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VARIATION IN PLANT VOLATILES AND ATTRACTION OF THE PARASITOID *Diadegma semiclausum* (HELLÉN)

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Abstract—Differences in allelochemistry of plants may influence their ability to attract parasitoids. We studied responses of *Diadegma semiclausum* (Hellén), a parasitoid of the diamondback moth (*Plutella xylostella* L.), to inter- and intraspecific variation in odor blends of crucifers and a non-crucifer species. Uninfested Brussels sprout (*Brassica oleracea* L. gemmifera), white mustard (*Sinapis alba* L.), a feral *Brassica oleracea*, and malting barley (*Hordeum vulgare* L.) were compared for their attractivity to *D. semiclausum* in a Y-tube bioassay. Odors from all plants were more attractive to the parasitoid than clean air. However, tested against each other, parasitoids preferred the volatile blend from the three cruciferous species over that of malting barley. Wasps also discriminated between uninfested crucifers: mustard was as attractive as feral *B. oleracea*, and both were more attractive than Brussels sprout. Attractivity of uninfested plants was compared with that of plants infested by larvae of the host *P. xylostella*. Host-infested mustard and Brussels sprout were more attractive than uninfested conspecifics. Interestingly, the volatile blends of uninfested white mustard and infested Brussels sprout were equally attractive. We also compared the volatile composition of different plant sources by collecting headspace samples and analysing them with GC-MS. Similarities of volatile profiles were determined by hierarchic clustering and non-metric scaling based on the Horn-index. Due to the absence of several compounds in its blend, the volatile profile of barley showed dissimilarities from blends of crucifers. The odor profile of white mustard was distinctly different from the two Brassicaceae.

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Feral *Brassica oleracea* odor profile was different from infested Brussels sprout, but showed overlap with uninfested Brussels sprout. Odor blends from infested and uninfested Brussels sprout were similar, and mainly quantitative differences were found. *D. semiclausum* appears to discriminate based on subtle differences in volatile composition of odor blends from infested and uninfested plants.

Key Words—*Diadegma semiclausum*, *Plutella xylostella*, *Hordeum vulgare*, *Sinapis alba*, *Brassica oleracea*, olfactometer, headspace volatiles, GC-MS.

INTRODUCTION

Plant-derived infochemicals are important for parasitoids of herbivores in the process of host location (Vinson, 1976; Vet and Dicke, 1992; Tumlinson et al., 1993; Völkl and Sullivan, 2000). The dietary breadth of both herbivores and their parasitoids may influence the degree to which plant odors are used in this process (Vet and Dicke, 1992). In general, odors from uninfested and mechanically damaged plants are easier to detect by a parasitoid than cues from the host, but they represent a weak predictor of host presence (Vet et al., 1991). On the other hand, information from the host itself (i.e., feces, frass, silk) is a more reliable indicator of a host, but is usually more difficult to detect than plant-derived volatiles. The solution to this reliability-detectability problem may rely on herbivore-induced volatiles. These are emitted upon damage by the host and are both reliable and detectable. In natural ecosystems, host-parasitoid interactions take place in habitats composed of several to many plant species, where both the expectancy of the host's presence and the specificity of volatile infochemicals may show great between- and within-plant variation (Takabayashi et al., 1994; De Moraes et al., 1998; Vet, 1999; Gouinguené, 2001). Variation in odors among plant species and cultivars can be greater than between damaged and undamaged conspecific plants (Geervliet et al., 1997), and such differences can be reflected in the attractance of parasitoids to plants (Elzen et al., 1983, 1986; Fox and Eisenbach, 1992; Geervliet et al., 1996). The differential ability of plants to attract natural enemies may even be responsible for further dietary specialization of herbivores exploiting specific plant taxa like the Cruciferae (Yano, 1994). For example, opposing choices at the plant-level could benefit the herbivore and lead to enemy-free space shaping host-parasitoid interactions (Fox and Morrow, 1981; Fox and Eisenbach, 1992; Bigger and Fox, 1997; Gratton and Welter, 1999; Oppenheim and Gould, 2002). If host-parasitoid interactions in ecosystems are to be understood, foraging behavior of parasitoids must be studied in relation to inter- and intraspecific variation in plant-derived infochemicals.

Crucifers are characterized by the presence of glucosinolates and their volatile by-products. These compounds play a role in the host searching behavior of parasitoid species that forage on hosts associated with plants of this family (Read et al., 1970, 1985; Shiojiri et al., 2001; Smid et al., 2002). Other studies show

effects of inter- and intraspecific variation in volatiles of cruciferous plants on their attractivity to parasitoids (Geervliet et al., 1996; Liu and Jiang, 2003; Kalule and Wright, 2004). Fox and Eisenbach (1992) found that *Diadegma insulare*, a parasitoid of larvae of *Plutella xylostella* L., preferred wild crucifers to collards. Higher levels of parasitism of *P. xylostella* by *Cotesia plutellae* were observed on common cabbage than on Chinese cabbage, which was attributed to differences in attractivity of plant odors for the parasitoid (Liu and Jiang, 2003).

Breeding programs involving glucosinolate chemistry largely focus on mammalian toxicity, and the demands of consumers in the utilization of plant organs (Mithen, 2001). Members of the Brassicaceae have undergone extensive breeding, resulting in huge variation in both the composition and the allocation of plant chemicals in different plant organs (Benrey et al., 1998; Mithen, 2001). Besides, the efforts to select for resistance in breeding programs mainly focused on direct defenses, ignoring effects on the third trophic level (Dicke, 1999; Bradburne and Mithen, 2000). It is possible that crucifer breeding programs have changed the apparency of plants not only for herbivores, but also for those parasitoids that use plant-derived infochemicals in habitat and host location. Therefore, domesticated plants might have an altered capacity to attract natural enemies, but experimental evidence is needed to test this assumption (Loughrin et al., 1995; Benrey et al., 1998; Cortesero et al., 2000).

