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SEX-RELATED PERCEPTION OF INSECT AND PLANT VOLATILES IN *Lygocoris pabulinus*

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Abstract—We recorded electroantennograms of male and female *Lygocoris pabulinus* antennae to 63 insect and plant volatiles. EAGs were between 100 and 500 μV. Overall, male EAGs were about twice the size of female EAGs. In both sexes, largest EAGs were recorded to (*E*)-2-hexenyl butanoate and (*E*)-2-hexen-1-ol. Response profiles were similar in both sexes. However, male antennae were more sensitive to a number of esters, especially the butanoates and pentanoates. Female antennae were more sensitive to nine of the 19 plant volatiles, i.e., to hexan-1-ol, heptan-1-ol, 1-octen-3-ol, 2-heptanone, (*R*)-carvone, linalool, geraniol, nerol, and methyl salicylate. Sexual differences in responses suggest that males are more sensitive to insect-produced pheromone-type compounds, whereas females are more sensitive to plant compounds for their orientation towards oviposition sites.

Key Words—Heteroptera, Miridae, green capsid bug, sex pheromone, electroantennogram, odors, plant volatiles, esters, (*E*)-2-hexenyl butanoate, (*E*)-2-hexen-1-ol.

INTRODUCTION

Female-produced sex pheromones are present in at least 10 mirid bug species (Strong et al., 1970; King, 1973; Smith, 1977; Boivin and Steward, 1982;

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Graham, 1987; Graham et al., 1987; Smith et al., 1991, 1994; Chinta et al., 1994; Millar et al., 1997; Millar and Rice, 1998). However, identification of the components and their active ratio has been elucidated in three species only (Smith et al., 1991; Millar et al., 1997; Millar and Rice, 1998). The pheromones of these species have been identified by analyzing chemical differences between male and female extracts. A sex pheromone from the green capsid bug *Lygocoris pabulinus* (L.) (Heteroptera: Miridae) is active in the field, where males are attracted to traps baited with virgin live females caged on a potato shoot (Blommers et al., 1988). The pheromone of this species is needed for development of integrated pest management in fruit orchards in northwestern Europe where *L. pabulinus* is a serious pest (Blommers, 1994; Ravn and Rasmussen, 1996). Pheromone traps are widely used for monitoring lepidopterous pests (e.g., Minks and Van Deventer, 1992), and since 1990, also for monitoring the mirid pest *Campylomma verbasci* (McBrien et al., 1994). In our quest to identify the sex pheromone of *L. pabulinus*, consistent chemical differences between the sexes have not yet been found (unpublished data). In order to screen for potential attractants, perception of a number of volatiles was studied by means of electroantennogram (EAG) recordings.

The EAG technique is regularly used as a bioassay to test olfactory perception in insects (e.g., Dickens et al., 1993a,b; Visser and Piron, 1995; Visser et al., 1996). In mirids, the technique has been applied to *Lygus lineolaris* (Chinta et al., 1994; Dickens et al., 1995), revealing olfactory receptors on the antennae that are responsive to insect and plant volatiles.

Two groups of volatiles were chosen for testing. The first consisted of esters that have been identified in other bug species (Knight et al., 1984; Graham, 1988; Smith et al., 1991; Chinta et al., 1994; Aldrich, 1995; Dickens et al., 1995; Millar et al., 1997; Millar and Rice, 1998). The second consisted of general plant volatiles, of which some may play a synergistic role in the sexual attraction of *L. pabulinus* (Groot et al., 1996). EAGs of both males and females were recorded because volatiles eliciting larger EAGs in males could indicate a role in sexual attraction.

METHODS AND MATERIALS

Insects. L. pabulinus was reared under summer conditions (22 ± 2°C, 65 ± 5% relative humidity, 18L : 6D) on potted potato plants (Blommers et al., 1997). Males and females were separated 0–2 days after the final molt to adult. *L. pabulinus* becomes sexually active about four days after the final molt (Groot et al., 1998a), and so for EAG recordings, sexually mature, virgin adults 4–10 days old were used. Prior to EAG recordings, bugs were collected from a rearing cage containing potato plants and sexed conspecifics.

