Journal of Chemical Ecology, Vol. 31, No. 8, August 2005 (©2005)
DOI: 10.1007/s10886-005-5923-8

METHYL SALICYLATE, A SOYBEAN APHID-INDUCED PLANT VOLATILE ATTRACTIVE TO THE PREDATOR *Coccinella septempunctata*

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(Received September 21, 2004; revised March 14, 2005; accepted April 18, 2005)

Abstract—Induced volatiles provide a signal to foraging predatory insects about the location of their prey. In Iowa, early in the growing season of soybean, *Glycine max*, many predacious seven-spotted lady beetles, *Coccinella septempunctata*, were observed on plants with heavy infestations of soybean aphid, *Aphis glycines*. We studied whether the attraction of this beetle is caused by the release of specific volatile compounds of soybean plants infested by aphids. Volatile compounds emitted by soybean plants infested by aphids were compared with those of undamaged, uninfested, and artificially damaged plants. Gas chromatography–mass spectrometry analyses revealed consistent differences in the profiles of volatile compounds between aphid-infested soybean plants and undamaged ones. Significantly more methyl salicylate was released from infested plants at both the V1 and V2 plant growth stages. However, release patterns of two other induced plant volatiles, (D)-limonene and (*E*,*E*)-α-farnesene, differed between the two plant growth stages. Gas chromatographic–electroantennographic detection of volatile extracts from infested soybean plants showed that methyl salicylate elicited significant electrophysiological responses in *C. septempunctata*. In field tests, traps baited with methyl salicylate were highly attractive to adult *C. septempunctata*, whereas 2-phenylethanol was most attractive to the lacewing *Chrysoperla carnea* and syrphid flies. Another common lady beetle, the multicolored Asian lady beetle, *Harmonia axyridis*, showed no preference for the compounds. These results indicate that *C. septempunctata* may use

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methyl salicylate as the olfactory cue for prey location. We also tested the attractiveness of some selected soybean volatiles to alate soybean aphids in the field, and results showed that traps baited with benzaldehyde caught significantly higher numbers of aphids.

Key Words—*Glycine max*, soybean volatile, induced plant volatile, methyl salicylate, attraction, enhanced biological control, seven-spotted lady beetle, *Aphis glycines.*

INTRODUCTION

The soybean aphid, *Aphis glycines*, is a new, invasive insect species that threatens U.S. soybean, *Glycine max*, production. It is the only aphid species to develop large colonies on soybean in North America. Infestation stunts the plants so that fewer pods and seeds are developed, thereby lowering yield. Soybean aphids also transmit several plant viruses, including alfalfa mosaic, soybean mosaic, soybean dwarf, soybean stunt, and bean yellow mosaic, that distort soybean's growth and further reduce yield.

In soybean fields, soybean aphids are attacked by several predatory insects, including lady beetles (*Harmonia axyridis* and *Coccinella septempunctata*), lacewings (*Chrysoperla carnea*), true bugs (*Orius insidiosus*), and syrphid flies (Zhu, unpublished data). The complex of these natural enemies seems to play a key role in regulating aphid populations (Han, 1997; Fox et al., 2004). Among these predatory insects, *C. septempunctata* dominates early in the growing season, with an increasing abundance of *C. carnea* and *H. axyridis* as the season progresses.

Studies have shown that predators, parasitoids, and predatory mites locate their hosts by using volatile semiochemicals emitted from their hosts or from food plants infested by their hosts (Noldus, 1989; Vet and Dicke, 1992; Bernasconi et al., 1998; Dicke et al., 1998; De Moraes et al., 1998; Du et al., 1998; Ninkovic et al., 2001; Van den Boom et al., 2004; De Boer and Dicke, 2004). During our soybean aphid field experiments, we observed increased abundance of *C. septempunctata* in soybean fields where higher soybean aphid infestation occurred during the early growing season, compared with fields with lower soybean aphid infestation. We report here the identification of volatile compounds released from soybean plants at vegetative growth stages 1 and 2 (V1 and V2, defined when leaflets on the first through the third node leaf are unrolled). A soybean aphid-induced volatile compound that is attractive to *C. septempunctata* is discussed. We also report a volatile compound emitted from the undamaged soybean plant that is attractive to alate soybean aphids.

