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BEHAVIORAL AND ELECTROPHYSIOLOGICAL RESPONSES OF APHIDS TO HOST AND NONHOST PLANT VOLATILES

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Abstract—Alate and apterous virginoparae of *Aphis fabae* Scop. and alate virginoparae of *Brevicoryne brassicae* (L.), walking in a linear track olfactometer, were attracted by odor from leaves of their host plants. *A. fabae* responded to odor from undamaged but not damaged bean leaves. Gynoparae (autumn migrants) of *A. fabae*, however, did not respond to their host plant (spindle, *Euonymus europaeus*) odor. Odors of certain nonhost plants masked the attractiveness of the host plant leaves, but tansy (*Tanacetum vulgare*) and summer savory (*Satureja hortensis*) volatiles repelled *B. brassicae* and *A. fabae*, respectively. 3-Butenyl isothiocyanate attracted *B. brassicae* and *Lipaphis erysimi* (Kalt.), the latter species being more sensitive in both behavioral and electrophysiological studies. Isothiocyanate receptors were found on the antennae of *A. fabae*, which was repelled by these compounds, 4-pentenyl isothiocyanate being the most active.

Key Words—Aphid, *Aphis fabae*, *Brevicoryne brassicae*, Homoptera, Aphididae, *Lipaphis erysimi*, olfaction, plant volatiles, isothiocyanate, electrophysiology, repellent, odor masking.

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INTRODUCTION

The role that host plant odor plays in aphid host finding and selection is still uncertain. For many years, odor was thought not to be involved in long-range host finding. Field studies demonstrated equal landing rates on host and nonhost plants by gynoparae and alate virginoparae of *Myzus persicae* and *Aphis fabae* and alate virginoparae of *Brevicoryne brassicae* (Kennedy et al., 1959a,b; Müller, 1962), suggesting that hosts were only selected after landing, with aphids having differential leaving rates from hosts and nonhosts. However, electrophysiological responses to plant volatiles have been shown in *Nasonovia ribis-nigri* (Bromley and Anderson, 1982), *Sitobion avenae* (Yan and Visser, 1982), *Lipaphis erysimi* (Dawson et al., 1987), and *A. fabae* (Wadhams, 1990), and behavioral responses have been shown in olfactometers (*A. fabae*, Alikhan, 1960; *B. brassicae* and *Rhopalosiphum padi*, Pettersson, 1970, 1973; *Aphis gossypii*, Pospisil, 1972), in the field (*Cavariella aegopodii*, Chapman et al., 1981; *Phorodon humuli*, Campbell et al., 1990), and in a wind-tunnel experiment on walking *Cryptomyzus korschelti* (Visser and Taanman, 1987), which demonstrated an odor-conditioned upwind anemotaxis. In addition, herbs have been recommended in the popular and organic gardening literature for many years as a means of repelling or deterring aphid pest species. For example, savory (*Satureja* spp.) and tansy (*Tanacetum vulgare*) are suggested as companion plants to deter aphids (e.g., Yepson, 1984) and reductions in *M. persicae* populations on bell peppers (*Capsicum luteus*) were reported after interplanting with tansy (Matthews et al., 1983). Thus, there is evidence that volatiles are implicated in host finding and that this behavior can be modified by nonhost odors.

This study was designed to reassess the role of host and nonhost plant odors in the orientation behavior of the black bean aphid, *A. fabae*, the cabbage aphid, *B. brassicae*, and the turnip aphid, *Lipaphis erysimi*. *A. fabae* alternates between a primary host, usually spindle (*Euonymus europaeus* L.), and a range of herbaceous secondary hosts, including broad bean (*Vicia faba* Moench). *B. brassicae* and *L. erysimi* complete their life-cycles on plants in the Cruciferae (Brassicaceae) and Resedaceae, families characterized by the presence of glucosinolates. These compounds have been implicated in the attraction of *B. brassicae* to rape buds and flowers (Pettersson, 1973); they are also reported to stimulate feeding in *B. brassicae* (Wensler, 1962) and *L. erysimi*, but to deter feeding in other species, including *A. fabae* (Nault and Styer, 1972). Glucosinolates are decomposed by enzymic action to produce volatile isothiocyanates (Kjaer, 1960; Ju et al., 1982). Behavioral responses of *B. brassicae*, *L. erysimi*, and *A. fabae* to a range of isothiocyanates were therefore examined in an olfactometer. As *L. erysimi* is known to possess olfactory receptors for isothiocyan-

ates (Dawson et al., 1987), such receptors were also sought in *A. fabae* and *B. brassicae*.