Chemicals. Olfactory stimuli used are listed in Table 1. A series of esters was tested, comprising acetates, propionates, butanoates, pentanoates, and hexanoates. A series of plant-related volatiles were also tested, comprising one arbitrarily chosen nitrile (4-methoxy phenylacetonitrile), methyl salicylate, six monoterpenes, three ketones, five alcohols, and one aldehyde. (*E*)-2-Hexenyl acetate and (*Z*)-3-hexenyl acetate were tested in both series, since these compounds are insect-produced esters as well as general green leaf volatiles (see references in Table 1). Chemicals were obtained from commercial sources or were synthesized (Table 1). Newly synthesized esters [except (*E*)-2-butenyl and (*E*)-2-octenyl esters] were prepared by refluxing a twofold excess of the appropriate carboxylic acid with the corresponding alcohol for 5 hr, followed by base extraction and partition into diethyl ether with removal of the solvent in vacuo. The (*E*)-2-butenyl and (*E*)-2-octenyl esters were prepared by refluxing 1 equivalent (eq) of the acid chloride with 1 eq of the corresponding alcohol for 1 hr, following Vogel (1989). (*E*)-2-Butenyl alcohol contained ~5% of the *Z* isomer; (*E*)-2-octenyl alcohol was prepared by reducing (*E*)-2-octenal with $NaBH_4$. Purity was determined by GC-MS. The (*E*)-2-butenyl esters contained ~5% of the *Z*-isomer, which was in correspondence with the 5% *Z* isomer in the starting material. For the EAG recordings, all chemicals were dissolved in paraffin oil at 1% v/v, following Visser and Piron (1995).

Antennal Preparation. An individual bug was anesthetized with CO_2 for a few seconds. The head was clipped off, and the distal tip of the terminal segment of one antenna cut off. The ground electrode was inserted into the open side of the head, and the recording electrode was sleeved over the tip of the antenna. The electrodes consisted of two glass capillaries filled with 0.1 M KCl solution. *L. pabulinus* antennae prepared this way showed a life-span of 15–30 min.

EAG Protocol. Ag–AgCl wires in the glass electrodes connected the antennal preparation to the amplification and recording devices consisting of an input probe and DC amplifier (Grass HIP 16A and P16D, rise time set at 30 msec), an oscilloscope (Philips PM3302), and a transient recorder (Krenz TRC 4010, 12 bits ADC) connected to a personal computer (Estate 80386 and 80387). Stimulation cartridges were prepared by applying 25 μl of each paraffin oil solution onto a piece of filter paper that was subsequently placed in a Pasteur pipet. The antenna, placed perpendicularly 1–2 cm in front of a glass tube, was stimulated for 2 sec by pushing air (1 ml/sec) through the pipet into the tube with a continuous airflow of 40 cm/sec (30 ml/sec). The interstimulus time interval was 30 sec. In order to compare responses within an individual and among individuals, all responses were normalized by using a standard of 1% (*E*)-2-hexenal in paraffin oil. The stimulation of each chemical was, thus, preceded and followed by the standard.

All chemicals were tested with 11–14 different individuals of each sex. Chemicals were tested in series of 10–18 compounds per antenna, each time

TABLE 1. VOLATILES USED FOR EAG RECORDINGS OF *L. pabulinus* MALES AND FEMALES

Volatile	Source	Purity (%)	Referred to as insect-produced odor[a]	Referred to as plant-produced odor[a]
Esters				
Butyl acetate	Acros[b]	>99	5	
(*E*)-2-Butenyl acetate	[c]	93		
Pentyl acetate	Roth[d]	>99		
Hexyl acetate[e]	Fluka[f]	99	1, 2a, 3a, 4, 5, 6	22
(*E*)-2-Hexenyl acetate	ICN/K&K[g]	99	2, 3, 4, 6, 7	23, 24, 25
(*Z*)-3-Hexenyl acetate	Roth	99	2, 7	19, 20, 21, 22, 24, 25, 26
Heptyl acetate	Roth	>99		
Octyl acetate	Roth	>99	2, 3, 5	
(*E*)-2-Octenyl acetate	[c]	62[h]	2, 3a, 4, 5, 7, 8	
Butyl propionate	Acros	>99		
(*E*)-2-Butenyl propionate	[c]	93		
Pentyl propionate	[c]	97		
Hexyl propionate	Roth	>99		19
(*E*)-2-Hexenyl propionate	ICN/K&K	98		25
(*Z*)-3-Hexenyl propionate	ICN/K&K	>99		25
Heptyl propionate	[c]	96		
Octyl propionate	[c]	96		
(*E*)-2-Octenyl propionate	[c]	79[i]		
Butyl butanoate	Roth	>99	1a, 4, 5, 6	
(*E*)-2-Butenyl butanoate	[c]	93	1a	
Pentyl butanoate	Roth	>99		
Hexyl butanoate[e]	Roth	>99	1, 2, 3, 4, 5, 6, 9	23
(*E*)-2-Hexenyl butanoate[e]	[c]	85[i]	6, 10	
(*Z*)-3-Hexenyl butanoate	[c]	92		19, 21, 20
Heptyl butanoate	[c]	97		
Octyl butanoate	Roth	>99		

