

# Similar attractiveness of maize volatiles induced by *Helicoverpa armigera* and *Pseudaletia separata* to the generalist parasitoid *Campoletis chloridae*

Zeng-Guang Yan<sup>1,2</sup> & Chen-Zhu Wang<sup>1\*</sup>

<sup>1</sup>State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, the Chinese Academy of Sciences, 25 Beisihuanxi Road, Haidian, Beijing, 100080, China, <sup>2</sup>Graduate School of the Chinese Academy of Sciences, Beijing, 100039, China

Accepted: 28 August 2005

**Key words:** herbivore-induced plant volatiles, behavioral response, *Zea mays*, Hymenoptera, Ichneumonidae, Lepidoptera, Noctuidae, Poaceae

## Abstract

*Campoletis chloridae* Uchida (Hymenoptera: Ichneumonidae), a major larval endoparasitoid of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), also attacks many other noctuid caterpillars. We investigated the attractiveness of *H. armigera*- and *Pseudaletia separata* (Lepidoptera: Noctuidae)-infested maize [*Zea mays* L. (Poaceae)] plants to *C. chloridae*, and analyzed the volatiles emitted from infested plants and undamaged plants. Considering the reported specific induction of plant volatiles by elicitors in the caterpillar regurgitant, we also tested the response of the parasitoid to mechanically damaged plants treated with caterpillar regurgitant or water and measured the volatiles released by these plants. In wind-tunnel bioassays, *C. chloridae* was strongly attracted to herbivore-induced maize volatiles. Mechanically damaged plants, whether they were treated with caterpillar regurgitant or water, were more attractive to the parasitoid than undamaged plants. The parasitoid did not distinguish between maize seedlings infested by the two noctuid insects, nor did they show a difference in attraction to mechanically damaged plants treated with caterpillar regurgitant or water. Coupled gas chromatography–mass spectrometer (GC-MS) analysis revealed that 15 compounds were commonly emitted by herbivore-infested and mechanically damaged maize plants, whereas only two compounds were released in minor amounts from undamaged plants. Infestation by *H. armigera* specifically induced four terpenoids,  $\beta$ -pinene,  $\beta$ -myrcene, *D*-limonene, and (*E*)-nerolidol, which were not induced by infestation of *P. separata* and mechanical damage, plus caterpillar regurgitant or water. Two compounds, geranyl acetate and  $\beta$ -sesquiphellandrene, were also induced by the infestation of *H. armigera*, but not by the infestation of *P. separata*. All treated maize plants released volatiles in significantly larger total amounts than did undamaged plants. Maize plants infested by *H. armigera* emitted greater amounts of volatiles than plants infested by *P. separata*. The treatment with caterpillar regurgitant resulted in larger amounts of volatile emission than the treatment with water did in mechanically damaged plants. The amounts of emissions of individual compounds were also different between differently treated plants.

## Introduction

In the past two decades, tritrophic interactions between plants, herbivores, and natural enemies have aroused intense interest among ecologists and show potential for exploitation in the management of arthropod pests (Tscharrntke & Hawkins, 2001). Infochemicals play essential roles as

mediators in tritrophic interactions (Vet & Dicke, 1992; Dicke & van Loon, 2000), and herbivore-induced plant volatiles, in particular, have been shown to be key signals that guide parasitoids to their host herbivores (see reviews in Dicke, 1999; Paré et al., 1999; Turlings et al., 2001).

Plant volatile emissions can be triggered by mere tissue damage. However, plant responses to herbivory may differ from generalized wound responses (Turlings et al., 1990). Elicitors in oral secretions of the herbivores are at least

\*Correspondence: E-mail: czwang@ioz.ac.cn

partly responsible for the differences in response. In the regurgitant of *Pieris brassicae* caterpillars, the main elicitor was identified to be the enzyme  $\beta$ -glucosidase (Mattiacci et al., 1995), whereas in the oral secretions of *Spodoptera exigua*, volicitin [N-(17-hydroxylinolenoyl)-L-glutamine] was isolated and identified as a potent non-protein elicitor of volatile biosynthesis (Alborn et al., 1997; Turlings et al., 2000). Volicitin and its analogues are now known to occur in the oral secretions of numerous insect species (Pohnert et al., 1999; Halitschke et al., 2001; Mori et al., 2001, 2003; Alborn et al., 2003) and of different larval stages of *Spodoptera littoralis* (Gouinguéné et al., 2003).

Herbivory can result in both quantitative and qualitative changes of volatile emissions (e.g., Dicke et al., 1990a; Turlings et al., 1990; Takabayashi et al., 1991). The release of herbivore-induced plant volatiles is an active process, and some herbivore-induced terpenoids are synthesized de novo (Paré & Tumlinson, 1997a,b). Emission of induced volatiles often occurs throughout the whole plant rather than the restricted area of feeding damage (e.g., Turlings & Tumlinson, 1992; Röse et al., 1996). Consistent differences in volatile blends have been observed in different plant and herbivore species. The differences could also be due to varying plant ages and developmental stages of the attacking herbivores (e.g., Takabayashi et al., 1995; De Moraes et al., 1998; Guerrieri et al., 1999). Exploitations of such specificities have been shown in several parasitoids (Takabayashi et al., 1995; Du et al., 1996; De Moraes et al., 1998).