METHODS AND MATERIALS

Insects. A. fabae were reared on tick beans (*Vicia faba*) in environmental cabinets held at 15°C. Apterae were obtained from continuous cultures, while alate virginoparae (summer migrants) were produced by crowding early instar aphids in long-day (light–dark 16 : 8) conditions. Gynoparae (autumn migrants) were induced by short days (light–dark 12 : 12). *B. brassicae* and *L. erysimi* were reared on Brussels sprouts (*Brassica oleracea* L., Bedford Darkmar) and turnip (*Brassica campestris* var. *rapifera* Metz.), respectively, in long days, with alates again being induced by crowding. All experimental aphids were young adults, starved for 24 hr, and used only once.

Plant Material. Host plants, bean (*Vicia faba*: Sutton dwarf bean or tick bean) and Brussels sprouts (*B. oleracea*: Bedford Darkmar) were greenhouse-grown, while spindle (*Euonymus europaeus*) leaves were field-picked. Non-hosts, winter savory (*Satureja montana* L.), summer savory (*Satureja hortensis* L.), tansy (*Tanacetum vulgare* L.), basil (*Ocimum basilicum* L.), thyme (*Thymus vulgaris* L.), and sage (*Salvia officinalis* L.) were grown in the greenhouse. All host and nonhost plant leaves were freshly picked and weighed prior to experiments.

Olfactometer. A linear track olfactometer, based on a design by Sakuma and Fukami (1985) and modified for aphids (Hardie et al., 1990), was constructed from transparent Plexiglas tubing and steel rods. The rods formed a T junction at the point where equal airstreams met from two side arms in the olfactometer. Twenty-five adult aphids were placed in a Fluon-lined dish at the base of the vertical rod and those that climbed up were scored for their direction of turn along the horizontal rod. All subsequent movement was ignored. An airflow of 1 liter/min was maintained in all experiments, with the air being subsequently exhausted from the room. The apparatus was housed within a black box and aphids were attracted upwards by a diffuse light. When plant material was used as a treatment, filter papers (Whatman No. 1; 4.25 cm) saturated with water were included to create equivalent humidities. Treatment and control sides were alternated for each new replicate and runs lasted for 10 min. Experiments were conducted at 19–23°C; between replicates the olfactometer was washed with methanol and soapy water. All data were analyzed using paired t tests, with means quoted $\pm$ SE and significance taken as $P < 0.05$.

Responses of alate and apterous *A. fabae* to three different levels of host plant leaf damage were tested: (1) undamaged, where leaves were gently picked

off the plant; (2) light damage, where leaves were rolled between the fingers; and (3) heavy damage, where leaves were crushed prior to use. All treatments employed whole leaves weighing 2 g (± 0.2 g). In bioassays with *B. brassicae*, and all host and nonhost experiments, undamaged leaf material was used. Host and nonhost leaves were presented together, and separately, in experiments with alate virginoparae of *A. fabae* and *B. brassicae*. Two ratios of host to nonhost leaf weight were used (2.0:2.0 g and 2.0:0.5 g).

Chemicals. Allyl, 3-butenyl, 4-pentenyl, and phenylethyl isothiocyanates (Figure 1) were obtained commercially or synthesized by standard methods. Isothiocyanates in hexane (10 μl) were applied to filter paper (Whatman No. 1; 4.25 cm) and placed in the treatment side of the olfactometer. Hexane (10 μl) alone served as the control.

Electrophysiology. Recordings from cells associated with the olfactory receptors on the proximal primary rhinaria of alate virginoparous *A. fabae* and *B. brassicae* were obtained using tungsten microelectrodes. Signals were amplified and recorded by standard methods (Wadhams et al., 1982; Dawson et al., 1987). The stimulus was delivered into a purified airstream (1 liter/min) that flowed continuously over the preparation. The delivery system, which utilized a filter paper in a disposable Pasteur pipet cartridge, has been described previously (Wadhams et al., 1982). The impulse frequency was determined as the number of impulses elicited during the first 1 sec after stimulus application.