(*E*)-2-Octenyl butanoate	*c*	92	2a, 3	
Butyl pentanoate	*c*	95		
(*E*)-2-Butenyl pentanoate	*c*	95		
Pentyl pentanoate	*c*	96		
Hexyl pentanoate	*c*	95		
(*E*)-2-Hexenyl pentanoate	*c*	86[i]		
(*Z*)-3-Hexenyl pentanoate	*c*	97		
Heptyl pentanoate	*c*	93		
Octyl pentanoate	*c*	93		
(*E*)-2-Octenyl pentanoate	*c*	88[i]		
Butyl hexanoate	Roth	>99	4	23
(*E*)-2-Butenyl hexanoate	*c*	95		
Pentyl hexanoate	*c*	97		
Hexyl hexanoate	*c*	97	5	
(*E*)-2-Hexenyl hexanoate	*c*	92	5, 11	
(*Z*)-3-Hexenyl hexanoate	*c*	84[i]		
Heptyl hexanoate	*c*	97		
Octyl hexanoate	*c*	97		
(*E*)-2-octenyl hexanoate	*c*	92		
Aldehydes				
Hexanal	Fluka	98	4, 7	19, 25, 26
(*E*)-2-Hexenal (standard)	Roth	96	4, 6, 7, 11, 12, 13, 14, 15, 16	6, 19, 22, 24, 25, 26, 27
Alcohols				
Hexan-1-ol[e]	Fluka	99	1, 3, 4, 7	10, 19, 21, 22, 25, 26, 27
(*E*)-2-Hexen-1-ol	Roth	97	7	19, 22, 24, 25, 26, 27
(*Z*)-3-Hexen-1-ol	Roth	97		6, 19, 20, 22, 25, 26, 27
Heptan-1-ol	Fluka	99		6, 22, 25
1-Octen-3-ol	Fluka	98		(1), 21, 25
Ketones				
2-Heptanone	Aldrich[j]	98	8, 12	25, 26
3-Heptanone	Aldrich	98		25
3-Octanone	Aldrich	99		25

TABLE 1. CONTINUED

Volatile	Source	Purity (%)	Referred to as insect-produced odor[a]	Referred to as plant-produced odor[a]
Monoterpenes				
(1S)-β-Pinene	Fluka	99	7, 17	19, 25, 26
Myrcene	Roth	91	17	20, 22, 25
(*R*)-Carvone	Aldrich	98		25, 26
Linalool	Fluka	97	7, 16, 18	6, 21, 22, 20, 25, 26
Geraniol	Fluka	99		6, 22, 25, 26
Nerol	Aldrich	97		6, 25, 26
Aromatics				
Methyl salicylate	Fluka	99		20, 21, 24
4-Methoxylphenylacetonitrile	Fluka	97		28

[a]Numbers in the list refer to the following references: **1.** Smith *et al.* (1991) (**1a:** sex pheromone compound *Campylomma verbasci*; **1:** from mold growing on mullein); **2.** Millar et al. (1997) (**2a:** sex pheromone compound *Phytocoris relativus*); **3.** Millar and Rice (1998) (**3a:** sex pheromone compound *Phytocoris californicus*); **4.** Aldrich and Yonke (1975); **5.** Knight et al. (1984); **6.** Chinta et al. (1994); **7.** Aldrich (1995); **8.** Blum (1985): **9.** Graham (1988); **10.** Dickens et al. (1995); **11.** Leal and Kadosawa (1992); **12.** Blum (1996); **13.** Ishiwatari (1974); **14.** Ishiwatari (1976); **15.** Borges and Aldrich (1992); **16.** Aldrich (1988); **17.** Staddon (1990); **18.** Aldrich et al. (1993); **19.** Bernays and Chapman (1994); **20.** Bolter et al (1997); **21.** Dicke et al. (1990); **22.** Dickens et al. (1993b); **23.** Fein et al. (1982); **24.** Takabayashi et al. (1994); **25.** Visser and Piron (1995); **26.** Visser et al. (1996); **27.** Visser et al. (1979); **28.** Cole (1976).