The degree at which natural enemies make use of specific differences in volatile blends is expected to depend on their dietary specialization and/or their host/prey species (Vet & Dicke, 1992). Although some generalist parasitoids use specific cues for host location (Steidle et al., 2003), generalists more often use general cues (see review in Steidle & van Loon, 2003). For generalist parasitoids, it is assumed that the use of general chemical cues present in all hosts or their respective food plants is an adaptive strategy (Vet & Dicke, 1992; Godfray, 1994). Behavioral responses of the parasitoids could be greatly affected by experience or learning (Turlings et al., 1993a). Learning to respond to infochemicals and the use of general cues were more often found in generalists than in specialists (Steidle & van Loon, 2003).

*Campoletis chloridae* Uchida (Hymenoptera: Ichneumonidae) is an important early larval endoparasitoid of many noctuid species (Lepidoptera: Noctuidae), including *Helicoverpa armigera*, *Helicoverpa assulta*, *Spodoptera litura*, *S. exigua*, *Agrotis ypsilon*, *Anomis flava*, *Pseudaletia separata*, and *Leucania loreyi* (Li et al., 1997; Sato, 1988; Yan et al., 2001; He et al., 2002a,b; Hou et al., 2002; Guo et al., 2003). In China, *C. chloridae* mainly occurs in the Yellow River and Yangtze River valleys as the predominant parasitoid of *H. armigera* (Zheng & Lu, 1981; You et al., 2002). The

parasitoid may have 8–10 generations per year (Zheng & Lu, 1981; Dai, 1990; You et al., 2002) and has been recorded on the insect pests of many crops, including cotton, maize, peanut, tomato, pepper, and tobacco (Lu et al., 1999; You et al., 2002). *Campoletis chloridae* has been extensively studied as a potential biological control agent for *H. armigera* in China, Korea, and India (e.g., Zheng & Lu, 1981; Dai, 1990; Nandihalli & Lee, 1995a,b; Kumar et al., 2000; Wang, 2001; You et al., 2002; Liu et al., 2004; Pandey et al., 2004). However, little is known about its host-foraging behavior. In the present study, we chose to investigate the attraction of *C. chloridae* to volatiles emitted by maize plants in response to the infestation by *H. armigera* and *P. separata*, two important maize pests in China. The studies not only reveal the relative importance of host-induced volatile emission for host location by *C. chloridae*, but also provide insight into how the parasitoid might deal with plant signals induced by distinctly different host herbivores.

## Materials and methods

### Plants

Maize [*Zea mays* L. (Poaceae)] cultivar ‘Zhongdan-306’ obtained from the Institute of Crop Breeding and Cultivation, the Chinese Academy of Agricultural Sciences (CAAS), was used in all experiments. Maize seedlings were cultivated in 16 cm (diameter)  $\times$  15 cm (deep) flower pots using fertilized soil obtained from the Institute of Vegetables and Flowers, CAAS. The seedlings were kept outdoors for growth under natural conditions at a temperature of 24–33 °C, and day length of 14–15 hours from June to September, 2003. Seedlings were watered every day. A net cage (3  $\times$  3  $\times$  2 m) was used to prevent any possible infestation by naturally occurring herbivores. Two-week-old maize seedlings with three to four leaves were used in the experiments.

### Insects

*Helicoverpa armigera* and *P. separata* were reared on artificial diets at 26  $\pm$  1 °C, 75% r.h., and L16:D8, as described in Wang & Dong (2001) and in Zhang & Wang (2003). A colony of the parasitoid *C. chloridae* was started with cocoons collected from Zhengzhou in Henan Province in China. The colony was maintained on *H. armigera* larvae fed with artificial diet. Mated female wasps were allowed to once or twice sting host larvae at the late 2nd or early 3rd instar, and these parasitized host larvae were kept in an incubator under the same conditions until cocoon formation. Fifteen cocoons were collected and kept in a glass tube (2 cm in diameter, 10 cm in length) plugged with cotton until adult emergence. Twenty adults were kept in a cage (10 cm in diameter, 20 cm in length) with a sex ratio of 1:1. A honey solution (20% v:v) was provided every day as a food source.

