J Chem Ecol (2008) 34:719–724
DOI 10.1007/s10886-008-9479-2

Sex Pheromone of the Plant Bug, *Phytocoris calli* Knight

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Received: 28 December 2007 / Revised: 14 March 2008 / Accepted: 10 April 2008 / Published online: 9 May 2008

Abstract Female *Phytocoris calli* Knight produce a sex pheromone from metathoracic scent glands. The pheromone consists of hexyl acetate (HA; present in both sexes), with the female-specific compounds (*E*)-2-hexenyl acetate (E2HA), octyl acetate (OA), and (*E*)-2-octenyl acetate (E2OA). HA and E2OA are key components of the pheromone, since deletion of either ester from the blend resulted in a total suppression of conspecific male trap catches. However, the binary blend of HA and E2OA was only slightly attractive to males, and was significantly less active than the four-component blend. The two ternary blends, HA/OA/E2OA and HA/E2HA/E2OA, were each as attractive as the full four-component blend. Evidence from previous research on the pheromones of *Phytocoris* species suggests that the apparent chemical redundancy in the pheromone of *P. calli* may actually be involved in maintaining reproductive isolation from other sympatric species. The patterns observed for pheromones of the five *Phytocoris* species whose pheromones have been directly (*P. californicus*, *P. relativus*, *P. difficilis*, and *P. calli*) or indirectly (*P. breviusculus*) studied are discussed vis-à-vis the pheromone intractable species of *Lygus* and *Lygocoris* plant bugs.

Keywords Electroantennogram · Plant bug · *Lygus* · Infochemicals · Metathoracic scent gland · Heteroptera · Miridae

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Introduction

Plant bugs (Miridae) are the most speciose heteropteran family that includes some 10,000 described members. The mirid genus *Phytocoris* is among the largest of the plant bug genera, containing about 650 species (Schuh and Slater 1995), 200 of which occur in western North America (Stonedahl 1988). Many *Phytocoris* are predacious, with mottled color patterns that render them cryptic on the bark of trees they inhabit. Some species, however, are serious pests of fruit and nuts (Wheeler 2001). Despite the abundance and agricultural importance of plant bugs, only 10 or so sex pheromones of mirids have been identified (Millar 2005). Millar (2005), somewhat casually, noted that mirid pheromones fall into two groups: "The first (e.g., *Campylomma verbasci* and *Phytocoris* spp.) is characterized by pheromones that were straightforward to identify, whereas pheromones of the second group, including *Lygus* and *Lygocoris* spp., have proven to be remarkably intractable despite decades of effort by numerous research groups." Since Millar's review, Innocenzi et al. (2005) reported that females of the European tarnished plant bug, *Lygus rugulipennis* Poppius, attract males with a blend of *(E)*-4-oxo-2-hexenal and hexyl butyrate, with the key to synthetic pheromone activity being the slow release of the active compounds; at higher release rates, the *(E)*-4-oxo-2-hexenal/ hexyl butyrate blend did not attract bugs (Innocenzi et al. 2004). For rice leaf bug, *Trigonotylus caelestialium* (Kirkaldy) (Miridae), high pheromone concentrations were also inhibitory (Kakizaki and Sugie 2001).

The first sex pheromone identifications of *Phytocoris* spp. were for two western US species, *P. californicus* (Millar and Rice 1998) and *P. relativus* (Millar et al. 1997). Our elucidation (Zhang and Aldrich 2003a) of the pheromone of the eastern US species, *Phytocoris difficilis*, and

concomitant inferences to the pheromone composition of the sympatric species, *P. breviusculus*, by default make the sex pheromones of *Phytocoris* spp. the best known of all 1400 mirid genera (Schuh and Slater 1995).

The present pheromone investigation of a fifth member of the genus *Phytocoris* was undertaken after the fortuitous discovery of this species by one of us (Q-HZ) in residential Spokane, WA, USA. Although *P. calli* is apparently not an economically significant pest or predator, we undertook the study to expand our understanding of the pheromone systems of these insects, and perhaps, to obtain new information that may suggest fruitful approaches to deciphering the pheromones of species in the group of "intractable" mirids.

Methods and Materials

Adult Insects and Preparation of Extracts *Phytocoris calli* adults were collected from residential porch lights around 9:30 P.M.—midnight during the summer of 2007 in Spokane, WA, USA. All bugs were dissected within 10–20 hr of capture for extraction of the metathoracic scent glands (MSG) and subsequent electrophysiological and chemical analyses. MSGs from male and female *P. calli* were excised from CO_2-anesthetized bugs submerged in tap water, and the glands were extracted individually in 50 µl of methyl-*tert*-butyl ether. Extracts were kept at −20 °C until analysis.

