

Journal of Chemical Ecology, Vol. 31, No. 7, July 2005 (©2005)

DOI: 10.1007/s10886-005-5796-x

OLFACTORY RESPONSES OF BANANA WEEVIL PREDATORS TO VOLATILES FROM BANANA PSEUDOSTEM TISSUE AND SYNTHETIC PHEROMONE

W. TINZAARA,^{1,2,*} C. S. GOLD,¹ M. DICKE,³ and A. VAN HUIS³

¹*International Institute of Tropical Agriculture, Eastern and Southern Africa Regional Centre, P.O. Box 7878, Kampala, Uganda*

²*National Agricultural Research Organisation, Kawanda Agricultural Research Institute, P.O. Box 7065, Kampala, Uganda*

³*Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands*

(Received January 3, 2005; accepted March 4, 2005)

Abstract—As a response to attack by herbivores, plants can emit a variety of volatile substances that attract natural enemies of these insect pests. Predators of the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae) such as *Dactylosternum abdominale* (Coleoptera: Hydrophilidae) and *Pheidole megacephala* (Hymenoptera: Formicidae), are normally found in association with weevil-infested rotten pseudostems and harvested stumps. We investigated whether these predators are attracted to such environments in response to volatiles produced by the host plant, by the weevil, or by the weevil–plant complex. We evaluated predator responses towards volatiles from banana pseudostem tissue (synomones) and the synthetic banana weevil aggregation pheromone Cosmolure+ in a two-choice olfactometer. The beetle *D. abdominale* was attracted to fermenting banana pseudostem tissue and Cosmolure+, whereas the ant *P. megacephala* was attracted only to fermented pseudostem tissue. Both predators were attracted to banana pseudostem tissue that had been damaged by weevil larvae irrespective of weevil presence. Adding pheromone did not enhance predator response to volatiles from pseudostem tissue fed on by weevils. The numbers of both predators recovered with pseudostem traps in the field from banana mats with a pheromone trap were similar to those in pseudostem traps at different distance ranges from the pheromone. Our study shows that the generalist predators *D.*

* To whom correspondence should be addressed. E-mail: w.tinzaara@kari.go.ug

abdominale and *P. megacephala* use volatiles from fermented banana pseudostem tissue as the major chemical cue when searching for prey.

Key Words—Aggregation pheromone, *Cosmopolites sordidus*, Curculionidae, infochemicals, prey searching, synomone, olfactometer, natural enemies, plant volatiles.

INTRODUCTION

During host searching, natural enemies of herbivorous insects (predators and parasitoids) are known to utilize volatile chemicals emitted by plants or herbivorous insects (Vinson, 1976; Vet and Dicke, 1992; Turlings et al., 1995; Dicke and Vet, 1999). Predators and parasitoids that forage for herbivorous prey by using infochemicals may have a problem concerning reliability and detectability of these stimuli (Vet and Dicke, 1992; Wiskerke et al., 1993). Stimuli from the prey's food are detectable but are not reliable in indicating prey presence. In contrast, prey-derived stimuli are generally the most reliable sources of information but usually not easily detectable at long distances (Vet and Dicke, 1992). Natural enemies have evolved different mechanisms to cope with this reliability–detectability problem (Vet and Dicke, 1992). One of these mechanisms is that natural enemies can exploit pheromones from their victim as kairomones in long distance herbivore location (Lewis et al., 1982; Noldus et al., 1991; Wiskerke et al., 1993; Hedlund et al., 1996; Hendrichs and Hendrichs, 1998; Hoffmeister and Gienapp, 1999; Wertheim et al., 2003; Francis et al., 2004; Fatouros et al., 2005). The use of chemical information that is both reliable and easy to detect enhances natural enemy searching efficiency (Vet and Dicke, 1992).

Infochemicals, both those used within and between species, can be utilized in pest management by either exploiting the way the natural enemy responds, or by manipulating the source of the infochemical (Dicke et al., 1990; Vite and Baader, 1990; Foster and Harris, 1997; Degenhardt et al., 2003; Powell and Pickett, 2003). For example, infochemicals can be used to enhance the searching efficiency, host utilization, and reproductive capacity of natural enemies (Renwick, 1992; Turlings et al., 1995; Scutareanu et al., 1997; Steidle and van Loon, 2003; McGregor and Gillespie, 2004). There are a few studies on the application of infochemicals to manipulate the behavior of predators or parasitoids in the field (e.g., Drukker et al., 1995; Shimoda et al., 1997; Bernasconi et al., 2001; James, 2003; James and Price, 2004). However, data on the role of infochemicals in predator foraging have become available for several groups such as predatory mites (Sabelis and Dicke, 1985), pentatomids (van Loon et al., 2000), anthocorids (Dwumfour, 1992; Drukker et al., 1995; James and Price, 2004), chrysopids (Reddy et al., 2002; James and Price, 2004), and

coccinellids (Le Ru and Makosso, 2001; Ninkovic et al., 2001; Steidle and van Loon, 2002; James and Price, 2004). The predator *Rhizophagus grandis* (Gyll.) (Coleoptera: Rhizophagidae) is attracted to traps baited with a kairomone produced by the bark beetle *Dendroctonus micans* Kug (Coleoptera: Scolytidae) (Aukema et al., 2000), and this can be exploited to monitor the predator's distribution in the field.

The banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae) is a major pest of bananas in East Africa. Yield losses of up to 100% have been reported (Sengooba, 1986, unpublished). The weevil oviposits in the leaf sheaths and corm at the base of the banana mat (a banana mat consists of plants arising from a common corm/rhizome) (Abera et al., 2000). The larvae tunnel in the corm and pseudostem (the plant part between the corm and leaves), damaging the vascular system and weakening the stability of the plant. In Uganda, distribution studies showed that over 60% of the adult weevils in the banana field were associated with crop residues such as rotting pseudostem (Gold et al., 2004). The weevil has predators that have been mostly found in environments harboring weevils such as banana pseudostem traps and fermenting banana pseudostem tissue, often in larval weevil tunnels (Koppenhofer et al., 1992; Koppenhofer, 1993; Tinzaara et al., 1999; Abera, 2004). Some ant species that have the potential to control *C. sordidus* include *Pheidole megacephala* and *Tetramorium guineense* (Mayr) (Hymenoptera: Formicidae) (Gold et al., 2001; Abera, 2004). Nonant predators known to prey on weevil eggs and larvae include *Dactylosternum abdominale* (Fabricius) (Coleoptera: Hydrophilidae), *Euborellia annulipes* (Lucas) (Dermaptera: Carcinophoridae), and *Thyreocephalus interocularis* (Eppelsheim) (Coleoptera: Staphylinidae) (Koppenhofer et al., 1992). Of these five predator species, *D. abdominale* and *P. megacephala* are the most abundant predators in environments preferred by weevils in Uganda (Tinzaara et al., 1999; Gold et al., 2001; Abera, 2004).