RESULTS AND DISCUSSION

There was no preferred direction of turn for apterous or alate *A. fabae* or for alate *B. brassicae* when the two chambers of the olfactometer contained only damp filter paper. However, *A. fabae* virginoparae were attracted to undamaged, but not to damaged, bean leaves (Table 1); apterae were attracted

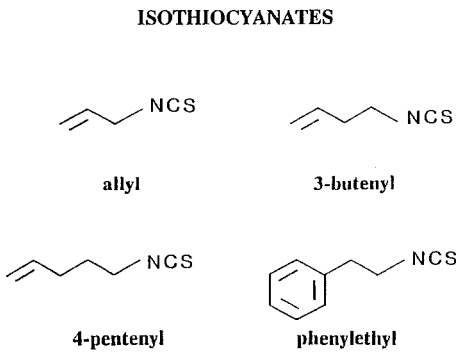

FIG. 1. Structures of isothiocyanates.

TABLE 1. RESPONSE (±SE) OF APTEROUS AND ALATE VIRGINOPARAE OF *Aphis fabae* TO BEAN LEAVES[a]

	Apterous virginoparae		Alate virginoparae	
	Treatment	Control	Treatment	Control
1. Undamaged tick bean	7.1 ± 0.5	4.6 ± 0.5 A	8.3 ± 0.8	6.4 ± 0.5 ns
2. Undamaged Sutton bean	6.9 ± 0.5	4.3 ± 0.5 A	7.9 ± 0.8	5.4 ± 0.4 A
3. Lightly damaged bean	4.6 ± 0.6	5.4 ± 0.8 ns	6.5 ± 0.6	6.3 ± 0.7 ns
4. Heavily damaged bean	4.3 ± 0.5	5.5 ± 0.7 ns	6.4 ± 0.8	6.5 ± 1.0 ns

[a] 3 and 4: apterous virginoparae with tick beans and alate virginoparae with Sutton dwarf beans, respectively. A = attraction, ns = not significantly different at $P < 0.05$, two-tailed paired t tests (eight replicates).

to both undamaged tick beans and Sutton dwarf beans, while alates were only significantly attracted by the Sutton dwarf beans. The lack of response to damaged plants may be due to an inability to recognize the altered volatile profile as that of a host plant. The degree of leaf damage, however, would have been greater than that normally encountered in the field. Alate virginoparae were not attracted to odor from mature leaves of spindle, the primary host (6.8 ± 0.4 cf. 6.4 ± 0.6; $N = 8$), and gynoparae did not respond to bean leaves or to mature (7.4 ± 0.7 cf. 6.1 ± 1.1; $N = 8$) or scenescent spindle leaves (6.5 ± 0.5 cf. 6.8 ± 0.4; $N = 8$). No response to spindle was observed even after 72 hr of starvation (3.6 ± 0.5 cf. 2.8 ± 0.3; $N = 8$), which should have ensured that the insects had completed any migratory or host-ignoring behavioral phase associated with olfactory cues, i.e., comparable to that observed with visual cues (Nottingham and Hardie, 1989). Previous olfactometer studies have produced variable results for responses of *A. fabae* to host plant odor. Alikhan (1960) reported attraction of apterous and alate virginoparae to bean and sugar beet leaf extracts, while Jones (1944) found no evidence for olfactory responses of alate virginoparae to bean, spindle, or leaf extracts. The present results suggest that plant volatiles play a role in host location by some aphid morphs.

Although alate virginoparae of *A. fabae* were attracted to Sutton dwarf beans alone and to beans in 4:1 ratios with winter savory and tansy and in a 1:1 ratio with sage, no significant attraction was elicited from 1:1 ratios of beans with winter savory, summer savory, tansy, thyme, or basil (Table 2). Summer savory alone appeared to be repellent. Similarly, alate virginoparae of *B. brassicae* were attracted to Brussels sprouts (host) odor, but combinations

of sprouts and winter savory or tansy odor were either unattractive or repellent (Table 3). Tansy alone also proved to be repellent.