[b]Geel, Belgium.

[c]Synthesized de novo.

[d]Karlsruhe, Germany.

[e]Compound found in both sexes of *L. pabulinus* (F.P. Drijfhout, unpublished research).

[f]Buchs, Switzerland.

[g]Costa Mesa, California.

[h]About ~32% of the rest product is 1-octenyl acetate, the remaining 5% consists of the alcohol and the acid from which (*E*)-2-octenyl acetate was synthesized.

[i]The remaining percentage consists of the starting compounds, i.e., the alcohol and the acid, from which the listed compounds were synthesized.

[j]Zwijndrecht, The Netherlands.

offered in a different order. As a control, an EAG to 25 μl of paraffin oil was recorded during each series. EAGs of all chemicals were expressed as percentage responses relative to the responses of the adjacent standards. If the magnitude of the EAG of the adjacent standard was below 100 μV, the EAG was omitted. Means and 95% confidence intervals were calculated for each compound. Differences in volatility among compounds were not corrected for.

Statistical Analysis. The series of 45 esters was analyzed separately from the series of plant compounds. (*E*)-2-Hexenyl acetate and (*Z*)-3-hexenyl acetate were tested and analyzed in both series. Both series were analyzed by using a mixed linear model, fitted with the procedure MIXED of the computer program SAS (1997) version 6.12. Data were square-root transformed after addition of a constant in order to normalize and stabilize the variance. After fitting the mixed linear model with fixed main effects and interaction for gender and chemicals and a random effect for the antenna, the following comparisons were made:

- A1: Response to the control paraffin oil versus response to each of the tested esters in female antennae.
- A2: Response to the control paraffin oil versus response to each of the tested esters in male antennae.
- A3: Female versus male antennal response to each of the tested esters.
- B1: Response to the control paraffin oil versus response to each of the tested plant compounds in female antennae.
- B2: Response to the control paraffin oil versus response to each of the tested plant compounds in male antennae.
- B3: Female versus male antennal response to each of the tested plant compounds.

The significance level of each series was corrected for multiple comparisons through the Bonferroni method, and, therefore, set at: for A1 and A2, $P = 0.05/45 = 0.0011$; for A3, $P = 0.05/46 = 0.0011$; for B1 and B2, $P = 0.05/20 = 0.0025$, and for B3, $P = 0.05/22 = 0.0023$.

RESULTS

The absolute peak EAG response of *L. pabulinus* to the standard (*E*)-2-hexenal was larger in males than in females; the male response was -308 ± 142 μV (mean ± SD; $N = 9$), the female response was -149 ± 51 μV (mean ± SD; $N = 9$).

Esters (Figure 1, Table 2)

A1. Responses in Female Antennae. Female antennae were most responsive to (*E*)-2-hexenyl butanoate (166 ± 13% (mean ± CI) relative to the stan-