**Caterpillar regurgitant preparation**

Regurgitant of 3rd- and 4th-instar larvae of *H. armigera* and *P. separata* feeding on artificial diet was collected following the methods of Turlings et al. (1993b). About 5–10  $\mu$ l of regurgitant could be collected from each caterpillar of *H. armigera* and *P. separata*. All regurgitants were centrifuged for 10 min at 10 000 g, and the supernatant was filtered through a 0.22- $\mu$ m sterile millipore filter to remove large particles and microorganisms, and subsequently stored at  $-20^{\circ}\text{C}$  until use.

**Plant treatment**

Maize seedlings used for volatile collection or bioassay were either left undamaged, or infested by *H. armigera* or *P. separata*, or artificially damaged, and treated with caterpillar regurgitant or water. Briefly, maize seedlings were excavated from pots and the soil was gently washed off the roots with tap water. The seedlings were then transferred to a vial (100 ml) filled with water. A batch of three maize seedlings was either left undamaged (control), or subjected to infestation by 12 3rd-instar *H. armigera* larvae or nine 3rd-instar *P. separata* larvae, which caused comparable amounts of damage during the experiments (ca. 20% of the total leaf surface was removed). Caterpillars were starved for about 10 h before being transferred to the plants. Once in contact with plants, most caterpillars started feeding on the leaves within 1 h. For artificial damage, plants were scratched with a razor blade over an area of ca. 3 cm<sup>2</sup> per leaf on the upper surface of the second and the third leaf, and a 10- $\mu$ l aliquot of distilled water or caterpillar regurgitant was subsequently applied onto the damaged areas. In all cases, the plants were treated at 08:00–09:00 hours.

**Wind tunnel bioassay**

To prevent the caterpillars from escaping after having received insects or artificial damage, plants used for bioassays were caged with a fine net bag. As controls, undamaged plants were also caged with the net bag. The bag and caterpillars were removed after 6 h of initial treatments, and the plants were subsequently used for bioassays. Behavioral responses of the parasitoid *C. chloridae* to plant volatiles were tested in a Plexiglass wind tunnel (interior measurements of 90  $\times$  30  $\times$  30 cm). A fan and a set of metal screens at the upwind end of the wind tunnel produced an airflow of 50 cm s<sup>-1</sup>. The wind tunnel was lit by two white fluorescent lamps (each 40 W), and indirect light was reflected from a white board, which together resulted in an intensity of 1500 lux inside the wind tunnel. Temperature was maintained at  $25 \pm 1^{\circ}\text{C}$  during the test. A batch of three maize seedlings that had undergone the same treatment was placed in one vial. Two vials each with undamaged or differently treated plants were placed 15 cm apart at the upwind end of the

tunnel. Two 3-day-old naive (no experience with hosts and plants) female wasps were released individually from a release device (2-ml vial) placed onto a take-off platform, which was located at 80 cm downwind from the plants with its top at mid height in the wind tunnel. The observation was stopped as soon as the wasp arrived at the plants within 5 min. Behavioral responses were categorized as: choosing, wasps flew upwind from taking-off, and arrived at plants within 5 min; not choosing, wasps flew upwind but ended by landing on the wind tunnel wall or inner top and did not arrive at plants within 5 min, or stayed on the platform for more than 5 min. The position of the plants was exchanged after testing two to three wasps to eliminate asymmetric effects. The wind tunnel and the take-off platform were cleaned with alcohol after each test. Each wasp was used only once. Each combination was tested three to four times with fresh batches of plants on different days. Some 10–15 wasps were tested each time. More than 40 wasps were tested for each of the eight combinations.

**Volatile collection**

Maize seedlings were immediately placed in a glass jar (12 cm in diameter and 21 cm high) after treatments. Volatiles were collected using a push-pull technique (compressed air and vacuum). Clean air was led through a water bubbler for humidification, a flowmeter for measuring and regulating the air flow, and a charcoal filter for purification. The moist and pure air then entered the jar at 300 ml min<sup>-1</sup> at the lower part of the jar, passed over the plant materials, and then passed through an outlet at the top of the jar. The blend of volatiles was trapped in a glass tube (10 cm long, 6 mm in diameter) that contained 25 mg of 80/100 mesh Super Q adsorbent (Alltech Assoc., Deerfield, IL, USA). The trap was connected with Teflon tubing to the outlet of the jar at one end and via another flowmeter at the other end to a vacuum pump. During collections, the jar containing the plant materials was kept on ice to keep the inner temperature at  $25 \pm 2^{\circ}\text{C}$ , and two fluorescent lamps (each 40 W) were suspended over the jar to illuminate the plants, producing a light intensity of about 2000 lux. Two collection systems were used in parallel every time, and the collections were run for 12 h. Each treatment was repeated five times with fresh batches of plants.