METHODS AND MATERIALS

Plants and Insects. V1- and V2-stage soybean plants (Garst Roundup Ready variety [80411203] grown in a greenhouse in small pots were used for infestation and entrainment. These two stages of plants were reported to be colonized by winged aphids emigrating from their overwintering host plant, buckthorn, *Rhamnus cathartica*, into soybean. Soybean aphids were collected from soybean fields at the University Farms in Ames, IA. They were maintained in a cabinet kept at 25 ± 2°C, with photoperiod of 14:10 (L:D) hr as a stock colony with only parthenogenetically produced females. Adults of *C. septempunctata* were collected from soybean fields during early summer and maintained under the same conditions as the soybean aphid colony, with 5% sugar water provided.

Volatile Collection. The collection apparatus for volatile compound collection consisted of two glass cells (9.5 cm ID × 12 cm in depth and 10 cm ID × 15 cm in depth), which when put together formed a chamber around the plant with the stem passing through a small slit. The remaining space around the slit was packed with glass wool held in place with Teflon tape. Moisturized and charcoal-filtered air was pumped into the chamber through the inlet, and the outlet of the chamber was connected with a prebaked (200°C overnight) glass tube (5 cm × 0.3 cm ID) containing 100 mg of Super Q (80/100 mesh, Alltech Associate, Deerfield, IL, USA) sandwiched with glass wool plugs. Airflow rates were measured at 2 l/min from the filtered house air pumped into the entrainment chamber (regulated by a flow meter, Barnant Company/Gilmont Instrument, Barrington, IL, USA) and 400 ml/min from the Super Q collector by using a digital flow meter (Hewlett Packard, Palo Alto, CA, USA). The entrainment was carried under the same condition as described for soybean growth.

Volatile entrainment was conducted from V1- and V2-stage soybean plants. Thirty second instars of soybean aphid were transferred onto leaves of one soybean plant, and collection was started 6 hr later. A control plant of the same stage was set up identically but without aphids (uninfested, undamaged). We also collected volatile emissions from a soybean plant of the respective stage by artificially damaging it with thin tungsten wires (5 μm ID). Leaves were punctured with 30 tiny holes. Volatiles were collected from d 1 to d 12, and the collection was extracted every other day. Volatile collection (24 hr) from only soybean aphids also was conducted in a 355-ml wide-mouth glass bottle with ~200 soybean aphids (second and third instars) under the same conditions described above but without soybean leaves. The trapped volatiles were eluted with 2 ml of HPLC-grade hexane (Burdick & Jackson Brand, High Purity, Des Plaines, IL, USA) containing 250 ng of pentadecane as an internal standard and then concentrated to 200 μl under a gentle nitrogen stream. Two microliters of extract were injected into either combined gas chromatography and electroantennographic detection (GC-EAD) or gas chromatography–mass spectrometry (GC-MS) for quantitative and qualitative analyses.

Chemical Analyses. For GC-EAD analysis, a Hewlett Packard 5890 Series II gas chromatography equipped with a DB-wax column (30 m × 0.25 mm i.d., J & W Scientific, Folsom, CA, USA) and a 50:50 effluent split allowed simultaneous flame ionization detection (FID) and EAD of the collected volatiles. Helium was used as the carrier gas with a flow rate of approximately 30 ml/min for both FID and EAD. Extracts were injected in splitless mode. The injector temperature was 250°C, and the split valve was opened 1 min after injection. The oven initial temperature was set at 50°C for 3 min and then increased to 250°C at a programmed rate of 15°C/min. The outlet for the EAD was continuously supplied with a purified, moisturized airstream flowing over the antennal preparation at 0.5 l/min. An adult of *C. septempunctata* was restrained on a block of dental wax with thin copper wires for the EAD recording. A glass capillary recording Ag–AgCl electrode filled with 0.5 M KCl solution was brought into contact with the distal segment of the antenna. A ground electrode, filled with the same saline solution, was introduced into the intersegmental membrane of the beetle body. A high-input impedance EAG amplifier (Syntech, Hilversum, the Netherlands) with automatic baseline drift compensation was used for the GC-EAD analysis. GC-EAD software (version 2.3, Syntech) was used to process, record, and analyze the EAD and FID signals on a PC (Micron Inc., Minneapolis, MN, USA).