It thus appears that attraction of aphids to host leaves can be disrupted by the presence of nonhost plant odor. This may be due to repellency, i.e., oriented movement away from an odor source (Dethier et al., 1960) or to odor masking,

TABLE 2. RESPONSE (±SE) OF ALATE VIRGINOPARAE OF *Aphis fabae* TO COMBINATIONS OF HOST AND NONHOST PLANT LEAVES[a]

	Ratio	Treatment	Control
Sutton beans		7.0 ± 0.4	4.0 ± 0.6 A
Sutton beans and winter savory	4:1	8.2 ± 0.5	5.5 ± 0.7 A
Sutton beans and winter savory	1:1	5.5 ± 0.8	7.3 ± 1.1 ns
Winter savory		6.5 ± 1.2	6.7 ± 0.6 ns
Sutton beans and tansy	4:1	7.5 ± 0.5	5.2 ± 0.5 A
Sutton beans and tansy	1:1	5.8 ± 0.8	6.3 ± 1.1 ns
Tansy		5.2 ± 0.9	8.2 ± 1.0 ns
Sutton beans and summer savory	1:1	7.7 ± 0.8	6.5 ± 0.6 ns
Summer savory		4.2 ± 0.6	6.2 ± 0.8 R
Sutton beans and thyme	1:1	6.3 ± 1.1	6.3 ± 0.8 ns
Thyme		5.0 ± 0.9	5.7 ± 0.6 ns
Sutton beans and basil	1:1	5.5 ± 0.6	7.3 ± 1.0 ns
Basil		5.8 ± 1.0	5.7 ± 0.6 ns
Sutton beans and sage	1:1	8.3 ± 0.5	6.0 ± 0.6 A
Sage		5.7 ± 0.5	5.8 ± 0.6 ns

[a] A = attraction, R = repulsion, ns = not significantly different at $P < 0.05$, two-tailed paired t tests (six replicates).

TABLE 3. RESPONSE (±SE) OF ALATE VIRGINOPARAE OF *Brevicoryne brassicae* TO COMBINATIONS OF HOST AND NONHOST LEAVES[a]

	Ratio	Treatment	Control
Brussels sprouts		7.3 ± 0.6	4.7 ± 0.4 A
Brussels sprouts and winter savory	4:1	3.7 ± 0.3	4.7 ± 0.7 ns
Brussels sprouts and winter savory	1:1	3.7 ± 0.7	6.3 ± 1.2 R
Winter savory		5.0 ± 0.9	6.7 ± 0.7 ns
Brussels sprouts and tansy	4:1	3.8 ± 0.6	4.5 ± 0.8 ns
Brussels sprouts and tansy	1:1	4.0 ± 0.6	7.5 ± 0.7 R
Tansy		4.0 ± 0.6	7.2 ± 0.7 R

[a] A = attraction, R = repulsion, ns = not significantly different at $P < 0.05$, two-tailed paired t tests (six replicates).

implying neutralization of an insect's orientation response without repellency (Thiery and Visser, 1986). Both effects were probably operating in this study; for example, tansy proved repellent to *B. brassicae*, while winter savory and thyme masked the attraction of *A. fabae* to host plant odor without in themselves being repellent. It is also of interest that the repellent action of tansy was masked by Brussels sprout odor.

Electrophysiological recordings from the proximal rhinaria on the antenna showed the presence of cells in *B. brassicae* (Figure 2) and *L. erysimi* (Dawson et al., 1987) that responded to isothiocyanates. Both species displayed strong electrophysiological responses to 3-butenyl isothiocyanate and were attracted by this compound in the olfactometer (Table 4). However, the electrophysiological threshold concentration was considerably lower for *L. erysimi* (ca. 10^{-11} g) than for *B. brassicae* (10^{-7} g), and this is reflected in its greater behavioral sensitivity. In *L. erysimi* isothiocyanates have the additional function of synergizing the action of the alarm pheromone, (*E*)-β-farnesene (Dawson et al.,