**Analysis of induced plant volatiles**

After collection, the trap was rinsed with 200  $\mu$ l redistilled hexane. Two internal standards (800 ng of n-decane and benzyl acetate in 10  $\mu$ l hexane) were added based on the knowledge obtained from the preliminary experiments showing that the two compounds were not released from all undamaged, mechanically damaged, and infested plants. Identifications and quantifications of volatiles were carried

out by coupled gas chromatography–mass spectrometry (GC-MS) on a Hewlett-Packard 6890 GC – 5973 MSD. The GC was equipped with a DB-WAX column (Agilent Technologies, Palo Alto, CA, USA) (polyethylene glycol 20000, 60 m × 0.25 mm ID; film thickness 0.15 μm). Helium was used as carrier gas with a constant flow of 26 cm s<sup>-1</sup>. A 2-μl aliquot of the volatile sample was injected, and then immediately split with a purge flow of 30 ml min<sup>-1</sup>. The injector temperature was 250 °C and the GC-MS transfer line temperature was 280 °C, source 230 °C, quadruple 150 °C, ionization potential 70 eV, and scan range 30–300 m z<sup>-1</sup>. Following injection, the column temperature was increased from 55 °C to 200 °C at 8 °C min<sup>-1</sup> and held at 200 °C for 20 min. Compounds were identified by comparing mass spectra with NIST library spectra (Agilent Technologies, Palo Alto, CA, USA), and some of them were confirmed with authentic reference compounds. Compounds were quantified by their total ion abundances relative to that of the internal standards.

#### Statistical analyses

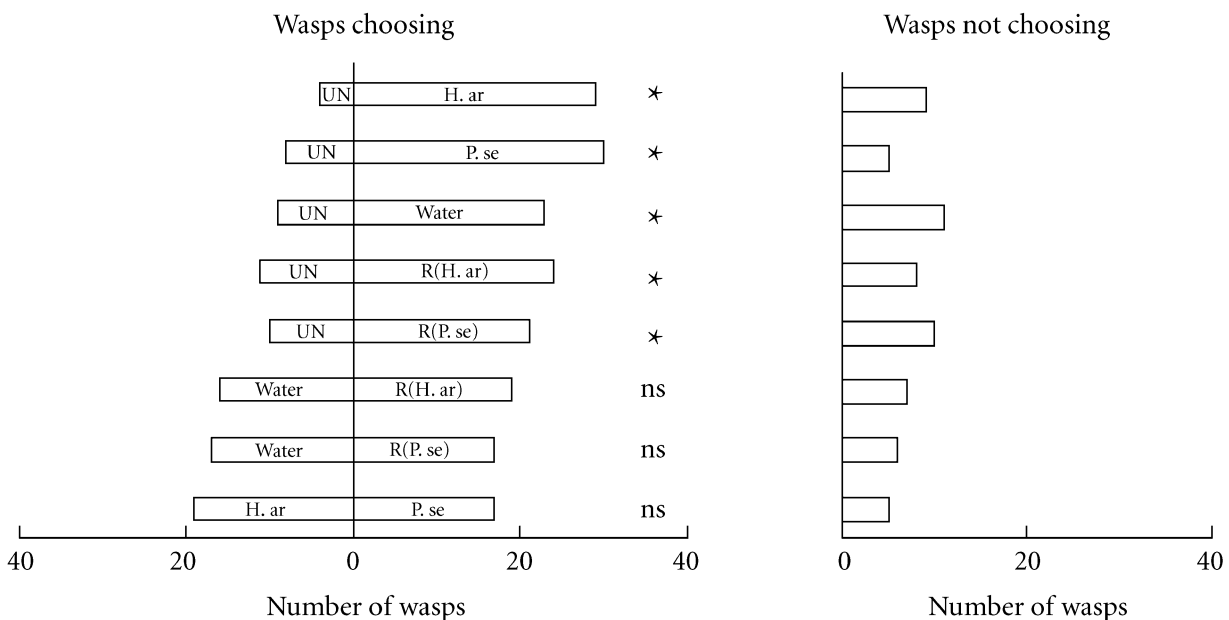
Tukey multiple comparison test after ANOVA was used to determine statistical differences of the average total amounts of the headspace volatiles emitted from undamaged, herbivore-infested, and mechanically damaged maize seedlings. Chi-squared analysis was performed to test differences

between numbers of wasps that chose undamaged and differently treated plants they were offered, and wasps defined as not choosing were not included in statistical analysis. All of these analyses were carried out with SPSS version 10.0 for Windows (SPSS Inc., Chicago, IL, USA) (Lu, 2000).