We chose members of the family *Brassicaceae* to study how inter- and intraspecific variation in odor blends influence their ability to attract larval parasitoids. We examined the responses of *Diadegma semiclausum*, a specialist parasitoid of the diamondback moth (*Plutella xylostella*), in olfactometer bioassays. The uninfested plants compared were Brussels sprout, a naturalized population of previously cultivated *Brassica oleracea*, white mustard, and malting barley. The latter species was included in comparisons as a species not related to crucifers and a non-host for *P. xylostella*. Comparisons of host-infested and uninfested plants involved Brussels sprout and mustard.

METHODS AND MATERIALS

Plants. Plants used were malting barley (*Hordeum vulgare* L. cv Video) (Cyperales, Gramineae), white mustard (*Sinapis alba* L. cv Carnaval) (Capparales, Brassicaceae), Brussels sprout (*Brassica oleracea* L. gemmifera cv Cyrus) (Capparales, Brassicaceae), and a naturalized population of *Brassica oleracea* L. This feral population was found in a roadside hollow in 2001, it probably "escaped" from a local farm, and it is unknown how long it has been growing in the wild (Harvey et al., 2003). Plants were reared in a greenhouse compartment under a 16L; 8D photoperiod, 20–28°C, and 40–80% R.H. Plants were sown in ca. 1.2 l pots filled with standard compost (Lentse Potgrond®) with no extra fertilizer

added. To standardize the biomass of the plants to about 25 g, a different number of plants per pot were grown for each species; eighteen for barley (3–4 wk old), nine for mustard (3–4 wk old), and one for Brussels sprout (6–7 wk old) and the feral *B. oleracea* (6–7 wk old). White mustard was tested, when the first flower buds had started to develop. Before testing, each plant was removed from the pot and below-ground plant parts were wrapped in aluminium foil. The plant was then used for behavioral assays or headspace sample collection.

Insects. Diadegma semiclausum (Hellén) (Hymenoptera, Ichneumonidae) was collected from Brussels sprout fields in a woodland area in the vicinity of Wageningen (The Netherlands) and was maintained on *Plutella xylostella* L. (Lepidoptera, Plutellidae) reared on Brussels sprout (8D: 16L photoperiod, 20 ± 2°C and 70% R.H). In the rearing cages, parasitized host larvae were allowed to pupate on paper strips, then transferred into a plastic cage with neither host nor plant material present. Wasps emerging from cocoons were provided *ad libitum* with water and honey. Mated females of 5–10 days of age with no oviposition experience were used in olfactometer bioassays. To obtain infested plants (mustard or Brussels sprout), 20 second or early third instar *P. xylostella* larvae were evenly distributed over a test plant 14–16 hr before the experiment.

Olfactometer Bioassay. To test behavioral responses of individual *D. semiclausum* females to plant odors, a glass Y-tube olfactometer (diam. 3.5 cm, length of stem section 22 cm) was used (for details see Takabayashi and Dicke, 1992). The two arms of the Y-tube were connected to glass vessels containing the odor source. The volume of the containers was five-liter in all comparisons except those involving the feral *B. oleracea*. As this plant had long petioles, we used 30 l containers to accommodate the plants. When an odor source was compared with clean air, a piece of cotton-wool humidified with water was placed into the empty container. While the 5 l containers were directly attached to the olfactometer, the two 30-l containers were attached with a silicon hose. Air was filtered over charcoal and led into each container at 4 l/min. The air was extracted at the base of the olfactometer at 8 l/min. The olfactometer was illuminated from above with high frequency fluorescent lights at an intensity of 30–35 μmol photons/m^2/sec. Wasps were individually tested in the olfactometer, and each wasp was used only once. In order to increase their motivation to search for hosts (Potting et al., 1999), females were transferred from the cage into the Y-tube on a piece of Brussels sprout leaf, damaged by the host but not containing the host itself or its products. The observation started by releasing the wasp at the base of the Y-tube, at 4 cm distance from the opening. Wasps were either walking or flying towards the odor source. A finish line was drawn 1 cm from the sieve at the end of each arm. A choice occurred when a wasp crossed the finish line and did not return to the junction for at least 15 sec. Wasps that did not make a choice within 10 min after release and wasps that did not reach the junction of the olfactometer within 5 min were considered non-responding individuals. Odor sources were replaced after testing

5–7 females, and at least 8 sets of new plants were used for each comparison. To control for possible asymmetries in the set-up, the odor source was moved from one arm of the olfactometer to the other after testing 3–4 females.

The attractiveness of the odor blends from the following uninfested plants were tested against clean air and each other. Brussels sprout, feral *B. oleracea*, mustard, and barley. Odor blends of host-infested Brussels sprout and mustard were compared to uninfested conspecifics, and uninfested mustard was compared to host-infested Brussels sprout. The tests were carried out from March–September 2003.

Collection and Analysis of Headspace Volatiles. Headspace volatiles were collected from all plant sources tested in Y-tube bioassays (except for the *Plutella*-infested mustard), and were analyzed by GC-MS. Four to five samples of each were taken in the period of June-August 2003. Plants prepared for sampling as described in section "*Plants*" were transferred into 30 l collection flasks. Pressurized air was filtered through silica gel, molecular sieves 4A and 13X (Linde), and activated charcoal before entering the flask. The air inlet, air outlet, filters, and sampling jar were connected with 0.8 cm diam. teflon tubing. After the plant was placed into the collection flask, the system was purged for 1 hr at an airflow rate of 500 ml/min to remove volatile contaminants. Subsequently, volatiles were collected in a glass tube containing 90 mg Tenax-TA (20/35 mesh) for 4–5 hr at a flow rate of 150–250 ml/min. Blanks were taken in duplicate from empty collection containers. The collected volatiles were released from the Tenax by heating the trap in a Thermodesorption Cold Trap Unit (Chrompack) at 250°C for 10 min and flushing with helium flowing at 12 ml/min. The released compounds were cryo-focused in a coldtrap (0.52 mm ID deactivated fused silica) at a temperature of −85°C. By ballistic heating of the cold trap to 220°C, the volatiles were transferred onto the analytical column (DB5, 60 m × 0.25 mm ID, 0.25-μm film thickness), which was connected to a Finnigan MAT 95 mass spectrometer. The temperature of the column oven was programmed from 40°C (4 min hold) to 250°C (4 min hold) at a rate of 4°C/min, and the initial helium velocity was 25 cm/sec. The mass spectrometer was operated in the 70 eV EI ionization mode and was scanning from mass 24 to 300 at 0.7 sec/decade. Compounds were identified by comparison of the mass spectra with those in the Wiley 7th/NIST98 library and in the Wageningen Mass Spectral Database of Natural Products and by checking the retention index. Emission rates were measured by quantifying peak areas. Compounds are presented as peak area per liter of trapped air per gram above-ground fresh weight.