GC-MS analyses of volatiles collected from soybean plants were performed with a Hewlett Packard 5890 Series II gas chromatography interfaced to a Hewlett Packard 5972 mass selective detector (MSD). The GC-MS was equipped with the same columns as those used in the GC-EAD system described above. The temperature program was the same as that described for the GC-EAD analyses. Mass spectra were recorded from 30 to 550 amu with electronic impact ionization at 70 eV. The assignments of chemical identities to the soybean volatile compounds were confirmed by comparison of the retention indices and mass spectra with those of authentic chemical standards and reference spectra in a mass spectral library (Wiley 138K, John Wiley & Sons, Inc., New York, NY, USA).

Chemicals. All synthetic standards of soybean volatile compounds were purchased from Sigma-Aldrich (St. Louis, MO, USA), and the purity of each compound was examined by GC-MS, ranging from 98 to 99.5% (from solutions containing 200 ng of each standard compound in 2 μl of hexane).

Field Tests. Field trapping tests were conducted in a 10,000-m^2 soybean field in 2003 in Ames, IA, USA. The first test was designed to test the attractivity of selected volatile compounds emitted from undamaged soybean plants to alate soybean aphids. Synthetic compounds at a dose of 100 mg were prepared in either hexane or methylene chloride. A second test examined the

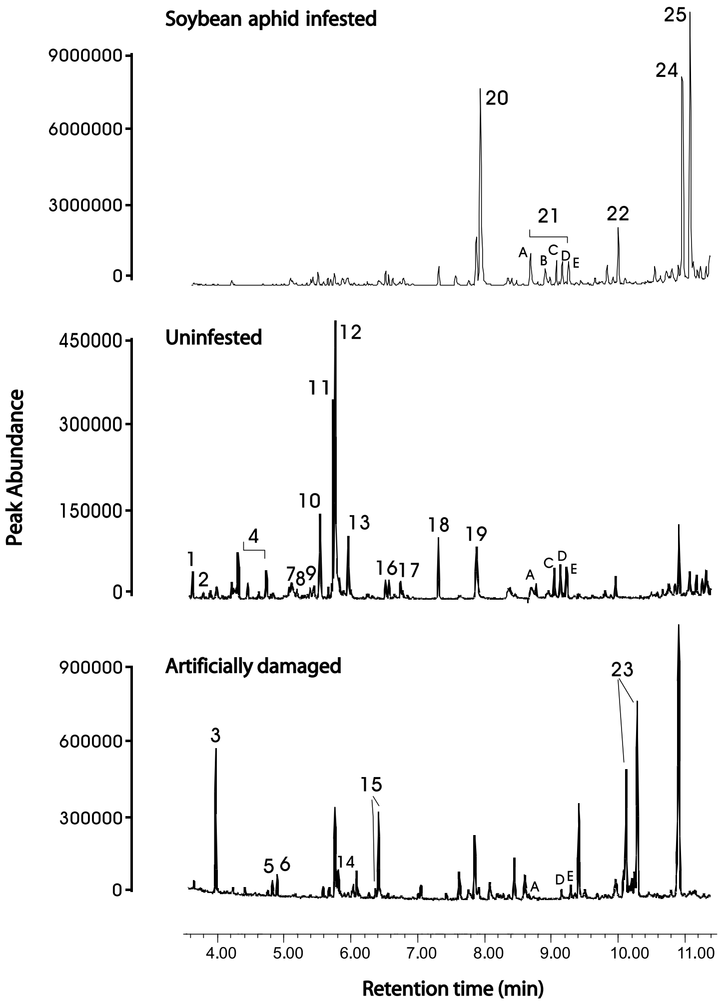

FIG. 1. Typical gas chromatograms (on a DB-5 column) of volatile compounds emitted from soybean aphid-infested, artificially damaged, and undamaged plants of *G. max* (V2 stage). Represented are (*E*)-2-hexenal (1), (*E*)-2-hexenol (2), unknowns (3 and 4), ethyl benzene (5), 1,3-dimethyl benzene (6), benzaldehyde (7), 6-methyl-5 heptanone (8), (*Z*)-3-hexenyl acetate (9), decane (10), 1,2,3-trimethyl benzene (11), dichlorobenzene (12), D-limonene (13), β-ocimene (14), unknown (15), linalool (16), 2-phenylethanol (17), unknown (18), naphthalene (19), methyl salicylate (20), unknown (21), tetradecane (22), unknown (23), α-humulene (24), and (*E*,*E*)-α-farnesene (25) (the labeled numbers on each peaks do not refer to those compounds that are only detected uniquely in each treatment, and the internal standard, *n*-pentadecane, is not shown due to its elution time is after 11.00 min).