## Results

#### Behavioral response of *C. chloridae*

Plants infested by *H. armigera* and *P. separata* were more attractive to *C. chloridae* than undamaged plants ( $\chi^2 = 18.939$ , d.f. = 1,  $P < 0.001$ , and  $\chi^2 = 12.737$ , d.f. = 1,  $P < 0.001$ , respectively; Figure 1). Mechanically damaged plants treated with water, *H. armigera* regurgitant or *P. separata* regurgitant attracted more parasitoids than the undamaged plants did ( $\chi^2 = 6.125$ , d.f. = 1,  $P = 0.013$ ,  $\chi^2 = 4.829$ , d.f. = 1,  $P = 0.028$ , and  $\chi^2 = 3.903$ , d.f. = 1,  $P = 0.048$ , respectively; Figure 1). Surprisingly, there was no significant difference in attractiveness of the mechanically damaged plants treated with water and either *H. armigera* regurgitant or *P. separata* regurgitant ( $\chi^2 = 0.257$ , d.f. = 1,  $P = 0.612$ , and  $\chi^2 = 0.000$ , d.f. = 1,  $P = 1.000$ , respectively; Figure 1). Furthermore, the plants infested by the two different herbivores were equally attractive to the parasitoid ( $\chi^2 = 0.111$ , d.f. = 1,  $P = 0.739$ ; Figure 1).



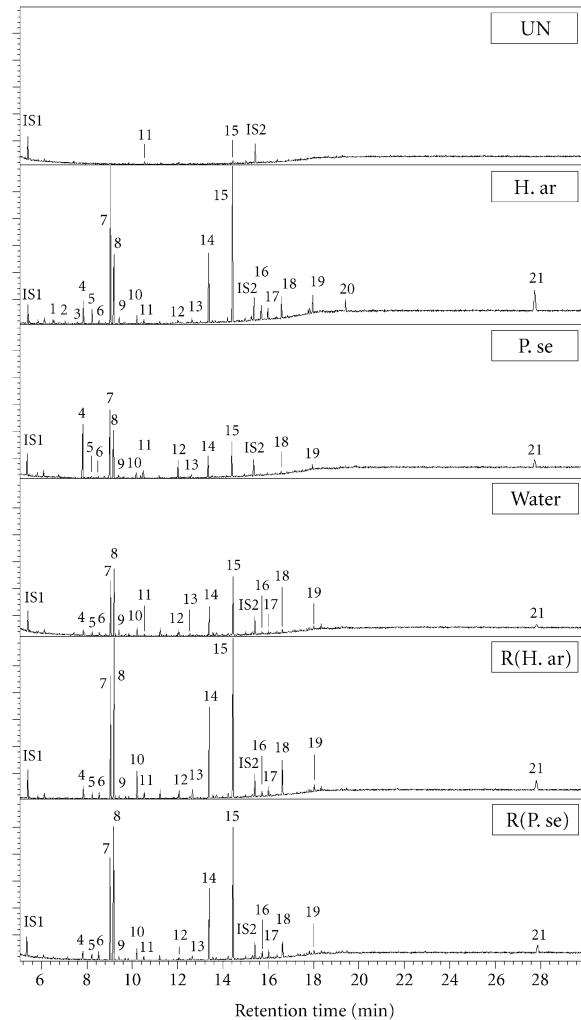
**Figure 1** Number of *Campoplex chloridae* wasps choosing and not choosing in wind tunnel bioassay with undamaged and differently treated maize seedlings. UN, undamaged; H. ar, infested by *Helicoverpa armigera*; P. se, infested by *Pseudaletia separata*; Water, mechanically damaged and treated with water; R(H. ar), mechanically damaged and treated with regurgitant of *H. armigera*; R(P. se), mechanically damaged and treated with regurgitant of *P. separata*. Asterisks indicate a significant difference within a choice test ( $P < 0.05$ ) and ns indicates no significant difference ( $\chi^2$  test).

### Variation in herbivore-induced plant volatiles

Figure 2 shows characteristic total ion current chromatograms of the headspace volatiles emitted from undamaged, herbivore-infested, and mechanically damaged maize seedlings. Total amounts of plant volatiles and average amount of each compound are listed in Table 1. Only two compounds (*E*-2-hexen-1-ol and *E*- $\beta$ -farnesene) were released in significant amounts by undamaged plants. Plants infested by *H. armigera* or *P. separata*, or damaged artificially and treated with water or caterpillar regurgitant, released largely the same compounds, including the green leaf volatiles (*E*-2-hexenal, hexyl acetate, (*Z*)-3-hexenyl acetate, (*E*-2-hexenyl acetate, (*Z*)-3-hexen-1-ol, and (*E*-2-hexen-1-ol; the terpenoids  $\gamma$ -terpinene, (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (*E*)- $\alpha$ -bergamotene, (*E*)- $\beta$ -farnesene, and linalool; the aromatics phenylethyl acetate and indole; and pentadecane and an unknown compound. Infestation by *H. armigera* induced the largest number of compounds (22), of which four terpenoids,  $\beta$ -pinene,  $\beta$ -myrcene, *D*-limonen, and (*E*)-nerolidol, were not found in the other treatments. Two compounds, geranyl acetate and  $\beta$ -sesquiphellandrene, were also induced by the infestation of *H. armigera*, but not by the infestation of *P. separata*. After having been infested by the two insects or damaged artificially, all maize plants released volatiles in significantly larger total amounts than did undamaged plants ( $F = 14.218$ , d.f. = 5,  $P < 0.001$ ; Table 1). Plants infested by *H. armigera* emitted greater amounts of volatiles than plants infested by *P. separata* ( $P = 0.001$ ). Treatment with caterpillar regurgitant resulted in larger amounts of volatile emission than treatment with water did in mechanically damaged plants. The emission amounts of individual compounds could also be different between differently treated plants (Table 1).