D. abdominale and *P. megacephala* are generalist predators that feed on microfauna and -flora of decomposing plant tissues, eggs, and small larvae of insects. Decomposing tissue is more attractive to these predators than fresh tissue (Koppenhofer, 1993). Generalist predators are known to use infochemicals during prey location (Dwumfour, 1992; Scutareanu et al., 1997; Haberkern and Raffa, 2003; Steidle and van Loon, 2003; McGregor and Gillespie, 2004). Information on how volatiles from decomposing banana pseudostem tissue influence prey location by generalist predators is not available. Therefore, we have investigated the behavior of *D. abdominale* and *P. megacephala* predators under laboratory and field conditions to assess whether they use volatile infochemicals associated with banana weevils and/or their food.

An aggregation pheromone has been identified for *C. sordidus*, which is specific to the weevil (Jayaraman et al., 1997). A synthetic pheromone source containing a mixture of the four sordidin isomers is sold under the trade name

Cosmolure+. The pheromone has been studied in the laboratory and in the field for the management of *C. sordidus* (Tinzaara et al., 2000, 2003) and attracts both male and female weevils (Alpizar et al., 1999; Tinzaara et al., 2000). The pheromone-baited trap captures up to 18 times more weevils than a conventional split pseudostem trap (Tinzaara et al., 2000). Information on the effect of this aggregation pheromone on the behavior of the weevil's predators has not been investigated. Several species of predators have been reported to use the aggregation pheromones of their hosts during host searching and location (Dwumfour, 1992; Vet and Papaj, 1992; Hedlund et al., 1996; Scutareanu et al., 1997; Haberkern and Raffa, 2003; Steidle and van Loon, 2003).

The objectives of this study were to determine whether: (1) volatiles from banana pseudostem tissue and *C. sordidus* pheromone attract the predators *D. abdominale* and *P. megacephala*; (2) the predators respond to host plant volatiles and whether this response is dependent on dose or weevil feeding; (3) the pheromone enhances the predators' response to weevil-damaged pseudostem tissue; and (4) the pheromone affects the predators' distribution around pheromone-baited traps in the field.

METHODS AND MATERIALS

Site Description

Laboratory and field studies were conducted at Kawanda Agricultural Research Institute (KARI) (0°25'N, 32°51'E, 1190 m), 13 km north of Kampala, Uganda. The site has two rainy seasons (March–May and September–November) with an average precipitation of 1180 mm per year. Average daily temperatures range between 16 and 29°C. Relative humidity in the laboratory ranged from 60 to 80%.

A field experiment was conducted in banana plots at KARI planted with cultivar Nabusa (*Musa* spp., AAA-EA group). The plot size was 12 × 10 mats at a spacing of 2.5 × 3 m (Figure 1). The plots were weeded after every 2 mo and were not mulched.

Odor Sources

Pieces of fresh pseudostem (less than a week after harvest) from the banana cv Nabusa collected from banana fields at KARI were placed in plastic containers for 7 d at room temperature to get fermented pseudostem tissue. Fresh pseudostem tissue was collected at the time of the bioassays. Fifty grams of either fresh or fermented pseudostem tissue was used for bioassays. This same dose was previously successfully used for studies of the weevil's response to infochemicals (Tinzaara et al., 2003).

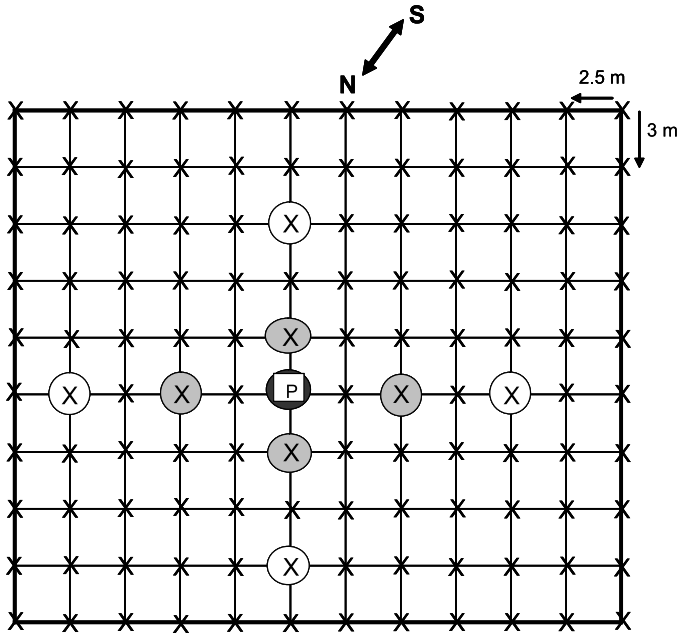


FIG. 1. A schematic diagram of the plot used in the field experiment to determine the effect of the aggregation pheromone on the distribution of predators. Pseudostem trap pieces were placed on banana mats (X) at different distance ranges indicated by circles (black = 0 m, grey = 0.1–5 m, white = 5.1–10 m) from the pheromone trap (P).

Pheromone lures for use in laboratory bioassays and field experiments were obtained from ChemTica International in San Jose, Costa Rica. They were sealed in plastic sent by a courier (transit time <1 wk) and subsequently stored in a freezer at -5°C upon arrival until use. Each pheromone pack contained 90 mg of Cosmolure+ with a release rate of 3 mg/day (Oehlschlager, personal communication). The pheromone packs were individually used as odor sources in their original plastic package material.