Statistical Analysis. A binomial test was used to determine whether preferences of parasitoids were significantly different from a non-preference situation ($p = q = 0.5$, two-tailed, $\alpha = 0.05$). Non-responding wasps were excluded from the analysis. To illustrate the dissimilarities between the odor blends of plants, classification (hierarchical clustering) and ordination (non-metric scaling)

methods were used. Those compounds not present in the blank and detected in at least two replicate samples were included in the analysis. The detected quantities of individual compounds within a sample were considered as variables, and dissimilarities among the 24 plant samples were calculated based on the Horn-index (average link method) (see Krebs, 1989, eqn. 1). We chose this index because the calculated similarities among the volatile blends are supposedly little affected by the number of compounds included in the analysis (Krebs, 1989).

$$R_0 = \frac{\sum[(x_{ij} + x_{ik})\log(x_{ij} + x_{ik})] - \sum(x_{ij}\log x_{ij}) - \sum(x_{ik}\log x_{ik})}{[(N_j + N_k)\log(N_j + N_k)] - (N_j \log N_j) - (N_k \log N_k)} \quad (1)$$

Where R_0 is the Horn's index of similarity for samples j and k, x_{ij}, and x_{ik} are the detected amounts of compound i in sample j and sample k, where N_j is Σx_{ij} the total amount of volatiles in sample j and N_k is Σx_{ik} the total number of compounds in sample k. Analysis was performed by the Syntax 5.1 program package (Podani, 1997).

RESULTS

Olfactometer Bioassay. When volatiles from different plants were tested against clean humidified air, 60% to 95% of wasps made a choice. Wasps preferred volatiles from all plant sources over clean air ($P < 0.01$) (Figure 1).

When offered a choice between blends of uninfested plants, 61% to 88% of the tested females made a choice (Figure 2). Parasitoids discriminated clearly among volatiles from different species of uninfested plants. All cruciferous plants were preferred over malting barley ($P < 0.001$), with wasps discriminating between

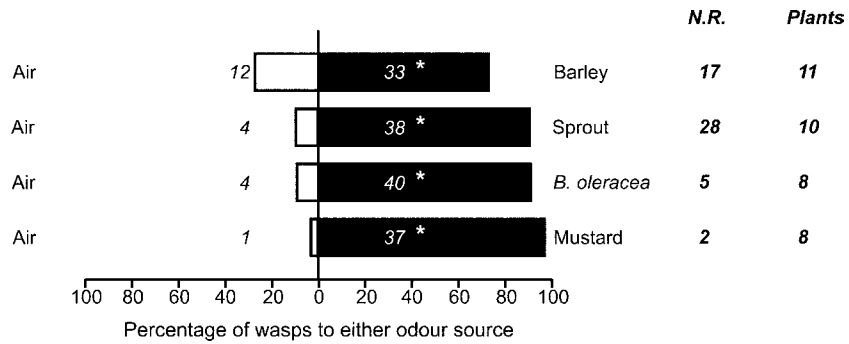

FIG. 1. Percentage of female *D. semiclausum* choosing either odor source when volatiles from uninfested plants are compared with clean air. Asterisks indicate significant preferences within tests (*$-P < 0.05$). Numbers next to graph are the number of non-responding (N.R.) individuals and the number of plants tested.

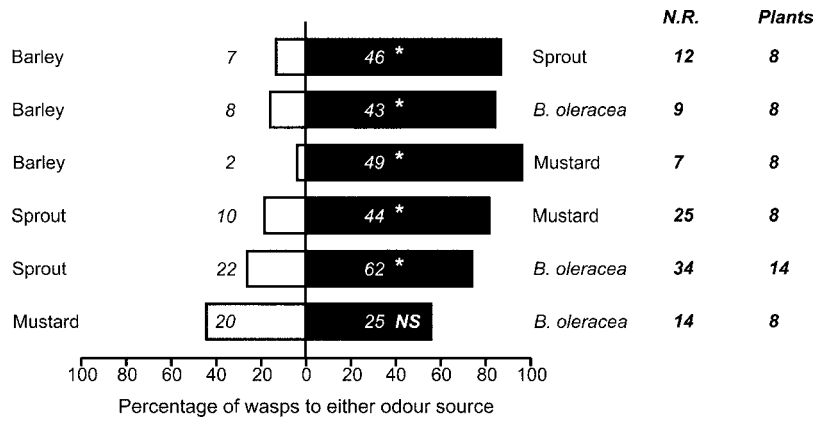

FIG. 2. Percentage of female *D. semiclausum* choosing either odor source from uninfested plants. Asterisks indicate significant preferences within tests ($^*-P < 0.05$). Numbers next to graph are the number of non-responding (N.R.) individuals and the number of plants tested.

the different cruciferous plants as well. Parasitoids preferred both mustard (82%) and the feral *B. oleracea* (74%) over Brussels sprout ($P < 0.001$) (Figure 2). The parasitoids were equally attracted to mustard and feral *B. oleracea*.

When parasitoids were exposed to volatiles from uninfested and host-infested cruciferous plants, 88% to 99% of individuals responded (Figure 3). Wasps discriminated between infested and uninfested conspecifics.