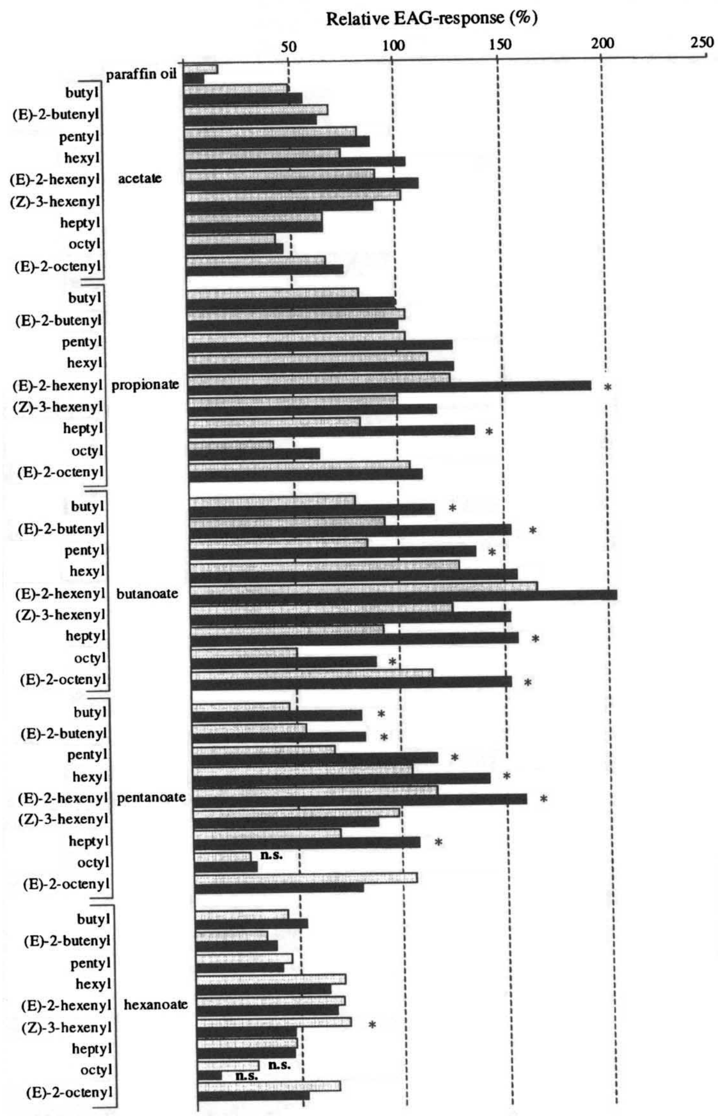

FIG. 1. EAG responses of male and female *L. pabulinus* to the series of esters. The response bars are based on the back-transformed least-square means. Grey: EAG response of female antennae; black: EAG response of male antennae; n.s.: EAG response not significantly different from the response to the control paraffin oil. *EAG response significantly different between the sexes (after correcting the significance level for multiple comparisons through the Bonferroni method). See text for further explanation.

TABLE 2. ANOVA TABLE OF SERIES OF ESTERS (RESPONSE PROFILES ARE SHOWN IN FIGURE 1)

Tests of fixed effects, source	NDF[a]	DDF[b]	Type III F	Pr > F	Covariance parameter	Estimate
Gender	1	122	27.28	0.0001	Antenna (gender)	0.5603
Chemical	45	1002	146.98	0.0001	Residual	0.9225
Gender × chemical	45	1002	8.47	0.0001		

[a]Numerator degrees of freedom.
[b]Denominator degrees of freedom.

dard). Slightly lower responses were elicited by hexyl propionate, (*E*)-2-hexenyl propionate, hexyl butanoate, (*E*)-3-hexenyl butanoate, (*E*)-2-octenyl butanoate, hexyl pentanoate, (*E*)-2-hexenyl pentanoate, and (*E*)-2-octenyl pentanoate. Lowest responses were recorded for the octyl esters and hexanoates, as in the male antennae. Octyl pentanoate and octyl hexanoate did not elicit a significant EAG response in female antennae.

A2. Responses in Male Antennae. The EAG profile of the males showed a distinct sensitivity for the array of esters. Largest EAGs were elicited by (*E*)-2-hexenyl propionate (195 ± 15% mean ± CI), and (*E*)-2-hexenyl butanoate (204 ± 15% mean ± CI). (*E*)-2-Butenyl butanoate, hexyl butanoate, (*Z*)-3-hexenyl butanoate, heptyl butanoate, (*E*)-2-octenyl butanoate, hexyl pentanoate, and (*E*)-2-hexenyl pentanoate elicited EAGs around 150% relative to the standard in male *L. pabulinus* antennae. The smallest EAGs were recorded in response to octyl esters and hexanoates. Octyl hexanoate did not elicit a significant EAG in male antennae.

A3. Female versus Male Antennal Responses. Regarding the five groups of esters tested, none of the acetates showed significant differences in EAGs between female and male antennae. Of the propionates, (*E*)-2-hexenyl propionate and heptyl propionate elicited larger responses in males. Most butanoates also elicited larger relative responses in males, except hexyl butanoate, (*E*)-2-hexenyl butanoate, and (*Z*)-3-hexenyl butanoate, for which there was no difference between sexes. Male antennae responded more to most of the pentanoates as well, although both sexes responded similarly to (*Z*)-3-hexenyl pentanoate, octyl pentanoate, and (*E*)-2-octenyl pentanoate. The hexanoates did not elicit larger EAGs in male antennae. (*Z*)-3-Hexenyl hexanoate even elicited a larger relative EAG response in female antennae.