Predators

Adults of the beetle *D. abdominale* and the ant *P. megacephala* were selected for use in laboratory bioassays to assay their response to infochemicals. Predators were collected by hand searching in rotten banana pseudostems and corms from the field and kept on a nonsubstrate tissue (wetted tissue paper) in the laboratory for 24–48 hr before use in bioassays. Neither age nor sex of the

collected *D. abdominale* beetles was known. Worker ants of *P. megacephala* of unknown age were used.

Olfactometer

An olfactometer similar to that employed by Lofgren et al. (1983) and Cordova-Yamauchi et al. (1998) to study laboratory response of ants to banana weevil aggregation pheromone was used in all experiments. The apparatus consists of a petri dish with 19-cm diam and 4 cm in height, without a lid. Two holes were made through the sides of the dish close to the base, and two delivery tubes were inserted into them. A filter paper was placed at the floor of the petri dish and wetted with about 50 ml of water before each test. One of the (arms) tubes of the olfactometer was connected to a jar (125 ml) containing a test odor source and the other to a jar containing clean air as control. Volatiles entered the arena by diffusion.

A single predator was placed at the center of the olfactometer arena. Each predator was observed for a maximum of 10 min and was considered to have responded when it entered one arm of the olfactometer or when at the end of the 10 min, the predator was within less than 1 cm from the entry port of the arms. After testing five individuals for each odor set, the odor sources were replaced with fresh ones. For all experiments, five individuals of each predator species were tested for all odor sets per day. The first experiment was repeated during 6 d ($N = 30$, total number of individuals per predator species per odor set), whereas the rest of the laboratory experiments were repeated on 10 d (50 individuals per predator species per odor set, unless mentioned otherwise). Each predator individual was tested only once and then discarded. Treatment and control arms were exchanged after testing each predator by connecting the tubes at the opposite side to avoid trail formation. This had been observed to occur especially in the case of *P. megacephala* in preliminary tests. This procedure also precluded the effects of unforeseen asymmetry in the setup. The apparatus was washed with ethanol and air-dried before using a new predator species (i.e., after testing five individuals).

Experiments

We conducted five experiments with *D. abdominale* and *P. megacephala*. The first four were done in the laboratory using the olfactometer, and the fifth was done in the field.

Testing of the Olfactometer. This experiment was conducted to test whether any directional bias interfered with the responses of the two predator species in the olfactometer. The following odor sets were compared in this

experiment: (1) clean air vs. clean air and (2) fermented pseudostem tissue vs. fermented pseudostem tissue.

Predator Response to Pseudostem Tissue and Weevil Pheromone. The response of the predators to banana pseudostem tissue and the weevil's aggregation pheromone was evaluated in this experiment. Odor sets that were tested in the olfactometer were (1) fresh pseudostem tissue vs. clean air, (2) fermented pseudostem tissue vs. clean air, (3) fermented vs. fresh pseudostem tissue, and (4) pheromone vs. clean air.

Predator Response to Different Doses of Fermented Pseudostem Tissue. This experiment was conducted to determine whether predator response to infochemicals was dose-dependent. Odor sources were 1, 5, 25, and 125 g of fermented pseudostem tissue. Predator response to volatiles emanating from these amounts of tissue was compared to clean air in the olfactometer.

Predator Response to Weevil-Damaged Pseudostem Tissue in the Absence and Presence of Pheromone. This experiment was conducted to determine whether feeding by weevil larvae influences predator response to the banana pseudostem tissue and to evaluate whether the presence of pheromone enhances the predators' responses to volatiles from banana pseudostem tissue without weevil larvae feeding. Treatments were as follows: (1) fresh pseudostem, fed on by weevil larvae for 48 hr and larvae removed (F-LR); (2) fresh pseudostem, fed on by weevil larvae for 48 hr and larvae present (F-LP); and (3) weevil larvae alone. The following odor sets were compared: (1) F-LR vs. clean air, (2) F-LP vs. clean air, (3) larvae vs. clean air, (4) F-LP vs. larvae, (5) F-LR vs. F-LP, and (6) F-LR plus pheromone vs. F-LR.

Pseudostems of the cultivar Nabusa were collected from the fields at KARI. Weevil larvae (third to fifth instar) collected from the field were allowed to feed on fresh pseudostem tissue for 48 hr. Five larvae were placed on a pseudostem piece measuring 30 × 10 cm. After 48 hr at 22–28°C, the tissue had been tunneled, and tissue had turned dark brown and was used in bioassays with or without the larvae present. The larvae that were tested without food were collected from the field 24 hr before bioassays. They were placed in petri dishes (9-cm diam) with a nonsubstrate food material (moist tissue paper).

Field Distribution of Predators Around the Pheromone-Baited Traps. A field experiment was conducted at KARI to determine the distribution of banana weevil predators around pheromone-baited traps. We evaluated the hypothesis that predators aggregate around the trap mat as a result of a response to the pheromone and/or weevil-related volatiles. A pitfall pheromone-baited trap (Tinzaara et al., 2000) was placed at the center of each plot (Figure 1). Soapy water was placed in the trap to retain the predators that had entered. The soapy water was renewed at every sampling occasion. Pheromone traps were checked every 37 d, and predators captured in the traps were recorded and taken to the laboratory in vials for sorting and identification.

Ten fresh split pseudostem pieces (each 30 cm long) were placed in the plots at the time of installing the pheromone traps. In each plot, pseudostem pieces were placed on the trap mat and on four mats in each of the distance range of 0.1–5 and 5.1–10 m from the trap. Selection of the distance ranges was based on previous data on response by the weevil to the aggregation pheromone (Tinzaara et al., 2000). Six replicate plots were used. To determine distribution of predators around the pheromone-baited traps, predators were searched for in banana pseudostem pieces after 30 d at different distances from the trap.

Statistical Analysis

The χ^2 -test for goodness of fit was used to determine the preference for one of the stimuli tested during the olfactometer bioassays (distribution of expected values 50:50). Field data on the number of predators and the weevils distributed around the pheromone-baited traps relative to distance were subjected to analysis of variance (ANOVA) using the GLM procedures of SAS software (SAS, 1990). The means were compared using the Student–Newman–Keuls (SNK) test. A regression analysis was used to determine the relationship between weevil and predator catches in pheromone-baited traps.