Parasitoids preferred both infested mustard (91%) and Brussels sprout (83%) to uninfested conspecifics. Interestingly, when females were offered a choice between host-infested Brussels sprout and uninfested mustard plants, no preference was observed.

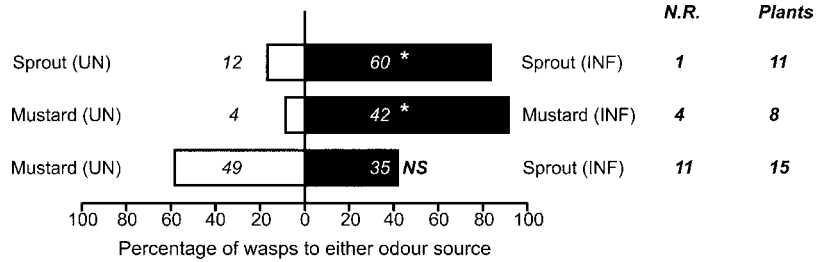

FIG. 3. Percentage of female *D. semiclausum* choosing either uninfested (UN) plants (Brussels sprout and mustard) or *P. xylostella*-infested plants (INF). Asterisks indicate significant preferences within tests ($^*-P < 0.05$). Numbers next to graph are the number of non-responding (N.R.) individuals and the number of plants tested.

Headspace Volatiles. In the 24 samples analyzed across treatments, 70 compounds were detected (Table 1). Compounds were identified as ketones, alcohols, aldehydes, esters, terpenoids, sulphides, nitrile, and others. In the headspace of barley, only 15 compounds were detected. Forty-six compounds were detected in the feral *B. oleracea* and in the mustard, 48 compounds were found in uninfested Brussels sprout and 59 in *Plutella*-infested Brussels sprout.

Characteristic GC traces of the plants tested are shown in Figure 4. Both quantitative and qualitative differences in headspace volatiles of tested plants were found. The smallest total amount of volatiles was emitted by barley, followed by mustard, feral *B. oleracea*, uninfested Brussels sprout, and host-infested Brussels sprout. Dissimilarities among the volatile profiles of different plants are presented in Figure 5. The volatile profile of barley showed the greatest dissimilarity among the treatments, with only 15 of the 70 compounds detected. Fourteen of these compounds were also present in the odor blend of at least one of the other plant sources. Compared to the crucifers, barley emitted few terpenoids. The dominant compounds produced by barley were the terpenoid linalool, which was also present in smaller amounts in the odor blend of infested Brussels sprout, 3-methyl-1-butanol, which was detected in smaller amounts both in the volatile blends of mustard and infested Brussels sprout, and the GLV (i.e., green leaf volatile) (*Z*)-3-hexen-1-ol, which was present in all samples.

The odor blend of the crucifers was dominated by the GLV (*Z*)-3-hexen-1-yl acetate, and the terpenoids sabinene, myrcene, limonene, and 1,8-cineole. The odor blend of mustard was more similar to the blends of the other crucifers than to that of barley, but it still grouped out from the blends of Brussels sprout and the feral *B. oleracea* (Figure 5). The 46 compounds detected in mustard greatly overlapped with those detected in the headspace of Brussels sprout and the feral *B. oleracea*. Four compounds, 2-methyl-1-butanol, 2-methyl-1-butyl acetate, 2-oxo-1,8-cineole, and germacrene D were detected in mustard alone. (*Z*)-3-hexen-1-yl 3-methylbutanoate and other compounds like 3-methyl-1-butanol, 3-methyl-1-butyl acetate, and indole were detected in mustard and infested Brussels sprout only. The compounds 3-methyl-1-butanol and 3-methyl-1-butyl acetate were also present in the odor blend of barley.

Infested Brussels sprout plants produced a similar odor blend to uninfested Brussels sprout and to a lesser extent to *B. oleracea*, but many of the compounds were emitted in considerably higher amounts by infested Brussels sprout. Four compounds, dehydroxylinalool oxide A, dehydroxylinalool oxide B, β-bisabolene, and cis-β-elemene were only present in the odor blend of feral *B. oleracea* (Table 1). (*E*,*E*)-α-Farnesene was found in high amounts in the feral *B. oleracea* and mustard only, whereas 3-methyl-2-pentanol was present in the volatile blend of the feral *B. oleracea* and that of infested Brussels sprout only.

The odor blends of infested and uninfested Brussels sprout plants showed the highest similarity. However, among the 59 compounds released by infested

TABLE 1. VOLATILE COMPOUNDS DETECTED IN THE HEADSPACE OF BARLEY, UNINFESTED MUSTARD (*S. ALBA*), BRUSSELS SPROUT, FERAL *B. OLERACEA* AND IN BRUSSELS SPROUT INFESTED BY LARVAE OF *P. XYLOSTELLA*[a]