trapping efficacy of the induced methyl salicylate and a previously identified lady beetle and lacewing attractant compound, 2-phenylethanol (also at 100-mg dose). In a third dose–response test, serial dilutions of synthetic methyl salicylate were made at doses ranging from 10 to 1000 mg. Medical peerless cotton wicks (5 cm in length, 100% cotton) were used as dispensers, and the trap used was constructed by stapling four yellow sticky traps together, which is similar to the Rebell trap described by Zhu et al. (1999), where the attractant lure was suspended in the center of this trap. The trap was hung from bamboo stakes, 1.2 m above the ground. Within a replicate (N = 10), the distance between traps was 15 m. The traps were checked daily and captured ladybugs were removed from sticky traps after checking. Trap position within a series

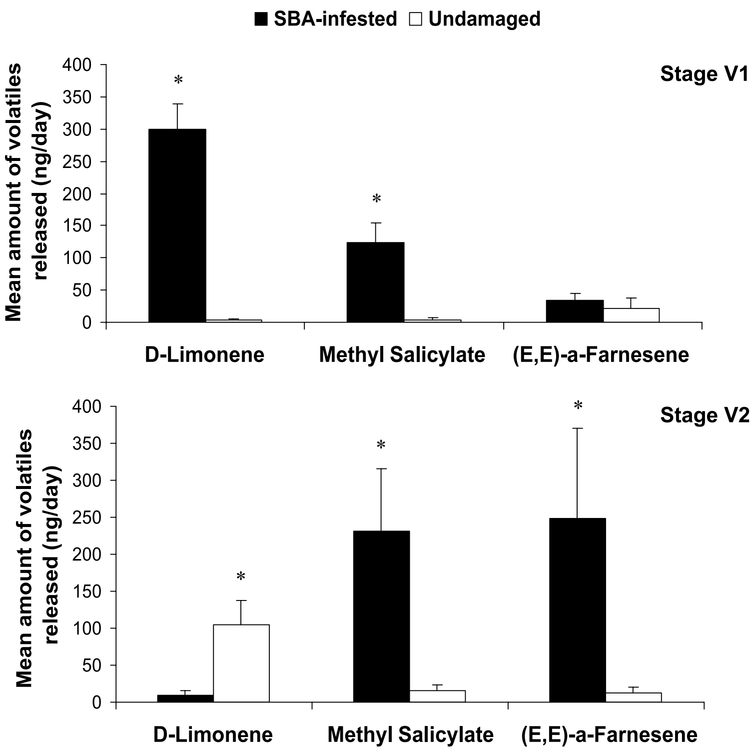

FIG. 2. Mean emission rates of three volatile compounds from plants at V1 (top) and V2 (bottom) stages of *G. max*. Asterisks indicate statistically significant differences in volatile release rates between soybean aphid-infested and undamaged plants (Student's t-test, N = 6, $P < 0.05$).

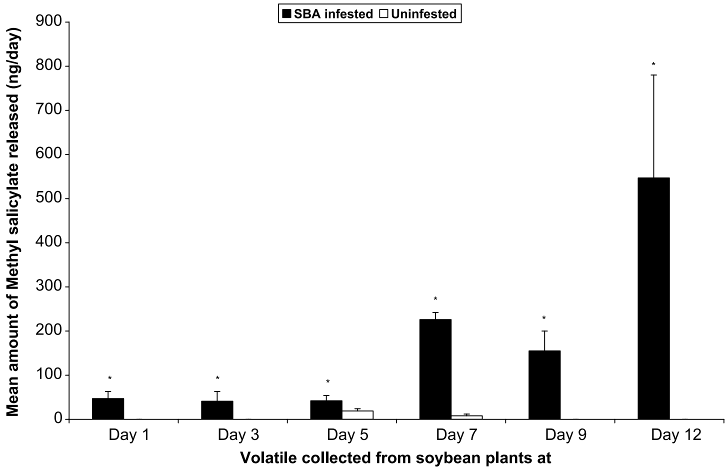

FIG. 3. Average released amounts of methyl salicylate at every other day from soybean aphid-infested and undamaged *G. max* plants during a 12-d collecting period. Asterisks indicate statistically significant differences in amounts of methyl salicylate released between soybean aphid-infested and undamaged *G. max* plants (Student's *t*-test, $N = 6$, $P < 0.05$).