RESULTS

Both predator species, *D. abdominalis* and *P. megacephala*, showed equal distributions when offered clean air vs. clean air and when offered fermented pseudostem tissue vs. fermented pseudostem tissue ($P > 0.05$) (Table 1). There were fewer nonresponders for *P. megacephala* (22%) than *D. abdominalis* (40%) in the olfactometer apparatus used. The data indicate that the apparatus has no symmetrical bias and can be used for evaluating responses of these predators to banana pseudostem tissue and the pheromone.

TABLE 1. NUMBER OF PREDATORS RESPONDING TO CLEAN AIR AND FERMENTED BANANA PSEUDOSTEM ODORS IN A TWO-CHOICE OLFACTOMETER ASSAY IN THE LABORATORY

Comparison odor sources (A/B)	<i>Dactylosternum abdominalis</i>			<i>Pheidole megacephala</i>		
	A	B	No response	A	B	No response
Clean air/clean air	10	9	11	12	11	7
Fermented/fermented tissue	9	8	13	11	13	6

A total number of 30 individual predators were tested per comparison set. The responses of the predators to the two odor sources did not differ significantly in either experiment ($P > 0.05$, χ^2 test).

Both *D. abdominale* and *P. megacephala* preferred fermented pseudostem tissue over clean air ($P < 0.001$ and $P < 0.05$, respectively). Neither predator species discriminated between fresh pseudostem tissue and clean air (Figure 2). In a direct comparison, more beetles and ants chose the fermented rather than the fresh pseudostem tissue, but this was only statistically significant for the ant *P. megacephala* ($P < 0.05$). Significantly more beetles moved to the side of the olfactometer with the pheromone ($P < 0.01$) than to the one with clean air, whereas the ants were not attracted to the weevil’s pheromone.

The response of both *D. abdominale* and *P. megacephala* to fermented pseudostem tissue was dose-dependent. At all doses, the number of *D. abdominale* and *P. megacephala* choosing the side of the olfactometer with

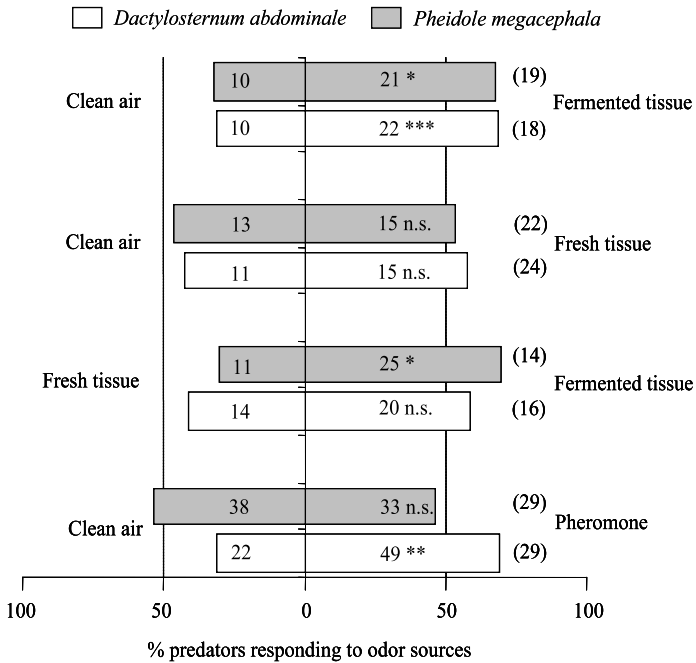


FIG. 2. Response of the banana weevil predators *Dactylosternum abdominale* and *Pheidole megacephala* to volatiles from banana pseudostem tissue and the pheromone in an olfactometer: percentage of responding individuals of each predator per comparison set, choosing one odor source or the other. Significantly different values are indicated with * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$; n.s. = nonsignificant at $P > 0.05$, χ^2 test. The total number of individuals tested per odor set was 50, except for pheromone vs. clean air when 100 individuals were tested for response. The nonresponding predators are indicated in brackets at the right of bars.

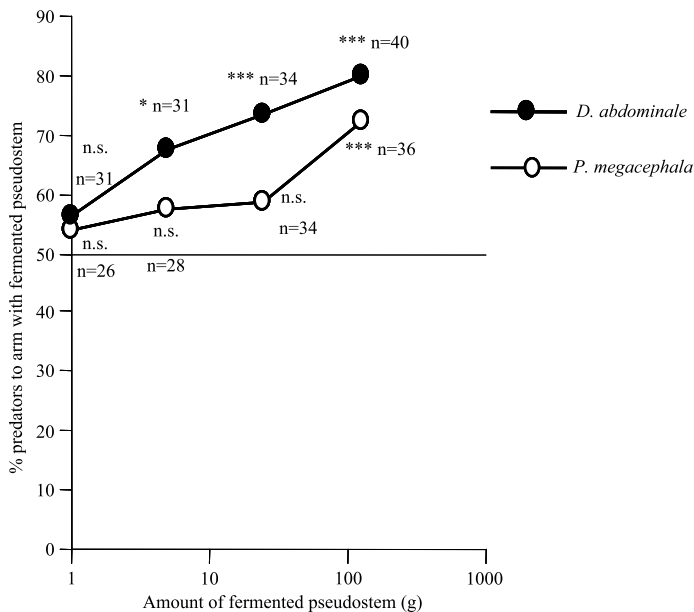


FIG. 3. Dose response of the predators *D. abdominalis* and *P. megacephala* to volatiles from fermented banana pseudostem tissue in an olfactometer when the alternative was clean air. * $P < 0.05$, *** $P < 0.001$, n.s. = nonsignificant ($P > 0.05$) (χ^2 test, N indicates total number of responding predators out of 50 individuals tested per dose).

the fermented banana tissue was higher than the number choosing the side with clean air (Figure 3), even when small amounts were used (down to 1 g). However, only the following responses were significant: more *D. abdominalis* chose for fermented pseudostem tissue when 5, 25, and 125 g were used than for clean air, and more *P. megacephala* chose for the pseudostem tissue when 125 g was used compared to clean air. Both *D. abdominalis* and *P. megacephala* also significantly preferred 50 g of fermented tissue over clean air (Figure 2).

