser and Avé (1978) found that the specificity of potato plant odor in eliciting a positive response from Colorado potato beetles depended on the ratios of the individual volatiles present rather than the presence of any particular volatile. On the other hand, the importance of all non-*Solidago* volatiles appeared to depend on the total diversity present rather than on the recognition of specific volatiles.

Experimental methods for testing insect orientation to chemical stimuli have been reviewed (Kennedy, 1977). Although Y-tube olfactometers have many advantages, they have the disadvantage of not enabling the actual mechanism of attraction to be unequivocally assayed since chemoklinotaxis cannot be distinguished from odor-conditioned positive anemotaxis. This ambiguity in ability to attribute the behavioral mechanism responsible for beetle choices in this study was not a problem since we were interested in actual beetle responses to plant odors rather than in determining the mechanism by which beetles responded.

Of the plant volatiles so far isolated, over 40% are derived from either terpenes or glucosides (Finch, 1980). Visser and Avé (1978) found that leaf alcohols, aldehydes, and derivatives, which they called "green leaf" volatiles, induced positive anemotaxis by the Colorado potato beetle. We are currently isolating volatiles from the plant species used in the present study and testing these to determine which are responsible for observed beetle behavior.

It is possible that attractiveness, neutrality, or repellency of the volatiles of a given plant species or mixture of species is strictly a function of the chemical structure of these volatiles, as determined, for example, by the presence of a particular functional group, although Harborne (1982) cautions that the relationship between chemical structure and odor is not likely to be a straightforward one. Whatever the mechanism, the varied responses of beetles to host, nonhost and host + nonhost volatiles suggest that in natural systems beetles

may respond not only to host odors but may also use nonhost odors to gain additional information about their environment. For example, given the same concentration of host plant volatiles, the presence either of increasing concentrations of the volatiles from one nonhost species or of increasing numbers of volatiles from a larger number of nonhost species may signal a host plant patch with higher total plant density. In such a patch, the host might be less vigorous and therefore a poor-quality source of food.

This study is the first to our knowledge that has focused on insect odor perception in a natural system where plants and insects have been associated over long periods of time. We have shown the effects of plant diversity (as represented by volatile diversity) on the responses of a specialist phytophagous insect at a fairly close range in the laboratory. In future field and laboratory experiments, we plan to test the effects of plant diversity on long-distance attraction of these beetles. More experiments such as these are needed, since such effects have not been tested for any insect species to date (Thery and Visser, 1986).

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