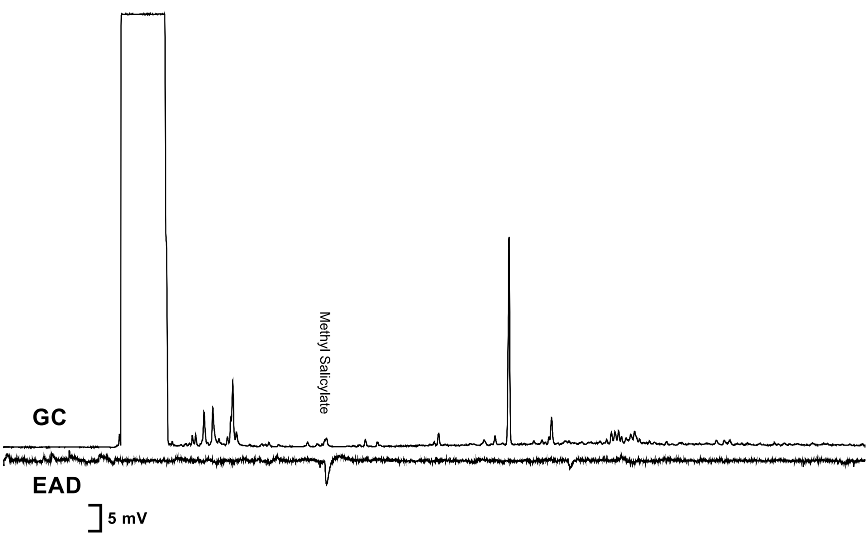

FIG. 4. Simultaneously recorded FID and EAD responses of antennae of a female adult *C. septempunctata* to extracts of soybean aphid-infested *G. max* (analyzed on a DB-Wax column).

was randomized after checking to minimize the effects of habitat heterogeneity. The trapping test lasted for 2 wk.

Statistical Analyses. Differences in volatile emission among treatments in the volatile collection experiments and field trap catches (means of trapped beneficial insects) were compared by either Student's *t*-test or analyses of variance (ANOVA) followed by Fisher's protected least significant difference test (FPLSD).

RESULTS

Volatiles from Soybean Aphid-Infested Soybean Leaves. In total, 19 volatile compounds were tentatively identified from emissions of both infested, uninfested and artificially damage soybean leaves by comparing their retention indices and mass spectra with those of synthetic standards (Figure 1). Most volatiles released from the soybean plants were common plant volatiles. Further quantitative GC and GC-MS analyses revealed consistent differences in emissions of D-limonene, methyl salicylate, and (*E*,*E*)-α-farnesene between the

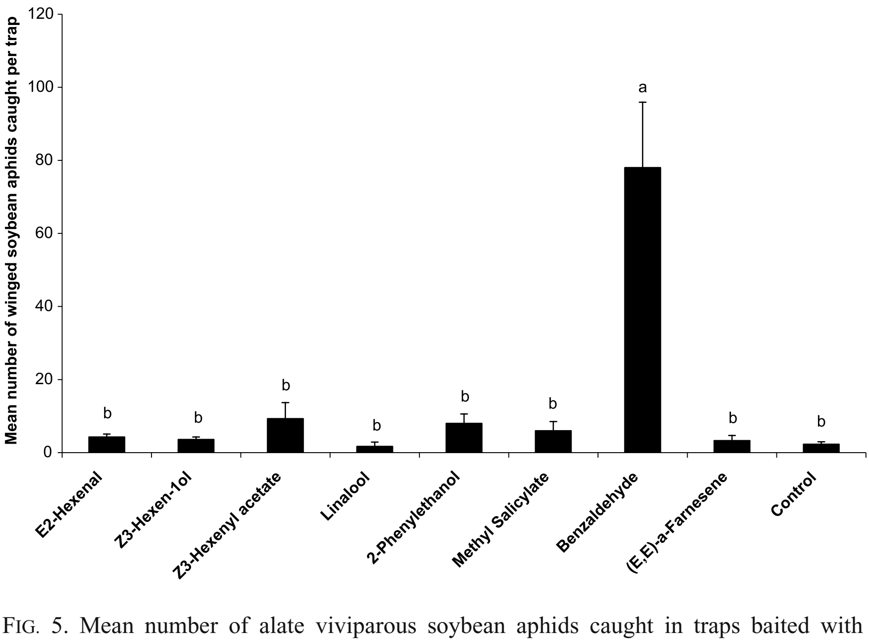

FIG. 5. Mean number of alate viviparous soybean aphids caught in traps baited with selected soybean associated volatile compounds (100 mg) in the soybean field (line indicates standard error). Columns with no letters in common are significantly different ($N = 10$, ANOVA followed by FPLSD test, $P < 0.05$).