The presence of weevil larvae did not influence the predators' responses to pseudostem tissue. More *D. abdominalis* chose fermented pseudostem tissue with or without feeding larvae present than clean air ($P < 0.05$) (Figure 4). There was no significant ($P > 0.05$) difference between the numbers of beetles choosing larvae vs. clean air, fermented pseudostem with larvae vs. larvae only, and fermented pseudostem tissue with larvae either present or absent. The effect of the pheromone when tested in the presence of fermented pseudostem tissue (without larvae) vs. the fermented tissue alone was not significant ($P > 0.05$).

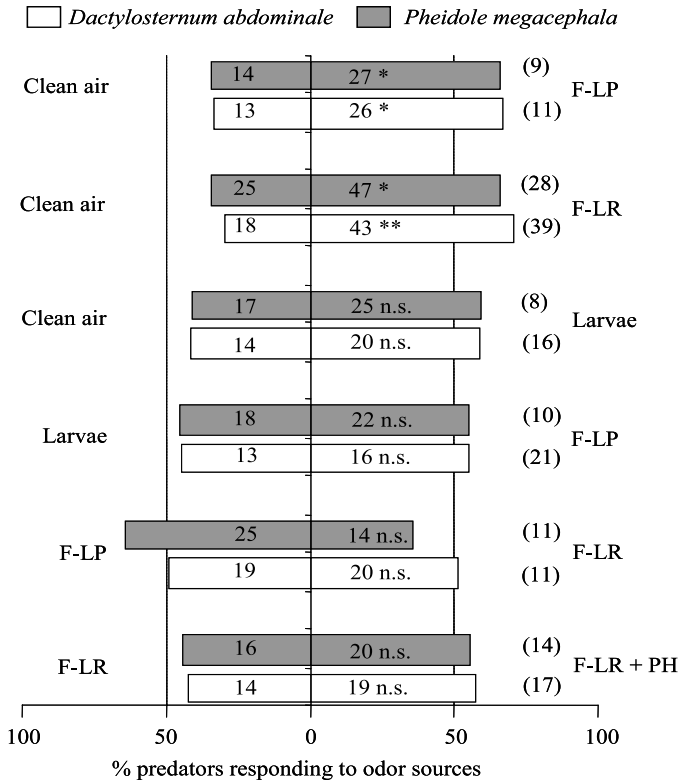


FIG. 4. Response of predators in an olfactometer to fermented tissue with (F-LP) or without (F-LR) feeding weevil larvae and in combination with the pheromone (PH): percentage of responding individuals of each predator per comparison set, choosing one odor source or the other. Significantly different values are indicated with * $P < 0.05$ and ** $P < 0.01$; n.s. = nonsignificant at $P > 0.05$, χ^2 test. The total number of individuals tested per odor set was 50, except for F-LR vs. clean air when 100 individuals were tested for response. Nonresponding predators are indicated in brackets at the right of bars.

More *P. megacephala* ants chose the side of the olfactometer with fermented pseudostem with larvae present or absent than the side with clean air ($P < 0.05$). There was no significant difference in the responses between the other odor sources tested.

The presence of pheromone traps had no effect on predator distributions in the field. The numbers of *D. abdominale* and *P. megacephala* that were recovered on the mats where pheromone traps were present compared to those that

TABLE 2. MEAN NUMBER (\pm S.E.) OF PREDATORS AND *C. sordidus* RECOVERED FROM PSEUDOSTEM PIECES PLACED AT DIFFERENT DISTANCES FROM THE PHEROMONE-BAITED TRAP IN BANANA PLOTS AT KARI, UGANDA

Predators and <i>C. sordidus</i>	Number of insects recovered from different distances (m)		
	0	0.1–5	5.1–10
<i>Labia</i> spp. (Dermaptera: Labiidae)	2.0 \pm 0.9a	0.8 \pm 0.3a	1.3 \pm 0.6a
<i>D. abdominale</i> (Coleoptera: Hydrophilidae)	4.8 \pm 1.0a	3.2 \pm 0.9a	3.3 \pm 1.0a
<i>P. megacephala</i> (Hymenoptera: Formicidae)	2.0 \pm 1.2a	0.3 \pm 0.3a	0.6 \pm 0.3a
Banana weevil larvae, <i>C. sordidus</i>	3.8 \pm 2.0a	1.1 \pm 0.4a	1.1 \pm 0.7a
Adult banana weevils, <i>C. sordidus</i>	21.5 \pm 6.3a	7.1 \pm 2.3b	6.5 \pm 1.2b

In each of the six plots, there were 10 pseudostem traps at each of the points per distance range. Means for each predator and *C. sordidus* followed by similar letter in a row are not significantly different ($P < 0.05$, SNK).

were recovered from mats less or more than 5 m from the trap were similar (Table 2). Numbers of adult weevils were significantly higher at the pheromone trap mat than on mats less than 5 m and in the range of 5.1–10 m from the trap. The numbers of weevil larvae recovered at all distances from the pheromone trap were similar.

The ants *P. megacephala* were the only predators that were captured in the pheromone-baited traps in the field. The mean number of weevils and *P. megacephala* captured in pheromone traps was 2.4 (\pm 0.4 S.E.) and 4.2 (\pm 1.2 S.E.) per plot per 3 d, respectively. There was no significant relationship between the numbers of *P. megacephala* and the number of weevils caught in pheromone-baited traps ($r^2 = 0.04$, $P = 0.61$).

DISCUSSION

Predators of the banana weevil are often observed in decomposing banana tissue such as harvested stumps, and often in tunnels where banana weevil eggs, larvae, and pupae are normally found (Koppenhofer, 1993). The results of our olfactometer experiments demonstrate that the predators *D. abdominale* and *P. megacephala* respond to volatiles from fermented banana pseudostem tissue. Attraction to the food of its host was similarly reported for several natural enemy species, such as *Leptopilina* parasitoids (Hymenoptera: Eucoilidae) (Vet, 1985; Vet and Van Opzeeland, 1985), *Anthocoris nemorum* (Heteroptera: Anthocoridae) (Dwumfour, 1992), *Orius tristicolor* (Hemiptera: Anthocoridae)

(Van Laerhoven et al., 2000), and *Chrysoperla carnea* (Neuroptera: Chrysopidae) (Reddy et al., 2002).