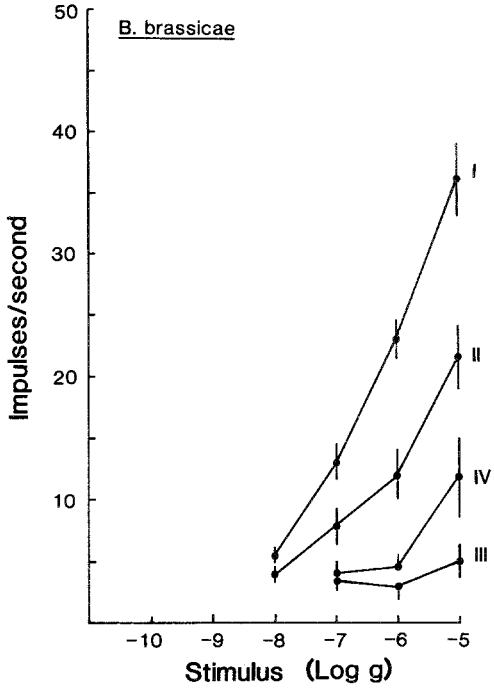

FIG. 2. Dose–response curves of *B. brassicae* olfactory cells to (I) 4-pentenyl, (II) 3-butenyl, (III) allyl, and (IV) phenylethyl isothiocyanates (means of five preparations ± SE). Where standard errors overlap, only half the SE bar is shown.

TABLE 4. RESPONSE (±SE) OF ALATE VIRGINOPARAE OF *Brevicoryne brassicae* AND *Lipaphis erysimi* TO 3-BUTENYL ISOTHIOCYANATE[a]

	B. brassicae		*L. erysimi*	
Amount (μg)	Treatment	Control	Treatment	Control
100	7.2 ± 0.4	4.8 ± 0.3 A	9.0 ± 0.7	5.5 ± 0.8 A
10	7.2 ± 0.8	5.2 ± 0.7 ns	8.8 ± 0.9	5.7 ± 0.4 A
1	6.7 ± 0.4	6.0 ± 0.7 ns	7.8 ± 1.0	5.3 ± 0.8 A
0.1	6.2 ± 0.9	6.2 ± 0.5 ns	8.3 ± 0.9	7.3 ± 1.2 ns
Hexane	5.8 ± 0.6	5.3 ± 0.6 ns	6.8 ± 0.6	6.5 ± 0.7 ns

[a] A = attraction, ns = not significantly different at $P < 0.05$, two-tailed paired t tests (six replicates).

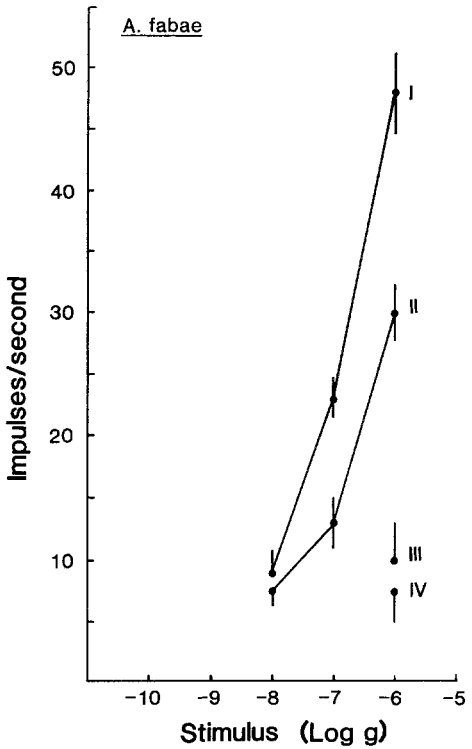

FIG. 3. Dose–response curves of *A. fabae* olfactory cells to (I) 4-pentenyl, (II) 3-butenyl, (III) allyl, and (IV) phenylethyl isothiocyanates (means of five preparations ± SE). Where standard errors overlap, only half the SE bar is shown.

FIG. 4. Olfactory cell in *A. fabae* proximal primary rhinarium: response to 1 μg of 4-pentenyl isothiocyanate. The stimulus duration (1 sec) is shown by the black bar.