aphid-infested and the undamaged, uninfested plants at the two growth stages (Figure 2). Among these three compounds, methyl salicylate was the only compound emitted in significantly higher quantities from aphid-infested plants at both V1 and V2 stages, relative to the undamaged, uninfested control. Significantly more D-limonene was released from the aphid-infested plants at the V1 stage, whereas more (E,E)-α-farnesene was produced by V2-stage plants. The amounts of methyl salicylate released from aphid-infested plants were significantly higher than those emitted from undamaged, uninfested plants, and amounts increased to maximum levels on d 12 of the collection period (Figure 3). No volatile compounds were found from extracts of soybean aphids only, except a trace of (E)-β-farnesene was identified.

Antennal Responses of Seven-Spotted Lady Beetles to Volatiles from Aphid-Infested Soybean Plants. Only one compound of the headspace of aphid-infested plants elicited a significant EAD response in *C. septempunctata.* The

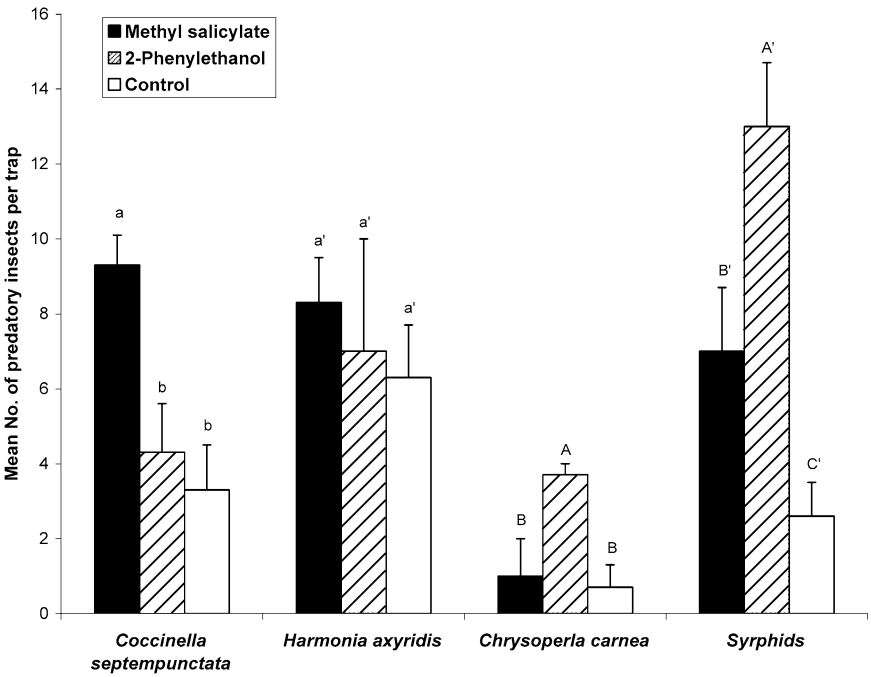

FIG. 6. Mean number of predatory insects (both sexes) caught in traps baited with 100 mg of methyl salicylate and 2-phenylethanol, and the control from an Iowa soybean field in 2003. Columns with no letters in common in four different categories are significantly different (N = 10, ANOVA followed by FPLSD test, $P < 0.05$).

retention time of this compound matched that of synthetic methyl salicylate (Figure 4). Further GC-MS analyses of the same extract confirmed its chemical identity as methyl salicylate.

Attraction of Aphids and Their Predators to Soybean Leaf Volatiles. Results from field-trapping tests using Rebell-type yellow sticky traps baited with either soybean leaf volatiles identified from this study or with previously reported leaf volatiles (Liu et al., 1989) showed that among eight common soybean plant-associated volatiles tested, benzaldehyde was the only compound attractive to alate soybean aphids (Figure 5). Relatively high numbers of four predatory insect species were captured in traps baited with 100 mg of methyl salicylate and 2-phenylethanol (Figure 6). Adults of *C. septempunctata* were significantly attracted only to methyl salicylate, whereas both adults of *C. carnea* and syrphid flies were attracted to 2-phenylethanol. However, there were no differences in catches of *H. axyridis* among traps baited with either of the two tested attractant compounds, compared with the control. A subsequent dose–response test with the synthetic methyl salicylate demonstrated that the highest attraction to adult *C. septempunctata* was at doses from 100 to 300 mg (Figure 7). A significant reduction in trap catch was observed at the highest tested dose of this compound.