Compound[b]	Barley ($N = 4$)	*S. alba* ($N = 5$)	*B. oleracea* ($N = 5$)	Brussels sprout ($N = 5$)	B. sprout +*Plutella* ($N = 5$)
Ketones					
1 3-pentanone$^{\Delta,\#,\circ}$	—	—	—	—	2.3 ± 1.6
2 2-hexanone	0.2 ± 0.2	0.1 ± 0.1	0.5 ± 0.2	1.5 ± 0.8	3.1 ± 1.7
3 1-cyclopropyl-2-propen-1-one$^{\circ}$	—	1.3 ± 0.5	0.9 ± 0.6	1.9 ± 1	10.7 ± 4.9
4 3-heptanone	—	1.3 ± 0.6	2.5 ± 0.4	3.3 ± 1.1	4.5 ± 1
5 2-heptanone	—	0.7 ± 0.2	1.1 ± 0.3	1.7 ± 0.4	1.9 ± 0.4
6 2-methyl-2-cyclopenlen-1-one (t)	1.7 ± 1	—	0.5 ± 0.5	0.8 ± 0.8	6.4 ± 4.8
7 3-octanone$^{\circ}$	—	—	2.6 ± 2.3	0.2 ± 0.2	2.4 ± 1.6
8 1,7-octadiene-3-one, 2-methyl-6-methylene	—	0.7 ± 0.5	2 ± 0.9	5.4 ± 2.7	8.6 ± 2.8
Alcohols					
9 1-penten-3-ol$^{\Delta,\square,\circ,\#}$	—	4.6 ± 0.9	1.2 ± 0.7	18.6 ± 11.4	117.5 ± 60.9
10 3-pentanol$^{\Delta,\square,\circ}$	—	0.3 ± 0.2	0.7 ± 0.2	2.6 ± 0.9	21.9 ± 11.5
11 3-methyl-3-buten-1-ol	—	—	—	—	0.7 ± 0.4
12 3-methyl-1-butanol$^{\circ}$	28.3 ± 6.2	6.5 ± 1.6	—	—	2.6 ± 0.8
13 2-methyl-1-butanol	—	1.1 ± 0.5	—	—	—
14 1-pentanol$^{\Delta,\square,\circ}$	0.4 ± 0.4	0.8 ± 0.1	1.3 ± 0.9	1.5 ± 0.7	8.2 ± 4
15 (*Z*)-2-penten-1-ol$^{\Delta,\square}$	—	—	0.2 ± 0.1	1.1 ± 0.7	12.5 ± 8.7
16 3-methyl-2-pentanol$^{\Delta,\square}$	—	—	1.3 ± 0.7	—	1 ± 0.8
17 (*Z*)-3-hexen-1-ol$^{\Delta,\square,\circ,\times,\#}$	17.5 ± 8.2	11.3 ± 2.8	9.5 ± 2.6	46 ± 22.5	358.8 ± 252.9
18 1-hexanol$^{\Delta,\square,\circ}$	1.6 ± 0.6	2.3 ± 0.4	3.9 ± 2.1	5.3 ± 2.5	28.3 ± 18.2
Esters					
19 3-methyl-1-butyl acetate$^{\circ}$	1.3 ± 0.6	6.5 ± 2.5	—	—	0.8 ± 0.4
20 2-methyl-1-butyl acetate	—	0.4 ± 0.2	—	—	—
21 (Z)-2-penten-1-yl acetate	—	1.7 ± 1	0.1 ± 0.1	24.4 ± 16.9	182.2 ± 112.3
22 pentyl acetate$^{\circ}$	—	1.3 ± 0.5	—	2.7 ± 1.7	17.6 ± 10.8

TABLE 1. CONTINUED

Compound[b]	Barley ($N = 4$)	*S. alba* ($N = 5$)	*B. oleracea* ($N = 5$)	Brussels sprout ($N = 5$)	B. sprout +*Plutella* ($N = 5$)
23 (*Z*)-3-hexen-l-yl acetate$^{\Delta,\circ,\times,\#,\blacktriangle,\bullet}$	—	231 ± 73.4	46.1 ± 17.4	381.7 ± 256.2	2175.8 ± l325.7
24 hexylacetate$^{\Delta,\circ,\#,\blacktriangle}$	—	11.5 ± 3.6	4.8 ± 1.9	18.2 ± 11.6	111.5 ± 76.8
25 (*Z*)-3-hexen-l yl-propanoate$^{\circ}$	—	—	—	—	2.2 ± 1.2
26 heptyl acetate$^{\circ}$	—	0.9 ± 0.5	0.3 ± 0.3	1.5 ± 1	4.7 ± 2.3
27 2-ethylhexyl acetate	5.5 ± 2.7	6.4 ± 1.5	11.3 ± 4.7	37.5 ± 10.5	33.9 ± 10.4
28 (*Z*)-3-hexen-l-ylbutanoate	—	0.2 ± 0.2	—	—	3.6 ± 2.8
29 methyl salicylate$^{\Delta}$	—	3.2 ± 1.8	0.9 ± 0.6	0.8 ± 0.6	1.5 ± 0.6
30 (*Z*)-3-hexen-l-yl 2-methylbutanoate	—	0.3 ± 0.2	—	0.4 ± 0.4	6.9 ± 3.7
31 (*Z*)-3-hexen-l-yl 3-methylbutanoate	—	3 ± 0.6	—	—	3.2 ± 2.3
Terpenoids					
32 α-thujene$^{\times,\Delta,\circ,\bullet}$	—	1.5 ± 0.8	27.9 ± 6.1	49.7 ± 17.8	83.8 ± 29
33 α-pinene$^{\Delta,\times,\#,\blacktriangle,\bullet}$	—	0.7 ± 0.3	6.1 ± 1.8	11.5 ± 2.3	19 ± 4
34 thuja-2,4,(10)-diene	—	—	1.4 ± 0.4	2.7 ± 0.4	4.4 ± 1.3
35 sabinene$^{\Delta,\circ,\times,\#,\blacktriangle,\bullet}$	—	31.2 ± 10.6	233.5 ± 45.1	345.7 ± 112.2	595 .9 ± 2 12.2
36 β-pinene$^{\Delta,\circ,\times,\#,\blacktriangle}$	—	2.4 ± 1	7.5 ± 1.5	15.1 ± 4.5	24.4 ± 7.2
37 myrcene$^{\Delta,\circ,\times,\#,\blacktriangle}$	8.8 ± 1.7	12.1 ± 5.4	59.9 ± 19.4	79.2 ± 36.7	150.4 ± 69.9
38 linalooloxide A, dehydroxy-	—	—	2.7 ± 1.8	—	—
39 linalooloxide B, dehydroxy-	—	—	3.5 ± 2.5	—	—
40 α-phellandrene	—	0.1 ± 0.1	—	0.7 ± 0.4	0.4 ± 0.3
41 α-terpinene$^{\Delta,\bullet}$	—	0.6 ± 0.6	0.6 ± 0.5	6.4 ± 2.7	8.9 ± 4.5
42 limonene$^{\Delta,\times,\#,\bullet}$	6.6 ± 1.3	18.9 ± 7.7	188.4 ± 49	257.2 ± 107.2	510.8 ± 209.5
43 β-phellandrene$^{\Delta,\times,\#}$	3 ± 1.2	1.2 ± 0.6	3.4 ± 1	4.9 ± 1.8	9.6 ± 3.6
44 l,8-cineole$^{\Delta,\circ,\times,\#,\blacktriangle}$	—	39.6 ± 14.6	41.2 ± 8.9	127.9 ± 40.6	255 ± 79.1
45 2-oxo-l,8-cineole	—	2.3 ± 1.6	—	—	—
46 (E)-β-ocimene$^{\times,\bullet}$	—	—	0.8 ± 0.5	1.4 ± 1.1	1.8 ± 0.8
47 γ-terpinene$^{\Delta,\circ,\bullet}$	—	0.6 ± 0.6	2.5 ± 0.6	7.5 ± 3.8	10.1 ± 4.2