Gas Chromatography-Electroantennogram Detector (GC-EAD) and GC-Mass Spectrometry (GC-MS) Analyses Mirid extracts were analyzed in the splitless mode with a Varian CP-3800 GC equipped with a polar column (HP-INNOWax; 30 m×0.53 mm×1.0 µm; Agilent Technologies), and a 1:1 effluent splitter that allowed simultaneous flame ionization and electroantennogram detection of separated compounds. Helium was used as the carrier gas, and the injector temperature was 220 °C. The column temperature was 50 °C for 1 min, rising to 240 °C at 10 °C min^{-1}, and then held for 10 min. The outlet for the electroantennogram detector (EAD) was held in a humidified air-stream flowing at 0.5 m sec^{-1} over the antennal preparation. A glass capillary indifferent electrode was filled with Beadle-Ephrussi Ringer solution (Zhang et al. 2000), grounded via a silver wire, and inserted into the open side of an excised mirid head. A similar recording electrode, connected to a high-impedance DC amplifier with automatic baseline drift compensation, was inserted over an antenna (the tip of the antenna was excised). Antennal signals were stored and analyzed on a computer equipped with a serial IDAC interface box and the program EAD ver. 2.5 (Syntech, Hilversum, The Netherlands). The MSG extracts were analyzed by GC-MS on an HP 6890 GC series coupled with an HP 5973 Mass Selective Detector by using the same type of GC column and conditions as described above. Compounds were identified by comparison of retention times and mass spectra with those of standards.

Chemical Standards The following authentic standards were obtained from commercial sources or were synthesized: 1-hexanol, (*E*)-2-hexenol, (*E*)-2-octenol, nonanal, hexyl acetate (HA), hexyl propanoate, octyl acetate (OA), and octyl butyrate (Aldrich Chemical Co., Milwaukee, WI, USA); (*E*)-2-octenyl acetate (E2OA), hexyl butyrate, (*E*)-2-hexenyl butyrate, (Bedoukian Research Inc., Danbury, CT, USA); heptyl acetate (Eastman Organics); and (*Z*)-3-octenyl acetate (J. G. Millar, Univ. California, Riverside). (*E*)-2-Hexenyl acetate (E2HA) was synthesized as described previously (Aldrich et al. 1997, 1999).

Field Trapping Two field-trapping experiments were carried out from August to September 2007 in a residential backyard with several apple, cherry, and other angiosperm trees that are common in residential Spokane, WA. Pherocon VI traps (Trécé Inc., Adair, OK, USA) with removable sticky inserts and baited with 10–80 µl of individual or mixed neat test compounds loaded onto gray rubber septa (5 mm sleeve-type, The West Co., Lititz, PA, USA) were used in the trials. Rubber septa were replaced every week. Traps were hung 1.5 m above the ground on a fence, ca. 5 m apart within each trap line. For each trapping experiment, one set of traps was deployed with their initial trap positions being random. The trap positions were systematically rotated after each visit, based on a procedure of Latin-square design (Byers 1991), so that traps appeared at least once per location. To minimize positional effects, mirid collections and trap rotations were carried out when ≥ 2 mirids were caught in a trap. Each replicate lasted several days to 1 wk, depending on mirid flight activity. Sticky inserts were taken to the laboratory for recording of species, gender, and number of bugs. Experiment 1 (August 7 to September 11, 2007) tested six treatments: a mixture of the EAD-active female MSG volatiles (4-compound "full blend"), subtraction of each EAD-active component from the full blend, and a blank. Experiment 2 (August 25 to September 24, 2007) was conducted to determine the potential activity of the two key EAD-active compounds, hexyl acetate, (*E*)-2-octenyl acetate, and their binary blend in comparison with the four-compound "full blend".

Statistical Analysis Trap catch data were transformed by log $(x+1)$ to fit the assumption of homogeneity of variance for analysis of variance (ANOVA). Means were compared by ANOVA followed by the Ryan–Einot–Gabriel–Welsh (REGW) multiple Q test (SPSS 8.0 for Windows) at $\alpha = 0.05$ (Day and Quinn 1989).