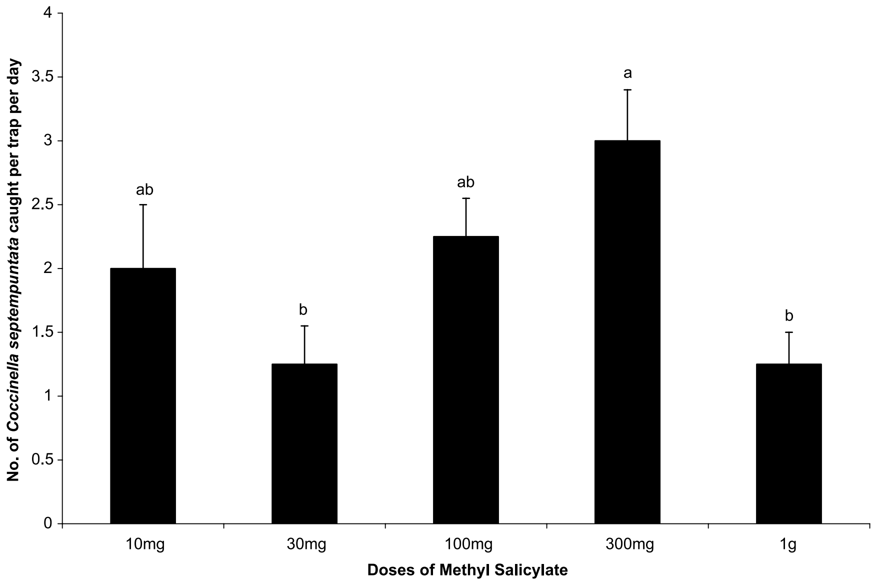

FIG. 7. Mean catches ±SE of *C. septempunctata* adults in traps baited with different doses of the synthetic methyl salicylate. Different letters on top of columns indicate significant differences (N = 10, ANOVA followed by Fisher FPLSD test, $P < 0.05$).

DISCUSSION

The analyses show that volatiles collected from soybean plants in their early growth stages (V1–V2) consist of aliphatic esters, aldehydes, alcohols, and ketones as well as some halogenated hydrocarbons and terpenoids. Some of these volatiles are similar to those that have been reported from a previous study (Liu et al., 1989), even though different cultivars of soybean were selected and different growth stages of plants were tested. Du et al. (1994) reported that alate viviparous soybean aphids are attracted or arrested by volatiles from soybean plants, and electroantennographic tests (EAG) have shown that these aphids show significant antennal responses to some volatiles from young leaves. Our field trapping experiments using the most common soybean volatile compounds also showed that alate viviparous soybean aphids are highly attracted to benzaldehyde, a component present in the headspace of soybean, and that this compound elicits significant EAG responses (Du et al., 1995; Zhu, unpublished data).

Despite large variation in the amounts of volatiles released from the plants we tested, methyl salicylate was consistently released at a significantly higher rate from aphid-infested plants compared with undamaged V1- and V2-stage plants or from artificially damaged leaves. This finding demonstrates that the infestation of aphids induces the emission of methyl salicylate, which is a volatile derivative of the plant hormone salicylic acid (Shulaev et al., 1997; Ozawa et al., 2000). Methyl salicylate has been identified in herbivore-induced plant volatile blends from at least 10 plant species infested with mites, aphids, beetles, and caterpillars (Walling, 2000; James, 2003; De Boer and Dicke, 2004; Van den Boom et al., 2004). This volatile plays an important role in the activation of plant defense responses (Yang et al., 1997), which also has been reported from tobacco plants inoculated with tobacco virus (Shulaev et al., 1997). The temporal emission patterns of two other volatile compounds, D-limonene and (*E*,*E*)-α-farnesene, differ between infested and undamaged plants at the two growth stages. Even though these two terpenes have been reported as herbivore-induced volatiles from several plant species (Paré and Tumlinson, 1999), it remains to be tested whether their emissions are triggered by soybean aphid infestation, or differ with plant growth stage.