Many predator species are known to discriminate between volatiles from herbivore-damaged and undamaged plants (Geervliet et al., 1994; Dicke, 1999). Damaged plants become more attractive soon after the herbivores start feeding on them (Dicke et al., 1990; Turlings et al., 1990; Vet and Dicke, 1992; Geervliet et al., 1994). In our study, the predators did not discriminate between volatiles from larva-damaged pseudostem tissue with or without the larvae present. In addition, neither predator species discriminated between volatiles from weevil larvae and clean air. Similar data have been reported for other tritrophic systems as well (e.g., Turlings et al., 1990; Vet and Dicke, 1992; Geervliet et al., 1994), including a system consisting of fermenting substrates, a fungivore, and its parasitoid (Dicke et al., 1984). Fermented pseudostems that had not been damaged by weevil larvae were also attractive to the predators, which has also been recorded for parasitoids of fungivores (Dicke et al., 1984; Vet, 1985). Stimuli originating from the host habitat may influence host habitat location, although volatile stimuli originating from the host are more reliable (Vet and Dicke, 1992). Our results indicate that the predators *D. abdominale* and *P. megacephala* exploit volatiles from fermented pseudostem tissue, and that prey-related odors do not play a role in prey location.

Several species of natural enemies have been reported to use the aggregation pheromones of their hosts during host searching and location (Aldrich et al., 1984; Wiskerke et al., 1993; Hedlund et al., 1996; Bruni et al., 2000; Reddy et al., 2002; Wertheim et al., 2003, 2005). In our study, the predatory beetle *D. abdominale* was observed to respond significantly to the pheromone compared to clean air in the laboratory. Contrary to what was expected, the pheromone did not enhance the response of *D. abdominale* to volatiles from weevil-damaged pseudostem tissue in the laboratory. The ant *P. megacephala* was not attracted to the banana weevil's aggregation pheromone in the laboratory.

Our field data indicate that banana weevil aggregation pheromone has no effect on the predator distribution around the trap. Although volatiles from the herbivore itself would provide reliable information to the predator (Vet and Dicke, 1992; Wiskerke et al., 1993), the distribution of both predator species in the field was not related to the number of adult weevils captured in pheromone traps indicating that the aggregation pheromone released by male *C. sordidus* is not used by the predators in the field. In addition to the lack of response to the aggregation pheromone, generalist predators such as formicine ants have not been reported to use prey-derived chemicals as kairomones during foraging (Cosens and Toussaint, 1985). In contrast, several other predator species have been reported to use pheromones of their prey during prey searching and location (Dwumfour, 1992; Hedlund et al., 1996; Haberkern and Raffa, 2003; Steidle and van Loon, 2003).

Acknowledgments—The research was funded by the Rockefeller Foundation through a grant to International Institute of Tropical Agriculture and the Wageningen University fellowship Program. We are grateful to Dr. A.C. Oehlschlager of Chemtica International, Costa Rica, for providing the pheromone lures used in the study. We thank Dr. J.J.A. van Loon for comments on earlier versions of this manuscript. Dr. W. Tushemereirwe is acknowledged for his support. F. Sebulime, A. Namirimu, and H. Nakaro assisted in collecting weevil larvae and predators from the field.

REFERENCES

- ABERA, K. A. M. 2004. Patterns of predation by natural enemies of the banana weevil (Coleoptera: Curculionidae) in Indonesia and Uganda, Ph.D. Thesis, University of Massachusetts, Amherst.
- ABERA, K. A. M., GOLD, C. S., KYAMANYA, S., and KARAMURA, E. B. 2000. Banana weevil *Cosmopolites sordidus* Germar ovipositional preferences, timing of attack and larval survival survivorship in a mixed cultivar trial in Uganda. *Acta Hortic.* 540:487–496.
- ALDRICH, J. R., KOCHANSKY, J. P., and ABRAMS, C. B. 1984. Attractant for a beneficial insect and its parasitoids: Pheromone of the predatory spined soldier bug, *Podisus maculiventris* (Hemiptera: Pentatomidae). *Environ. Entomol.* 13:1031–1036.
- ALPIZAR, D., FALLAS, M., OEHLISCHLAGER, A. C., GONZALEZ, L. M., and JAYARAMAN, S. 1999. Pheromone-based mass trapping of the banana weevil, *Cosmopolites sordidus* (Germar) and the West Indian sugarcane weevil *Metamasius hemipterus* L. (Coleoptera: Curculionidae) in banana and sugarcane. *Memorias XIII Reunion ACORBAT*, 23–27 November 1998. Guayaquil, pp. 515–538.
- AUKEMA, B. H., DAHLSTEN, D. I., and RAFFA, K. F. 2000. Improved population monitoring of bark beetles and predators by incorporating disparate behavioural responses to semiochemicals. *Environ. Entomol.* 29:618–629.
- BERNASCONI, M. L., TURLINGS, T. C. J., EDWARDS, P. J., FRITSCHZE-HOBALLAH, M. E., AMBROSETTI, L., BASSETTI, P., and DORN, S. 2001. Response of natural populations of predators and parasitoids to artificially induced volatile emissions in maize plants (*Zea mays* L.). *Agric. For. Entomol.* 3:201–209.
- BRUNI, R., SANT'ANA, J., ALDRICH, J. R., and BIN, F. 2000. Influence of host pheromone on egg parasitism by scelionid wasps: Comparison of phoretic and nonphoretic parasitoids. *J. Insect Behav.* 13:165–173.
- CORDOVA-YAMAUCHI, L., GIANOLI, E., QUIROZ, A., and NIEMEYER, H. M. 1998. The argentine ant, *Linepithema humile* (Hymenoptera: Formicidae: Dolichoderinae) is sensitive to semiochemicals involved in the spacing behaviour in the bird chery-oat aphid *Rhopalosiphum padi* (Sternorrhyncha: Aphididae). *Eur. J. Entomol.* 95:501–508.
- COSENS, D. and TOUSSAINT, N. 1985. An experimental study of the foraging strategy of the wood ant *Formica aquilonia*. *Anim. Behav.* 33:541–552.
- DEGENHARDT, J., GERSHENZON, J., BALDWIN, I. T., and KESSLER, A. 2003. Attracting friends to feast on foes: Engineering terpene emission to make crop plants more attractive to herbivore enemies. *Curr. Opin. Biotechnol.* 14:169–176.
- DICKE, M. 1999. Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivorous arthropods? *Entomol. Exp. Appl.* 92:131–142.
- DICKE, M. and VET, L. E. M. 1999. Plant–carnivore interactions: Evolutionary and ecological consequences for plant, herbivore and carnivore, pp. 483–520, in H. Olff, V. K. Brown, and R. H. Drent (eds.). *Herbivore: Between Plants and Predator*. Blackwell and Scientific, Oxford, UK.
- DICKE, M., VAN LENTEREN, J. C., BOSKAMP, G. J. F., and VAN DONGEN-VAN LEEUWEN, E. 1984.