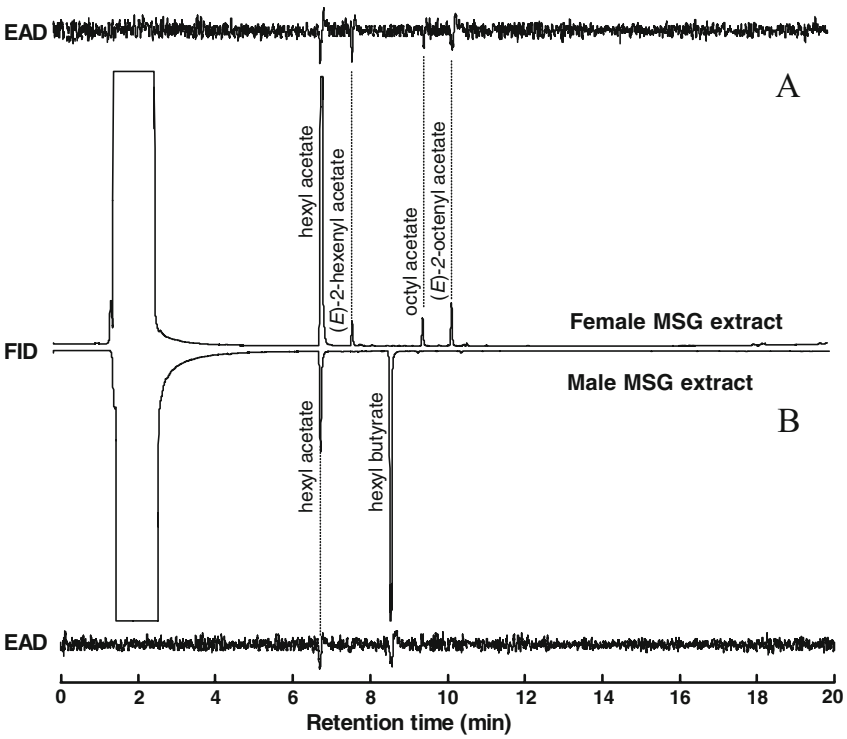

Fig. 1 Coupled flame ionization (FID) and electroantennogram (EAD) detection of *Phytocoris calli* male antennae to metathoracic scent gland (MSG) extracts of conspecific females (A) and males (B)

Results

GC-EAD and Chemical Identifications Antennae of *P. calli* males responded strongly to one major and three minor components from female MSG extracts. These compounds were identified by GC-MS as HA, E2HA, OA, and E2OA (in a ratio of ca. 20:1:1:1), respectively (Fig. 1A and Table 1). In male MSG extracts, there were only two major volatile components, HA and hexyl butyrate, each of which elicited strong responses from male antennae (Fig. 1B, Table 1). In addition to the EAD-active compounds, several other minor or trace amounts of chemicals also were

Table 1 Metathoracic scent gland components identified from *Phytocoris calli*

Chemical	Relative amount (%) ± SE		Male EAD activity
	Females (N=3)	Males (N=3)	
Hexyl acetate	**86.87±0.57**	**25.36±7.01**	***
***(E)*- 2-Hexeny acetate**	**3.16±0.37**	0.05±0.03	***
Hexyl propanoate		0.51±0.44	
1-Hexanol	0.81±0.16	0.19±0.08	
Heptyl acetate	0.05±0.03	0.02±0.02	
Nonanal		0.10±0.03	
(E)-2-Hexenol	0.28±0.21		
Hexyl butyrate	0.21±0.10	**73.05±7.56**	***
(E)- 2-Hexeny butyrate		0.46±0.05	
Octyl acetate	**3.58±0.41**		***
(Z)-3-Octenyl acetate	0.10±0.02		
***(E)*-2-Octenyl acetate**	**4.82±0.30**		***
(E)-2-Octenol	0.11±0.01		
Octyl butyrate		0.26±0.06	

Data for major and EAD-active compounds are in bold.