TABLE 1. CONTINUED

48 trans-4-thujanol	—	0.2 ± 0.1	10.1 ± 3.2	14 ± 7.5	36 ± 15.5
49 α-terpinolene[•]	—	0.2 ± 0.1	1.4 ± 0.9	1.7 ± 0.8	2.5 ± 1.1
50 linalool oxide B	0.7 ± 0.7	—	0.9 ± 0.6	—	—
51 p-cymene[Δ]	—	0.1 ± 0.1	0.5 ± 0.2	0.9 ± 0.5	2.1 ± 1
52 linalool[Δ,□,×,#]	53 ± 9.1	—	—	—	3.9 ± 3.9
53 cis-4-thujanol	—	—	3.3 ± 2	3.4 ± 3.3	10.8 ± 4.8
54 (E)-3,4,8-dimethyl-1,3,7-nonatriene[Δ,,○,•]	—	1.9 ± 1.2	47.8 ± 27.1	1.4 ± 0.5	34.7 ± 17.8
55 terpinen-4-ol	—	—	—	0.6 ± 0.4	1.6 ± 0.8
56 α-terpineol	1.3 ± 0.7	3.2 ± 1.7	0.2 ± 0.2	0.4 ± 0.4	0.6 ± 0.4
57 cis-β-elemene,[Δ,×,#]	—	—	73.8 ± 57.5	—	—
58 germacrene D tent[Δ,•]	—	3.2 ± 1.2	—	—	—
59 (E,E)-α-famesene[○,×]	—	0.4 ± 0.4	41.6 ± 29.9	—	—
60 β-bisabolene	—	—	5.3 ± 4.6	—	—
61 carvone	—	—	—	1.1 ± 0.7	1.2 ± 1.2
Aldehydes					
62 (E)-2-hexanal[Δ,○,#,▲,•]	—	—	—	—	2.9 ± 2.1
Sulphides					
63 dimethyl trisulphide[Δ,□,○,×,#,▲]	—	0.5 ± 0.0	0.8 ± 0.3	1.2 ± 0.3	1.7 ± 0.5
Nitrogen containing					
64 benzyl cyanide[Δ]	—	—	—	0.8 ± 0.8	11.5 ± 5.1
65 indole[Δ,×]	—	1.7 ± 1.1	—	—	7.8 ± 4.7
Unknown[c]					
66 unknown[57b,68,82]	—	0.2 ± 0.2	—	2.5 ± 1.1	5 ± 1.9
67 unknown[81b,135,150]	7.9 ± 0.8	—	—	—	—
68 unknown[mtxt]	—	—	—	1.9 ± 0.8	1.6 ± 1.3
69 unknown[107,108b,150]	—	—	0.1 ± 0.1	1.3 ± 0.8	2.9 ± 1.3
70 unknown[79,107,150b]	—	—	—	2.9 ± 1.3	2.3 ± 1.1
Total amount	139.1 ± 23	420.1 ± 130	857.8 ± 255	1503.2 ± 647	4939.7 ± 2586

[a] Amounts of individual compounds are given as average peak area (±SE) per liter of trapped air per gram above ground biomass.
[b] References related to volatile analysis on crucifers. [Δ]-compound detected by Geervliet et al., 1997; [□]-compound detected by Agelopoulos et al., 1995; [○]-compound detected by Mattiacci et al., 1994; [×]-compound detected by Tollsten and Bergström, 1988; [#]-compound detected by Blaakmeer et al., 1994; [▲]-compound detected by Agelopoulos and Keller, 1994; [•]-compound detected by Shiojiri et al., 2001.
[c] characteristic mass peaks, b denotes the base peak.

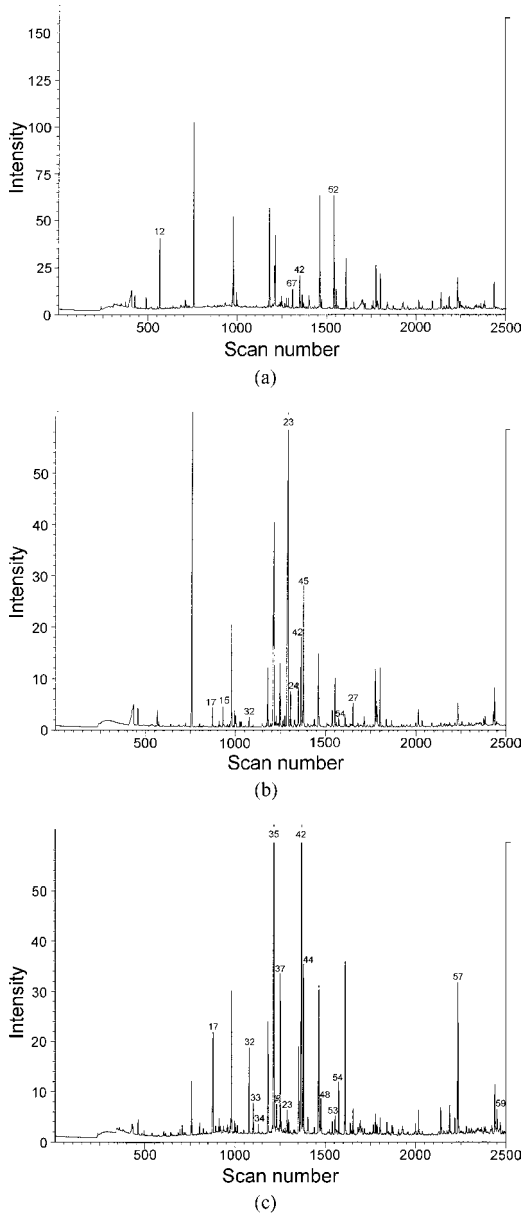

FIG. 4. Gas chromatograms of volatiles collected from (**a**) uninfested barley, (**b**) uninfested *S. alba*, (**c**) uninfested *B. oleracea*, (**d**) uninfested Brussels sprout, and (**e**) Brussels sprout infested by *P. xylostella*. Numbers next to peaks correspond to the compound numbers in Table 1.