### Discussion

In this study, we investigated the behavioral responses of *C. chloridae* to herbivore-induced plant volatiles. We showed that *C. chloridae* was strongly attracted by herbivore-induced maize volatiles in a wind tunnel. Mechanically damaged plants, whether they were treated with caterpillar regurgitant or water, were more attractive to the parasitoid than undamaged plants. The parasitoid did not distinguish between maize seedlings infested by the two different noctuid insects. Interestingly, there also were no significant differences in attraction to mechanically damaged plants treated with caterpillar regurgitant and those treated with water (Figure 1), although analyses of the collected volatiles showed a much higher release of the volatiles from the former than the latter plants (Table 1). At least 15 compounds were shared in blends of herbivore- and mechanical damage-induced volatiles (Figure 1).



**Figure 2** Representative total ion current chromatograms of the headspace volatiles from maize seedlings with different treatments: UN, undamaged; H. ar, infested by *Helicoverpa armigera*; P. se, infested by *Pseudaletia separata*; Water, mechanically damaged and treated with water; R(H. ar), regurgitant of *H. armigera*; R(P. se), regurgitant of *P. separata*. Peak numbers correspond with numbers in Table 1. IS1 and IS2 are the internal standards *n*-decane and benzyl acetate.

In response to the attack by herbivores, plants release large amounts of volatiles into the environment (Dicke et al., 1990b; Turlings et al., 1990). These herbivore-induced plant volatiles play important roles in host location of many parasitoids (Turlings et al., 1990; Whitman & Eller, 1990; McCall et al., 1993; Steinberg et al., 1993; Agelopoulos & Keller, 1994; Mattiacci et al., 1994; Turlings et al., 1995). Maize volatiles induced by herbivores have been found to be attractive to a wide range of parasitoids, including *Cotesia marginiventris* (Turlings et al., 1990), *Microplitis croceipes*

**Table 1** List of volatile compounds collected from maize seedlings with different treatments: undamaged (UN), infested by *Helicoverpa armigera* (H. ar) or *Pseudaletia separata* (P. se), mechanically damaged and treated with water (Water), regurgitant of *H. armigera* (R(H. ar)) or *P. separata* (R(P. se))

Code	Compound	Undamaged or infested by insects (ng/12 h/3 seedlings) <sup>a</sup>			Mechanically damaged (ng/12 h/3 seedlings) <sup>a</sup>		
		UN	H. ar	P. se	Water	R(H. ar)	R(P. se)
1	β-pinene	0a	115 ± 37b	0a	0a	0a	0a
2	β-myrcene	0a	110 ± 11b	0a	0a	0a	0a
3	D-limonene	0a	219 ± 72b	0a	0a	0a	0a
4	(E)-2-hexenal	0a	2439 ± 424b	2254 ± 281b	602 ± 183a	547 ± 75a	506 ± 48a
5	γ-terpinene	0a	325 ± 126c	48 ± 22ab	211 ± 20bc	335 ± 22c	296 ± 41c
6	Hexyl acetate	0a	339 ± 76d	97 ± 17ab	198 ± 36bc	381 ± 42d	288 ± 30cd
7	DMNT <sup>b</sup>	0a	9169 ± 2200d	2525 ± 395bc	1682 ± 251bc	4324 ± 898c	3916 ± 372c
8	(Z)-3-hexenyl acetate	0a	6531 ± 1655c	693 ± 176ab	3015 ± 513b	7244 ± 1178c	6699 ± 845c
9	(E)-2-hexenyl acetate <sup>c</sup>	0a	762 ± 221b	173 ± 50a	57 ± 26a	141 ± 24a	133 ± 23a
10	(Z)-3-hexen-1-ol	0a	762 ± 96c	346 ± 34b	589 ± 115bc	738 ± 176c	731 ± 124c
11	(E)-2-hexen-1-ol	76 ± 11a	307 ± 48c	431 ± 61d	162 ± 28ab	146 ± 39ab	203 ± 23bc
12	Pentadecane <sup>c</sup>	0a	108 ± 49a	1141 ± 628b	151 ± 18a	179 ± 30a	634 ± 134ab
13	Linalool	0a	1021 ± 411b	375 ± 181a	138 ± 58a	407 ± 107a	472 ± 75ab
14	(E)-α-bergamotene <sup>c</sup>	0a	2690 ± 625bc	711 ± 154a	1513 ± 267ab	3594 ± 904c	3101 ± 473c
15	(E)-β-farnesene	29 ± 18a	5015 ± 1283bc	1110 ± 232a	2546 ± 490ab	6801 ± 2042c	5029 ± 815bc
16	Geranyl acetate	0a	526 ± 115c	0a	86 ± 41a	334 ± 116bc	181 ± 54ab
17	β-sesquiphellandrene <sup>c</sup>	0a	349 ± 93bc	0a	173 ± 40ab	406 ± 120c	330 ± 76bc
18	Phenylethyl acetate	0a	925 ± 258b	174 ± 81a	193 ± 67a	966 ± 361b	950 ± 170b
19	Unknown compound	0a	346 ± 182b	111 ± 33ab	79 ± 37ab	111 ± 37ab	159 ± 123ab
20	(E)-nerolidol	0a	552 ± 302b	0a	0a	0a	0a
21	Indole	0a	2702 ± 673c	1355 ± 641b	101 ± 63ab	951 ± 376ab	553 ± 162ab
Total		106 ± 16a	35320 ± 7030c	11565 ± 1722b	11502 ± 451b	27613 ± 4002c	24190 ± 1323c