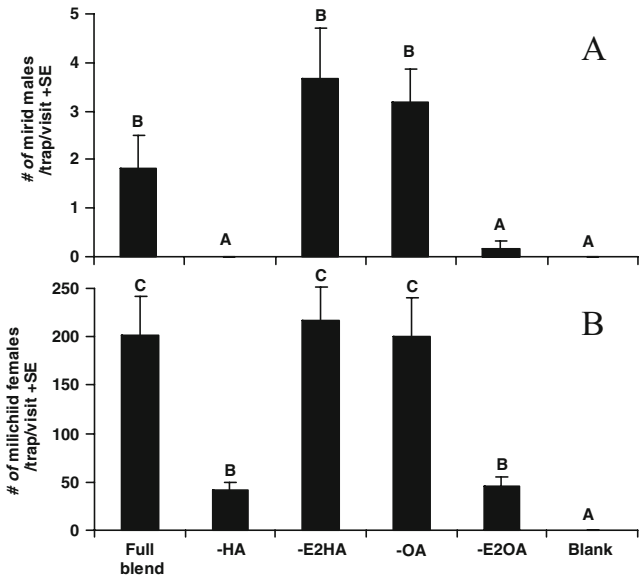

Fig. 2 Captures of *Phytocoris calli* males (A) and *Leptometopa latipes* females (B) in traps baited with full blend [HA (50 µl)/E2HA (10 µl)/OA (10 µl)/E2OA (10 µl)] or ternary blends of the four EAD-active female MSG volatiles (*HA* hexyl acetate, *E2HA* (*E*)-2-hexenyl acetate, *OA* octyl acetate, *E2OA* (*E*)-2-octenyl acetate). Means (N=6) followed by the same letter are not significantly different (P>0.05), ANOVA on log (x+1), followed by the Ryan–Einot–Gabriel–Welsh (REGW) multiple Q test

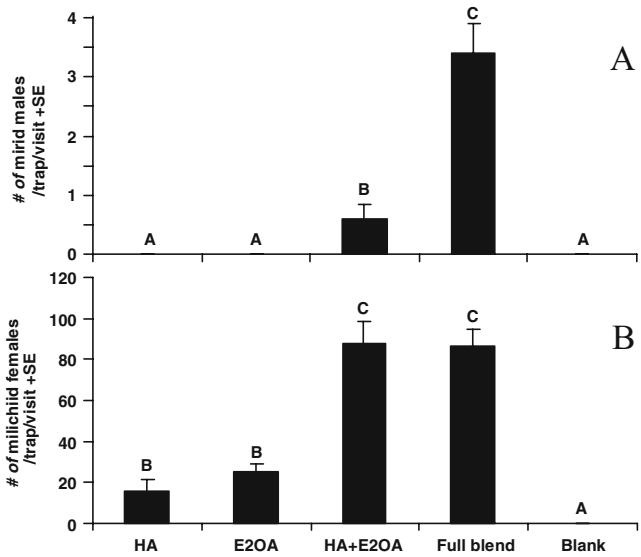

Fig. 3 Captures of *Phytocoris calli* males (A) and *Leptometopa latipes* females (B) in traps baited with hexyl acetate (50 µl), (*E*)-2-octenyl acetate (10 µl), and their binary blend (50 µl+10 µl) in comparison with the four-compound "full blend" (HA [50 µl]/E2HA [10 µl]/OA [10 µl]/E2OA [10 µl]). Means (N=5) followed by the same letter are not significantly different (P>0.05), ANOVA on log (x+1), followed by the Ryan–Einot–Gabriel–Welsh (REGW) multiple Q test

identified by GC-MS, including 1-hexanol and heptyl acetate from both sexes, (*E*)-2-hexenol, (*E*)-2-octenol, and (*Z*)-3-octenyl acetate from females, and hexyl propanoate, nonanal, (*E*)-2-hexenyl butyrate, and octyl butyrate from males (Table 1).

Field Experiments In experiment 1, traps baited with the blend of the four EAD-active components ("full blend") of female MSG volatiles (HA/E2HA/OA/E2OA) caught significant numbers of *P. calli* males (P<0.05, Fig. 2A). Subtraction of E2HA or OA from the four-component "full blend" had no effect on trap catches. However, deletion of HA or E2OA from the blend entirely eliminated catches of *P. calli* males (Fig. 2A), indicating that these two compounds may be key components of the pheromone. In experiment 2, traps baited with HA or E2OA alone caught a non-significant number of bugs, while traps baited with the binary blend caught some *P. calli* males, but significantly (>4 times) less in than traps baited with the four-component "full-blend" (Fig. 3A).

In addition to male bugs, large numbers of female milichiid flies (*Leptometopa latipes* Meigen) were captured in most traps. As for catches of mirid males, traps baited with the "full-blend" caught large numbers of *L. latipes* females, and deletion of E2HA or OA from the four-component "full blend" had no effect on the catches of flies. However, removal of HA or E2OA from the blend dramatically reduced trap catches of the milichiid females (Fig. 2B). Traps baited with HA or E2OA alone caught low numbers of milichiid females; however, the binary blend of these two compounds elicited much greater trap catch than did either compound individually (Fig. 3B). There was no difference in catches of milichiid females between traps baited with the binary blend or the four-compound "full-blend.".

Most mirids (males from traps or lights or females from lights) were collected or trapped during the first half of the scotophase (after sunset to midnight), whereas milichiids were captured exclusively during the daytime.

Discussion

Phytocoris sex pheromones, including that of *P. calli*, consist of HA, which is produced by both sexes, plus related female-specific esters (Millar 2005) (Table 2). Pheromone compounds are produced by adult females in the MSG (Zhang and Aldrich 2003a). Redundant pheromone esters in sympatric *Phytocoris* species (Millar et al. 1997; Millar and Rice 1998) and *P. calli* may help maintain reproductive isolation, although more research is needed to verify whether this possibility is correct or not.