- Chemical stimuli in host-habitat location by *Leptopilina heterotoma* (Thomson) (Hymenoptera: Eucoilidae), a parasite of *Drosophila*. *J. Chem. Ecol.* 10:695–712.
- DICKE, M., SABELIS, M. W., TAKABAYASHI, J., BRUIN, J., and POSTHUMUS, M. A. 1990. Plant strategies of manipulating predator–prey interactions through allelochemicals: prospects for application in pest control. *J. Chem. Ecol.* 16:3091–3118.
- DRUKKER, B., SCUTAREANU, P., and SABELIS, M. W. 1995. Do anthocorid predators respond to synomones from *Psylla*-infested pear trees under field conditions? *Entomol. Exp. Appl.* 77:193–203.
- DWUMFOUR, E. F. 1992. Volatile substances evoking orientation in the predatory flowerbug *Anthocoris nemorum* (Heteroptera: Anthocoridae). *Bull. Entomol. Res.* 82:465–469.
- FATOUROS, N. E., HUIGENS, M. E., VAN LOON, J. J. A., DICKE, M., and HILKER, M. 2005. Butterfly anti-aphrodisiac lures parasitic wasps. *Nature* 433:704.
- FOSTER, S. P. and HARRIS, M. O. 1997. Behavioural manipulation methods for insect pest management. *Annu. Rev. Entomol.* 42:123–146.
- FRANCIS, F., LOGNAY, G., and HAUBRUGE, E. 2004. Olfactory responses to aphid and host plant volatile releases: (*E*)-beta-farnesene an effective kairomone for the predator *Adalia bipunctata*. *J. Chem. Ecol.* 30:741–755.
- GEERVLIEET, J. B. F., VET, L. E. M., and DICKE, M. 1994. Volatiles from damaged plants as major cues in long-range host searching by the specialist parasitoid *Cotesia rubecula*. *Entomol. Exp. Appl.* 73:289–297.
- GOLD, C. S., PENA, J. E., and KARAMURA, E. B. 2001. Biology and integrated pest management for the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). *Int. Pest Manag. Rev.* 6:79–155.
- GOLD, C. S., NIGHT, G., RAGAMA, P. E., KAGEZI, G. H., and TINZAARA, W. 2004. Field distribution for banana weevil adults in cooking banana stands in Uganda. *Insect Sci. Appl.* 24:242–248.
- HABERKERN, K. E. and RAFFA, K. F. 2003. Phlophagous and predaceous insects responding to synthetic pheromones of bark beetles inhabiting white spruce stands in the Great Lakes region. *J. Chem. Ecol.* 29:1651–1663.
- HEDLUND, K., VET, L. E. M., and DICKE, M. 1996. Generalist and specialist parasitoid strategies of using odors of adult drosophilid flies when searching for larval hosts. *Oikos* 77:390–398.
- HENDRICH, M. A. and HENDRICH, J. 1998. Perfumed to be killed: Interception of Mediterranean fruit fly (Diptera: Tephritidae) sexual signaling by predatory foraging wasps (Hymenoptera: Vespidae). *Ann. Entomol. Soc. Am.* 91:228–234.
- HOFFMEISTER, T. S. and GIENAPP, P. 1999. Exploitation of the host's chemical communication in a parasitoid searching for concealed host larvae. *Ethology* 105:223–232.
- JAMES, D. G. 2003. Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. *Environ. Entomol.* 32:977–982.
- JAMES, D. G. and PRICE, T. S. 2004. Field-testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. *J. Chem. Ecol.* 30:1613–1628.
- JAYARAMAN, S., NDIEGE, I. O., OEHLSCHELGER, A. C., GONZALES, L. M., ALPIZAR, D., FALLAS, M., and AHUYA, P. 1997. Synthesis, analysis, and field activity of sordidin, a male-produced aggregation pheromone of the banana weevil, *Cosmopolites sordidus*. *J. Chem. Ecol.* 23:1145–1161.
- KOPPENHOFER, A. M. 1993. Egg predators of the banana weevil, *Cosmopolites sordidus* (Germar) (Col., Curculionidae) in Western Kenya. *J. Appl. Entomol.* 116:352–357.
- KOPPENHOFER, A. M., SESHU-REDDY, K. V., MADEL, G., and LUBEGA, M. C. 1992. Predators of the banana weevil *Cosmopolites sordidus* Germar (Coleoptera: Curculionidae) in Western Kenya. *J. Appl. Entomol.* 114:530–533.
- LE RU, B. and MAKOSSO, J. P. M. 2001. Prey habitat location by the cassava mealybug predator *Exochomus flaviventris*: Olfactory responses to odor of plant, mealybug, plant–mealybug