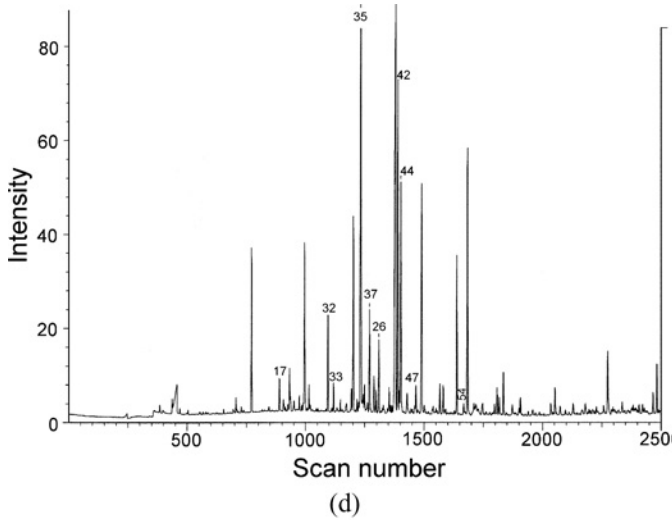

FIG. 4. Continued

Brussels sprout, 11 were not present in the odor blend of uninfested Brussels sprout (Table 1).

DISCUSSION

In this study, *D. semiclausum* preferred all plant species tested, including barley, over clean air. Yet, when uninfested plants of different species were tested

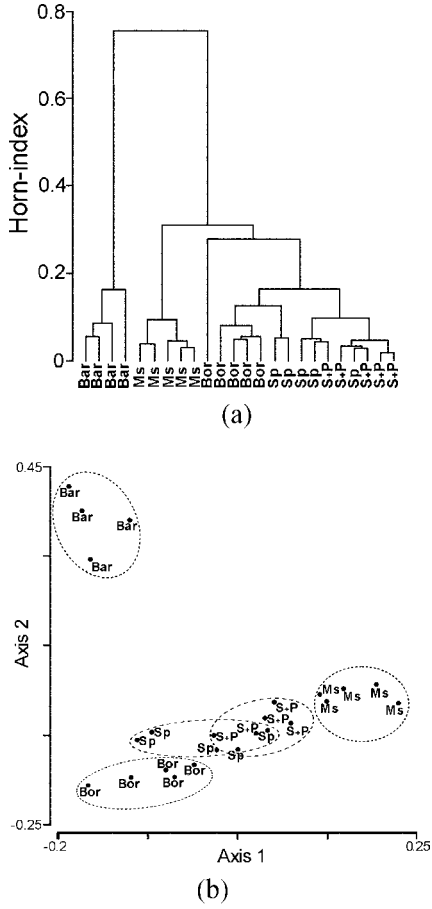

FIG. 5. Dissimilarities in volatile profiles of plants. (**a**) Hierarchic clustering and (**b**) non-metric scaling of dissimilarities in volatile profiles based on the Horn-index. "Bar"-barley, "Ms"-mustard, "Bor"-feral *B. oleracea*, "Sp"-uninfested Brussels sprout, "S+P"-Brussels sprout infested by *P. xylostella* larvae.

against each other, females preferred volatile blends of crucifers to barley. In a comparable study, *Cotesia kariyai* a parasitoid of the noctuid *Pseudaletia separata*, was attracted to several unrelated non-host food plants, which was explained by the presence of the same GLVs in the headspace of the different plant species (Takabayashi et al., 1991). Except for one compound, all the compounds produced by barley were also present in at least one of the crucifers. These included (*Z*)-3-hexen-1-ol, myrcene, and limonene. Linalool, the compound dominantly produced

by barley, was also detected in infested Brussels sprout. Therefore, the presence of those compounds in the odor blends of barley, which were present in the odor of crucifers, could explain the preference of wasps towards barley odors when compared with clean air.

Parasitoids also discriminated between odors of uninfested crucifers. Despite the lower amounts of total volatiles and the fewer compounds produced by both mustard and the feral *B. oleracea*, these plants were more attractive to *D. semiclausum* than Brussels sprout. Some alcohols and terpenoids emitted by mustard were present in this species only, and some alcohols, esters, and indole were detected both in mustard and infested Brussels sprout. The GLV (*Z*)-3-hexen-1-yl acetate is known to be produced by herbivore-infested Brussels sprout in greater quantities than by uninfested plants (Blaakmeer et al., 1994; Mattiacci et al., 1994; Geervliet et al., 1997). This was the dominant compound that mustard produced. However, this same compound was also the dominant compound in uninfested sprouts, and it was produced in larger quantities than in uninfested mustard. This finding indicates that (*Z*)-3-hexen-1-yl acetate alone was not responsible for the attraction of this parasitoid to mustard.

White mustard also contains specific aromatic hydroxy-benzyl and benzyl glucosinolates (McCloskey and Isman, 1993; Hopkins et al., 1998; Mewis et al., 2002). Aromatic derivatives of these glucosinolates were detected in the headspace of uninfested mustard (Tollsten and Bergström, 1988). We did not detect these derivatives in our samples, possibly due to differences in methodology for collecting and analyzing samples. Tollsten and Bergström (1988) used cut plants while we used potted plants.