Traps baited with HA and E2OA also were strongly attractive to the scavenging milichiid fly, *Leptometopa latipes* (Fig. 3B). Similar synergistic attraction between hexyl butyrate and *(E)*-2-hexenyl butyrate to *L. latipes* also was reported in a previous study of the tarnished plant bug, *Lygus lineolaris* (Zhang and Aldrich 2004). These results

Table 2 Known sex pheromone components (*), sex attractants (o), and an attraction-inhibitor (x) of *Phytocoris* mirids

Chemicals	*P. relativus*	*P. californicus*	*P. difficilis*	*P. breviusculus*	*P. calli*
Hexyl acetate	*	*	*	o	*
(*E*)-2-Hexenyl acetate			*	x	*
Octyl acetate					*
(*E*)-2-Octenyl acetate		*	*	o	*
(*E*)-2-Octenyl butyrate	*	x			
References	1	2	3	3	4

1 Millar et al., 1997; *2* Millar and Rice, 1998; *3* Zhang and Aldrich 2003a; *4* this paper.

suggest that milichiid females may use pheromonal compounds from plant bugs as kairomones to find freshly injured or dead bugs on which to feed.

The major volatiles from males, whether from aeration or MSG dissection, are almost identical among the five *Phytocoris* species studied, with hexyl butyrate being the dominant component (Millar et al. 1997; Millar and Rice 1998; Zhang and Aldrich 2003a, b) (Table 1). Hexyl butyrate elicited strong EAD responses from antennae of male *P. calli* (this paper), *P. difficilis*, and *P. breviusculus* (Zhang and Aldrich 2003a, b). For *P. difficilis*, we demonstrated that hexyl butyrate totally stopped attraction of males to the female-produced sex pheromone. We consider this signal to be a natural anti-sex pheromone, perhaps that repels other males from further mating attempts, or for precluding a male from remating with a female. A similar inhibitory effect of hexyl butyrate also has been reported in two other mirids, *Lygocoris pabulinus* (Groot et al. 2001) and *Lygus lineolaris* (Zhang et al. 2007). It remains to be determined whether hexyl butyrate is an anti-sex pheromone for *P. calli*. The phenomenon of a male-to-male inhibitory pheromone was reported long ago as one likely mode of action for hair pencil secretions of male Lepidoptera (Hirai et al. 1978).

Intractable and easily identified mirid pheromones are all female-produced, and apparently based on compounds (especially esters) biosynthesized in the MSG (Millar 2005). The MSG is characteristic of "true bugs" (Heteroptera) and is usually considered to be a defensive gland (Aldrich 1988). However, males or females of various seed bugs (Lygaeidae) (Aldrich et al. 1997, 1999; Marques et al. 2000) and broad-headed bugs (Alydidae) (Leal et al. 1995, 1996; Aldrich et al. 2000) release attractant pheromones from the MSG, while retaining the ability to release chemical irritants from the MSG when attacked by predators. In most bugs, the MSG consists of a pair of lateral accessory glands and a median reservoir in which the principal irritants (aldehydes and acids) are enzymatically derived from esters produced in the accessory glands (Aldrich et al. 1978). The sexual role of the MSG is evidently associated with compartmentalization of the MSG, such that the insects are able to release pheromone directly from the lateral accessory glands or accumulate defensive compounds in the median reservoir until needed for defense.

In mirids, species of *Phytocoris* and *Campylomma* seem to express the sexual manifestations of the MSG primarily, with little capacity to produce aldehydic or acidic allomones. At the other extreme is the aposematic mirid, *Lopidea robiniae* (Uhler), with a MSG secretion dominated by *(E)*-2-hexenal (Staples et al. 2002). Judging by the coexistence of *(E)*-4-*oxo*-2-hexenal with hexyl and *(E)*-2-hexenyl butyrates in the MSG of *Lygus* bugs (Aldrich et al. 1988; Innocenzi et al. 2004), the defensive and sexual roles of the MSG seem more entwined for *Lygus* bugs than is the case for *Phytocoris* spp., thus complicating the task of deciphering the sex pheromones.

Acknowledgments We thank T. J. Henry (Miridae) and Allen L. Norrbom (Milichiidae), Systematic Entomology Laboratory (SEL), USDA-ARS, Beltsville, Maryland, for identification of mirid and milichiid species, respectively. We are also grateful to J. G. Millar, Department of Entomology, University of California at Riverside, for the gift of chemical standards.

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