TABLE 5. RESPONSE (±SE) OF ALATE VIRGINOPARAE OF *Aphis fabae* TO ISOTHIOCYANATES[a]

Amount (μg)	4-Pentenyl		3-Butenyl		Allyl	
	T	C	T	C	T	C
1,000	4.2 ± 0.7	6.8 ± 0.5 R	5.0 ± 0.7	7.8 ± 0.7 R	4.8 ± 0.7	7.3 ± 0.8 R
100	5.7 ± 0.7	8.0 ± 0.8 ns	4.3 ± 0.7	7.5 ± 0.9 R	5.5 ± 0.4	7.7 ± 0.6 ns
10	4.0 ± 0.4	6.7 ± 1.0 R	6.2 ± 0.9	6.2 ± 0.6 ns	4.5 ± 0.6	6.5 ± 0.8 ns
1	6.7 ± 0.4	5.5 ± 0.8 ns	5.8 ± 0.7	6.0 ± 0.7 ns	6.5 ± 0.7	6.5 ± 0.8 ns
Hexane	4.7 ± 0.4	5.0 ± 0.4 ns				

[a] T = treatment, C = control. R = repulsion, ns = not significantly different at $P < 0.05$, two-tailed paired t tests (six replicates).

TABLE 6. RESPONSES (±SE) OF ALATE VIRGINOPARAE OF *Aphis fabae* TOWARD SUTTON DWARF BEANS ALONE AND BEANS WITH 3-BUTENYL OR 4-PENTENYL ISOTHIOCYANATE[a]

Amount (μg)	3-Butenyl		4-Pentenyl	
	Treatment	Control	Treatment	Control
100	5.5 ± 0.6	4.9 ± 1.1 ns	5.0 ± 0.7	6.6 ± 1.0 ns
10	6.3 ± 0.8	6.1 ± 0.6 ns	6.5 ± 0.8	6.1 ± 0.7 ns
1	8.8 ± 0.5	5.9 ± 0.7 A	7.9 ± 0.7	5.9 ± 0.5 A
Beans only	7.3 ± 0.6	5.1 ± 0.4 A	—	—

[a] A = attraction, ns = not significantly different at $P < 0.05$, two-tailed paired t tests (eight replicates).

1987). Thus, alone they are attractants, but in combination with (*E*)-β-farnesene their effect is to initiate an alarm response.

Alate virginoparae of *A. fabae* also were shown to have olfactory receptors sensitive to isothiocyanates (Figures 3 and 4), although these compounds are not associated with their host plants. The response characteristics of the cells were similar to those observed for *B. brassicae*, but the behavioral responses were markedly different. While 100 μg of 3-butenyl isothiocyanate attracted *B. brassicae*, it repelled *A. fabae* (Tables 4 and 5). Allyl isothiocyanate was also repellent to *A. fabae*, but only at high concentrations (Table 5). The low behavioral activity of this compound correlates well with its relatively low electrophysiological activity (Figure 3). 4-Pentenyl isothiocyanate was the most active compound in electrophysiological studies (Figure 3) and proved repellent at a

level of 10 μg (Table 5). Phenylethyl isothiocyanate did not elicit electrophysiological responses in either *A. fabae* or *B. brassicae* (Figures 2 and 3). Both 3-butenyl and 4-pentenyl isothiocyanates masked the attractant response of *A. fabae* to Sutton bean leaves at levels of 100 and 10 μg (Table 6). No repellency was observed. Therefore, the presence of host plant volatiles reduced the repellency of the isothiocyanates, presumably in a similar way to the interaction of tansy and host volatiles for *B. brassicae* described above.

It must now be accepted that plant volatiles play a role in host location and selection by aphids. The current study demonstrates behavioral responses of alate and apterous aphids, with attraction to host and repulsion by some nonhost odors. In addition, it reveals that nonhost volatiles can mask host attraction. In some cases, individual volatiles have been implicated, but the interaction of different odor components is undoubtedly complex. Although evidence of olfactory responses by flying aphids is restricted to *C. aegopodii* (plant volatiles; Chapman et al., 1981) and *P. humuli* (sex pheromone and plant volatiles; Campbell et al., 1990), these observations demonstrate a role for olfaction at a distance. After landing, local odor fields may also prove important. The present results indicate that host and nonhost odor interactions may provide a degree of crop protection in companion planting programs and suggest that manipulating behavior via plant volatiles or mimics may be a way forward for aphid control.

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