Qualitative and quantitative differences in the odor blends of plants may enable natural enemies to discriminate between odor sources while searching for their prey or host (De Boer, 2004). *D. semiclausum* discriminated between odor blends of plants, and presence or absence of compounds in the blend combined with quantitative differences in blend composition could have played a role in this. While presence/absence of compounds in volatile blends could have been important for females to discriminate between odors of barley and crucifers, differences in quantity and ratios of compounds could be important in the discrimination between mustard, the feral *B. oleracea*, and Brussels sprout. This was suggested by the finding that the volatile profile of the feral *B. oleracea* was similar to that of uninfested Brussels sprout, with a few compounds detected exclusively in the feral *B. oleracea*. Yet, wasps were able to discriminate between these lines of *B. oleracea*. Furthermore, the greater amounts of plant volatiles produced by uninfested Brussels sprout compared to the feral *B. oleracea* combined with few qualitative differences, did not result in a stronger attraction of *D. semiclausum*. This indicates that subtle differences in volatile profiles of uninfested plants could be important in the attractivity of these plants for *D. semiclausum*.

Brussels sprout plants damaged by hosts are more attractive for the parasitoids *Cotesia glomerata*, *C. rubecula*, and *C. plutellae* than artificially damaged or intact Brussels sprout plants (Steinberg et al., 1992, 1993; Blaakmeer et al., 1994; Geervliet et al., 1996; Shiojiri et al., 2000). A recent study by Ohara et al. (2003) showed that *D. semiclausum* females were attracted by the odor blends of uninfested and infested cruciferous plants. The observed attraction was not due to the host or products directly associated with the host (i.e., feces, silk exuviae), but the damaged plant itself (Ohara et al., 2003). Our results also suggest that *D. semiclausum* assesses changes in volatile blends as a result of herbivore damage. The odor blend of infested Brussels sprout was similar to that of uninfested Brussles sprout, but many of the compounds were emitted in higher amounts by infested plants, which was in line with findings of other studies (Blaakmeer et al., 1994; Geervliet et al., 1997; Reddy and Guerrero, 2000; Smid et al., 2002). Compounds like (*Z*)-3-hexen-1-yl acetate, (*Z*)-3-hexen-1-ol, and limonene, which were also detected in our samples, could play a role in the attraction of the parasitoids *C. rubecula*, *C. glomerata*, and *C. plutellae*, and of the predatory lacewing *Chrysoperla carnea* (Geervliet et al., 1997; Reddy et al., 2002; Smid et al., 2002). The volatile profile of *Plutella*-infested Brussels sprout shares many similarities with the odor profiles from white cabbage and Brussels sprout infested by different *Pieris* spp. (Geervliet et al., 1997; Blaakmeer et al., 1994). Moreover, parasitoid species associated with *P. xylostella* and *Pieris spp.* differ in their ability to distinguish odor blends of plants that are infested by hosts or non-hosts (Shiojiri et al., 2001). It is not yet known what compounds may be involved in the ability of *D. semiclausum* to discriminate between blends of infested and uninfested Brussels sprout, or how the volatile composition of mustard is influenced by herbivore damage. These may be important factors to understand its searching behavior, and interactions with its host in the field. We currently study how inter- and intraspecific variation in plant volatiles influence the ability of this parasitoid to discriminate between plants infested by hosts and non-hosts.

Based on dissimilarities in the volatile profiles, wasps were able to discriminate between infested and uninfested Brussels sprout plants. Interestingly, such discrimination was not observed when infested Brussels sprout was compared with mustard, although the dissimilarity in odor blends compared to the dissimilarity of blends of infested versus uninfested Brussels sprout plants were greater. Hence, the lack of discrimination by *D. semiclausum* between infested Brussels sprout and mustard was not because of the great similarity of odor blends. Despite the considerable differences in blends, wasps did not discriminate, possibly because the "values" of information (i.e., expectancy of the host's presence) from the odors of infested Brussels sprout and mustard were similar. Based on studies of *Leptopilina heterotoma*, a parasitoid of *Drosophila* spp., Vet et al. (1998) hypothesized that parasitoids may actively not discriminate among subtle, quantitative

differences and rely on qualitative differences until they learn to discriminate via experiences. Data from a separate study suggest that such a mechanism may play a role in the searching behavior of *D. semiclausum* (Bukovinszky, 2004). While host location by inexperienced females on Brussels sprout is hindered by the greater preference of wasps to search on uninfested mustard, oviposition experience redirects odor preference in favor of host-infested Brussels sprout and enhances the efficiency of females to locate subsequent host-infested plants, irrespective of neighboring plant species (Bukovinszky, 2004).

Relative to other herbivores that are specialists on crucifers, *P. xylostella* has a broad host plant diet (Yano, 1994; Bigger and Fox, 1997). Mustard is a preferred food plant of *P. xylostella* and is used as a trap crop (Palaniswamy et al., 1986; Talekar and Shelton, 1993). *P. xylostella* develops faster and reaches greater body weight on white mustard than on Brussels sprout (R. Gols, unpublished data). Hence, if the occurence of *P. xylostella* on these plant species is different, it could be a viable strategy for *D. semiclausum* to have a preference towards volatile blends that reflects the food-plant preference of the host.

As plant breeding and biological control developed independently, we have limited information on what mechanisms are responsible for triggering different responses of parasitoids to different plant species and genotypes of the same plant species (van Lenteren et al., 1995; Bottrell et al., 1998; Cortesero et al., 2000). The finding that feral *B. oleracea* is more attractive than cultivated conspecifics might indicate that artificial selection in cultivated plants has altered their ability to attract natural enemies compared with their wild relatives. However, further studies are needed to explicitly test this hypothesis. Our results indicate that volatile traits responsible for the attraction of natural enemies to plants would be valuable to consider in breeding programs enhancing biological control. Although plant traits that increase attractivity for the parasitoid may also attract herbivores, such traits could still be valuable tools in developing pest-suppressive diversification strategies (i.e., companion planting, intercropping).

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