Previous studies have shown that several parasitoids and predatory mites locate their hosts by using volatile semiochemicals emitted from their hosts and from the plants infested by their hosts (Vet and Dicke, 1992; Dicke and Vet, 1999). Recently, De Boer and Dicke (2004) and Van den Boom et al. (2004) showed that one of the major soybean volatiles induced by the herbivorous mite *Tetranychus urticae* is methyl salicylate, and that this compound is also attractive to its predatory mite *Phytoseiulus persimilis*. During the Iowa soybean growing season, we observed that a variety of insect predators attack soybean aphids. The complex of these natural enemies seems to play a key role in regulating aphid populations. *C. septempunctata* dominates early in the growing season, when heavy aphid infestation is first observed in the field. Both larva and adults of this beetle can consume up to 90 aphids per day (Han, 1997). Our GC-EAD analyses showed that antennae of this lady beetle species exclusively responded to methyl salicylate, which may be induced by the infestation of soybean plants with aphids. Field trapping tests conducted in soybean fields further confirmed that synthetic methyl salicylate-baited traps are highly attractive to *C. septempunctata*. Methyl salicylate also has been demonstrated to be attractive to predatory mites *P. persimilis* and predatory bugs *Anthocoris nemoralis* as well as minute pirate bugs, *Orius tristicolor*; bigeyed bugs, *Geocoris pallens*, and lady beetle *Stethorus punctum* (Dicke and Sabelis, 1988; Drukker et al., 2000; James, 2003). In addition, several studies have shown that methyl salicylate can act as a repellent to several aphid species when they leave their overwintering places to colonize host plants in spring (Lösel et al., 1996; Ninkovic et al., 2003).

Relatively higher numbers of syrphid flies are attracted to traps baited with methyl salicylate compared with non-methyl salicylate-baited traps, which coincides with a previous report (James, 2003). However, James (2003) has reported that the catches of coccinellids in traps baited with methyl salicylate are not significantly different from those of control traps. The discrepancy in trap catches of coccinellids with methyl salicylate between the current study and that of James' field experiment could be attributed to geographical variation in populations of these coccinellids, different trap designs, and different doses of methyl salicylate. In the field experiment, James (2003) used ~1 g methyl salicylate (~1 ml), a dose that has been shown in our field trapping experiment to reduce attraction of *C. septempunctata.* Similar examples have been documented for several parasitic wasp species that are attracted to low doses of green leaf volatiles but are repelled by high doses (Whitman and Eller, 1992). One of the most abundant lady beetle species, *H. axyridis*, which accounts for most of the soybean aphid feeding during the late growing season in Iowa, was not attracted to methyl salicylate. The number of *H. axyridis* caught in traps baited with methyl salicylate was not statistically different from that in the control traps. A minor soybean volatile, 2-phenylethanol, identified from both aphid-infested and undamaged soybean plants is highly attractive to adults of *C. carnea,* which is similar to findings of Zhu et al. (1999).

The use of natural enemies as biological control agents for soybean aphids has great potential to suppress aphid populations. However, the biggest concern for the success of biological control is how to recruit predaceous insects into natural or damaged soybean fields and synchronize their presence with the targeted aphid pest, thereby increasing their predatory efficacy. The present study provides a base to help further development of enhanced biological control strategies via applications of attractants of predatory insects that attack aphids early in the growing season, which is considered as an alternative to suppress their populations below the economic threshold level. The identification of methyl salicylate as a soybean aphid-induced plant volatile and the demonstration of its attractiveness to one of the most abundant lady beetle species (and to syrphid flies that also attack soybean aphids) may provide a tool to enhance the biological control of these aphids. This compound also has been reported to attract some *Orius* species, of which *O. insidiosus* has been considered as another key predator for soybean aphid biological control in the Midwest. The application of beneficial insect attractants such as methyl salicylate and 2-phenylethanol has been tested in soybean fields to enhance biological control of aphids. Although our preliminary results have shown positive impact on increasing predatory insect presence and on suppressing soybean aphid populations (Zhu et al., unpublished data), detailed further studies are necessary to implement such strategies. Negative effects caused by factors such as excessively high concentrations of attractants could repel predatory insects, and host deficiency might result in reduction of predation or parasitism due to relatively low-density prey in the natural habitat (Dicke et al., 1990).

Acknowledgments—We thank Jason Jones for field trapping assistance. This project was supported by funding from National Science Foundation (SBIR) and Iowa Department of Natural Resources and The Leopold Center for Sustainable Agriculture to J.Z.

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