- complex, and plant-mealybug-natural enemy complex, and plant-mealybug-natural enemy complex. *J. Insect Behav.* 14:557-572.
- LEWIS, W. J., NORDLUND, D. A., GUELDER, R. C., TEAL, P. E. A., and TUMLINSON, J. H. 1982. Kairomones and their use for management of entomophagous insects. XIII. Kairomonal activity for *Trichogramma* spp. of abdominal tips, excretion, and a synthetic sex pheromone blend of *Heliothis zea* (Boddie) moths. *J. Chem. Ecol.* 8:1323-1331.
- LOFGREN, C. S., GLANCEY, B. M., GLOVER, A., ROCCA, J., and TUMLINSON, F. 1983. Behaviour of workers of *Solenopsis invicta* (Hymenoptera: Formicidae) to the queen recognition pheromone: Laboratory studies with an olfactometer and surrogate queens. *Ann. Entomol. Soc. Am.* 76:44-50.
- MCGREGOR, R. R. and GILLESPIE, D. R. 2004. Olfactory responses of the omnivorous generalist predator *Dicyphus hesperus* to plant and prey odors. *Entomol. Exp. Appl.* 112:201-205.
- NINKOVIC, V., AL ABASSI, S., and PETTERSSON, S. 2001. The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. *Biol. Control* 21:191-195.
- NOLDUS, L. P. J. J., POTTING, R. P. J., and BARENDREGT, H. E. 1991. Moth sex pheromone adsorption to leaf surface: Bridge in time for chemical spies. *Physiol. Entomol.* 16:329-344.
- POWELL, W. and PICKETT, J. A. 2003. Manipulation of parasitoids for aphid pest management: Progress and prospects. *Pest Manag. Sci.* 59:149-155.
- REDDY, G. V. P., HOLOPAINEN, J. K., and GUERRERO, A. 2002. Olfactory responses of *Plutella xylostella* natural enemies to host pheromone, larva frass and green leaf cabbage volatiles. *J. Chem. Ecol.* 28:131-143.
- RENWICK, J. A. A. 1992. New directions in semiochemical research. *J. Appl. Entomol.* 114:431-438.
- SABELIS, M. W. and DICKE, M. 1985. Long range dispersal and searching behaviour, pp. 141-160, in W. Helle and M. W. Sabelis (eds.). *Spider Mites, Their Biology, Natural Enemies and Control*. World Crop Pests. Volume 1. Elsevier, Amsterdam.
- SAS, 1990. SAS Institute Inc., SAS/STAT Users' Guide Version 6, Fourth Edition, V.II.
- SCUTAREANU, P., DRUKKER, B., BRUIN, J., POSTHUMUS, M. A., and SABELIS, M. W. 1997. Volatiles from *Psylla*-infected pear trees and their possible involvement in attraction of anthocorid predators. *J. Chem. Ecol.* 23:2241-2260.
- SENGOوبا, T. 1986. Survey of banana pest problem complex in Rakai and Masaka districts, August 1986: Preliminary trip report. Ministry of Agriculture, Namulonge Research Station, Uganda. Unpublished, 10 pp.
- SHIMODA, T., TAKABAYASHI, J., ASHIRA, W., and TAKAFUJI, A. 1997. Response of predatory insect *Scolothrips takahashi* towards herbivore induced plant volatiles under laboratory and field conditions. *J. Chem. Ecol.* 23:2033-2048.
- STEIDLE, J. L. M. and VAN LOON, J. J. A. 2002. Chemoecology of parasitoids and predator oviposition behaviour, pp. 291-311, in M. Hilker and T. Meiners (eds.). *Chemecology of Insect Eggs and Egg Deposition*. Blackwell, Oxford.
- STEIDLE, J. L. M. and VAN LOON, J. J. A. 2003. Dietary specialisation and infochemical use in carnivorous arthropods: testing a concept. *Entomol. Exp. Appl.* 108:133-148.
- TINZAARA, W., KARAMURA, E. B., and TUSHEMERIRWE, W. 1999. Preliminary observations on natural enemies associated with the banana weevil *Cosmopolites sordidus* Germar in Uganda. *Infomusa* 8:28-29.
- TINZAARA, W., TUSHEMERIRWE, W., and KASHAJA, I. 2000. Efficiency of pheromones and trap types in the capture of the banana weevil *Cosmopolites sordidus* Germar in Uganda. *Uganda J. Agric. Sci.* 5:91-97.
- TINZAARA, W., DICKE, M., VAN HUIS, A., VAN LOON, J. J. A., and GOLD, C. S. 2003. Different bioassays for investigating orientation responses of the banana weevil, *Cosmopolites sordidus* (Germar) show additive effects of host plant volatiles and the synthetic pheromone. *Entomol. Exp. Appl.* 106:169-175.

- TURLINGS, T. C. J., TUMLINSON, J. H., and LEWIS, W. J. 1990. Exploitation of herbivore-induced plant odors by host seeking parasitic wasps. *Science* 250:1251–1253.
- TURLINGS, T. C. J., LOUGHRIN, J. H., MCCALL, P. J., ROSE, U. S. R., LEWIS, W. J., and TUMLINSON, J. H. 1995. How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proc. Natl. Acad. Sci. USA* 92:4169–4174.
- VAN LAERHOVEN, S., GILLESPIE, D. R., and MCGREGOR, R. R. 2000. Leaf damage and prey type determine search effort in *Orius tristicolor*. *Entomol. Exp. Appl.* 97:167–174.
- VAN LOON, J. J. A., DE VOS, E. W., and DICKE, M. 2000. Orientation behaviour of the predatory hemipteran *Perillus bioculatus* to plant and prey odors. *Entomol. Exp. Appl.* 96:51–58.
- VET, L. E. M. 1985. Olfactory microhabitat location in some eucoilid and alysiine species (Hymenoptera), larval parasitoids of Diptera. *Neth. J. Zool.* 35:720–730.
- VET, L. E. M. and DICKE, M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 32:141–172.
- VET, L. E. M. and PAPA, D. R. 1992. Effect of experience on parasitoid movement in odor plumes. *Physiol. Entomol.* 19:90–96.
- VET, L. E. M. and VAN OPZEELAND, K. 1985. Olfactory microhabitat selection in *Leptopilina heterotoma* (Thomson) (Hym.: Eucoilidae), a parasitoid of Drosophilidae. *Neth. J. Zool.* 35:497–504.
- VINSON, S. B. 1976. Host selection by insect parasitoids. *Annu. Rev. Entomol.* 21:109–134.
- VITE, J. P. and BAADER, E. 1990. Present and future use of semiochemicals in pest management of bark beetles. *J. Chem. Ecol.* 16:3031–3041.
- WERTHEIM, B., VET, L. E. M., and DICKE, M. 2003. Increased risk of parasitism as ecological costs of using aggregation pheromones: laboratory and field study of *Drosophila*–*Leptopilina* interaction. *Oikos* 100:269–282.
- WERTHEIM, B., VAN BALEN, E. J. A., DICKE, M., and VET, L. E. M. 2005. Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. *Annu. Rev. Entomol.* 50:321–346.
- WISKERKE, J. S. C., DICKE, M., and VET, L. E. M. 1993. Larval parasitoid uses aggregation pheromone of adult hosts in foraging behaviour: a solution to the reliability–detectability problem. *Oecologia* 93:145–148.