<sup>a</sup>Values are means ± SE (five replicates). Different letters in the same row indicate a significant difference (Tukey multiple comparison test after ANOVA, P<0.05) between differently treated plants.

<sup>b</sup>DMNT = (3E)-4,8-dimethyl-1,3,7-nonatriene.

<sup>c</sup>Compounds were tentatively identified when their mass spectra showed >90% identity with those of the mass spectra library NIST.

(Turlings et al., 1993b), *Cotesia kariyai* (Takabayashi et al., 1995), *Cotesia flavipes* and *Cotesia sesamiae* (Ngi Song et al., 1996), *Microplitis rufiventris* (Gouinguéné et al., 2003), and *Dentichasmias busseolae* (Gohole et al., 2003). The current study demonstrated that the herbivore-induced maize volatiles also function as attractants for *C. chloridae*.

Different herbivore species can induce emissions of different blends of volatiles by the plant, and the differences can be quantitative and/or qualitative (e.g., De Moraes et al., 1998; Du et al., 1998; Turlings et al., 1998). Here we observed a difference in the maize volatiles induced by the two noctuid species, *H. armigera* and *P. separata*. Infestation by *H. armigera* induced some specific compounds that were not detected for *P. separata* infested plants, and significant quantitative differences for the other compounds were observed (Table 1). Significant differences in quantity but not in quality were also shown between the blends of

volatiles from mechanically damaged plants treated with caterpillar regurgitant and water (Figure 1 and Table 1). The lack of qualitative differences between water-induced and caterpillar regurgitant-induced plant volatiles may be due to the use of caterpillar regurgitant from larvae that feed on artificial diet in the current study. Larvae reared on artificial diet might not contain the same elicitors in their regurgitant as larvae reared on a natural food plant (Tumlinson & Lait, 2005). Surprisingly, treatment with mechanical damage plus water also induced the emissions of significant amounts of several terpenoid compounds, DMNT, (E)-β-bergamotene, and (E)-β-farnesene (Table 1), which were considered to be typically associated with herbivory (Turlings et al., 1990, 1993b). This effect may be due to the maize cultivar used in this study. Other maize cultivars (e.g., Delprim) also tend to release herbivore-induced volatiles after mechanical damage (Hoballah et al., 2004).

It is anticipated that carnivores use the available information that is specifically associated with their prey to maximize efficiency of foraging behavior. Several studies have unraveled the biologically active compounds that cause the attractiveness of an odor blend to carnivorous arthropods (Dicke et al., 1990a; Turlings et al., 1991; Scutareanu et al., 1997; Du et al., 1998). Four compounds, linalool, methyl salicylate,  $\beta$ -ocimene, and DMNT are known to attract the predator *Phytoseiulus persimilis* as single compounds (Dicke et al., 1990a). Linalool and  $\beta$ -ocimene also attracted the parasitoid *Aphidius ervi* in a wind tunnel (Du et al., 1998). (*E,E*)- $\alpha$ -farnesene and methyl salicylate are attractive to the two predators *Anthocoris nemorum* and *Anthocoris nemoralis* (Scutareanu et al., 1997). Moreover, green leaf volatiles are also found to be attractive to many parasitoids. For example, the parasitoid *C. marginiventris* strongly responded to recently damaged cotton plants, which are known to release green leaf volatiles (Cortesero et al., 1997); furthermore, the preference of the parasitoid for cowpea odors to maize odors resulted from cowpea containing larger proportions of green leaf volatiles than maize (Fritzsche-Hoballah et al., 2002).

In a flight-tunnel test, the parasitoids *M. croceipes* and *Netelia heroica* were found to be attracted to green-leaf volatiles, especially to different hexenols and hexenals (Whitman & Eller, 1990). In a Y-tube experiment, the parasitoid *Aphidius rhopalosiphi* was strongly attracted to (*Z*)-3-hexenyl acetate and (*E*)-2-hexenal (Wickremasinghe & van Emden, 1992). Even though carnivores usually perceive and respond to more than one compound of herbivore-induced plant volatiles (Dicke et al., 1990a; de Bruyne et al., 1991; Du et al., 1998; Smid et al., 2002), the presence of certain key compounds is sometimes sufficient to attract the predators (Kessler & Baldwin, 2001; de Boer & Dicke, 2004). In our current study, the parasitoid *C. chloridae* was shown to be equally attracted to both blends of herbivore-induced plant volatiles (Figure 1). Also, mechanically damaged plants treated with water or caterpillar regurgitant showed equal attraction to the parasitoid (Figure 1). Because *C. chloridae* is a generalist and its predominant host *H. armigera* is a typically polyphagous herbivore, the parasitoid is potentially confronted with a large variety of herbivore-induced plant volatiles. In fact, at least 15 compounds were shared in blends of *H. armigera*- and *P. separata*-induced maize volatiles (Figure 2). It could be expected that certain shared compounds play important roles in the attraction to the parasitoid *C. chloridae*. Our further studies would aim at determining which parts of herbivore-induced blends of maize volatiles are important signals for the parasitoid response.

Non-discrimination between odor sources may not indicate a lack of ability to discriminate, but a functional

decision by the parasitoid (Vet et al., 1998). *Campoletis chloridae* may not need to discriminate between *H. armigera*- and *P. separata*-induced maize volatiles because the two noctuid species are natural hosts of the parasitoid. Alternatively, *C. chloridae* may need to learn to discriminate among volatiles emitted from caterpillar regurgitant and water-treated damaged plants. Many studies have revealed that parasitoids can learn to associate their hosts with host-induced plant volatiles (Turlings et al., 1993a; Godfray, 1994; Vet et al., 1995). Experiences can increase the response of the parasitoids to plant volatiles (e.g., Fukushima et al., 2002), but also change the preference of the parasitoids to different blends of volatiles. The females of the generalist parasitoid *C. marginiventris* that had no experience with hosts and associated odors preferred the odor of freshly damaged maize plants (mainly green-leaf volatiles) to the odor of maize plants with older damage (mainly terpenoids). This preference was changed in a combination of fresh and old damage odor after the wasps had an oviposition experience on older damaged maize plants (ME Fritzsche-Hoballah and TCJ Turlings, pers. comm.). In the generalist parasitoid *Cotesia glomerata*, previous experience modifies this wasps's preference for certain plant-host complexes through associative learning (Geervliet et al., 1998). It is likely that the experience will also affect the olfactory responses of *C. chloridae*. Learning by experience may confer the ability of *C. chloridae* to discriminate mechanically damaged and herbivore-infested plants, and aid the wasps to focus on profitable odor sources to determine which host is available in a field.

Attraction of natural enemies to herbivore-induced plant volatiles has mainly been demonstrated in laboratory studies. Recently, a potential defensive function of induced volatiles through attraction of natural enemies was suggested in the field experiments (Bernasconi et al., 2001; Kessler & Baldwin, 2001; James, 2003a,b). A positive effect of parasitization on plant fitness has also been demonstrated (van Loon et al., 2000; Fritzsche-Hoballah & Turlings, 2001). As a result, a prospect for the use of elicitors of plant volatiles in insect pest management was proposed (Thaler, 1999; Stout et al., 2002).

*Campoletis chloridae* preferentially lays eggs in 2nd and 3rd instar larvae of *H. armigera* (Dai, 1990; You et al., 2002). Parasitism by *C. chloridae* greatly deters the development and reduces the consumption of the host larvae within 2–3 days (Dai, 1990) and totally disables the feeding ability of the host larvae after 1 week. Thus, most parasitized *H. armigera* larvae die before they can molt into voracious stage, and their consumption is only 20% of that of unparasitized larvae (Zheng & Lu, 1981), which could be translated into a fitness benefit to the plant. Therefore, it is possible to exploit *C. chloridae* against some noctuid

species in biological control program, and the current study gives evidence to support the potential use of induced volatiles for improving the foraging efficacy of the parasitoid.

## Acknowledgements

We thank Yan Yunhua, Qin Xiaowei, and Zhao Chenghua for their help in GC-MS analysis, Zhao Xincheng, Wang Honglei, and Tang Qingbo for their technical assistances, and Feng Li for her help in rearing insects. Many thanks are given to Zhang Zhongning and Fang Yuling for providing some standard compounds. We are grateful to Ted C.J. Turlings of University of Neuchatel, the Switzerland, Kun Yan Zhu, Kansas State University, USA, and to three anonymous referees for their constructive advice and critical reviews of an earlier version of the manuscript. This work was supported by the National Natural Science Foundation of China (Grant no. 30330100).

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