Plant Volatiles (Figure 2, Table 3)

B1. Responses in Female Antennae. The largest EAGs in female antennae were elicited by (*E*)-2-hexen-1-ol (150 ± 18% mean ± CI) and 1-octen-3-ol (126

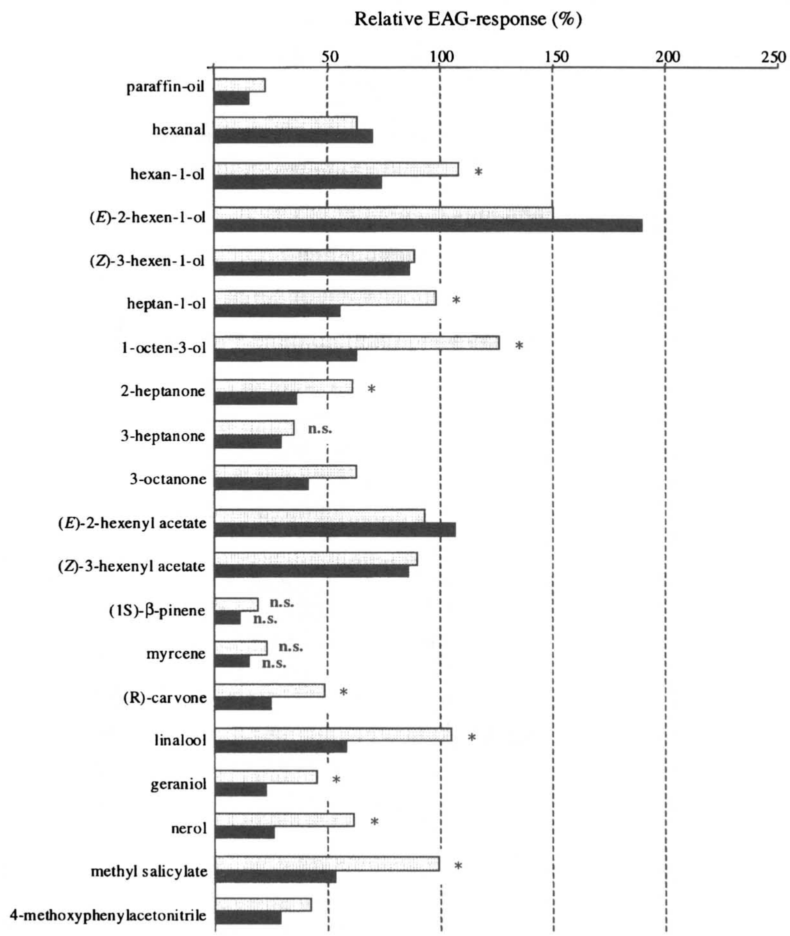

FIG. 2. EAG responses of male and female *L. pabulinus* to the series of plant volatiles. The response bars are based on the backtransformed least-square means. Grey: EAG response of female antennae; black: EAG response of male antennae; n.s.: EAG response not significantly different from the response to the control paraffin oil. *EAG response significantly different between the sexes (after correcting the significance level for multiple comparisons through the Bonferroni method). See text for further explanation.

± 16% mean ± CI). Hexan-1-ol, (*Z*)-3-hexen-1-ol, heptan-1-ol, (*E*)-2-hexenyl acetate, (*Z*)-3-hexenyl acetate, linalool, and methyl salicylate elicited about the same response as the standard (*E*)-2-hexenal. 3-Heptanone, (1*S*)-*β*-pinene, and myrcene did not elicit a significant EAG response in females.

B2. Responses in Male Antennae. The largest EAGs were elicited by (*E*)-

TABLE 3. ANOVA TABLE OF SERIES OF PLANT COMPOUNDS (RESPONSE PROFILES ARE SHOWN IN FIGURE 2)

Tests of fixed effects, source	NDF[a]	DDF[b]	Type III F	Pr > F	Covariance parameter	Estimate
Gender	1	126	19.96	0.0001	Antenna (gender)	0.3761
Chemical	20	438	81.76	0.0001	Residual	1.4271
Gender × chemical	20	438	6.67	0.0001		

[a]Numerator degrees of freedom.
[b]Denominator degrees of freedom.

2-hexen-1-ol (190 ± 21% mean ± CI). The other alcohols, as well as hexanal, the acetates, methyl salicylate, and linalool elicited ca. 50–100% response relative to the standard (*E*)-2-hexenal. Nerol, (*R*)-carvone, and 4-methoxyphenol acetonitrile elicited smaller EAGs, and the responses of male antennae to (1*S*)-*β*-pinene and myrcene were not different from the control.

B3. Female versus Male Antennal Response. Female antennae showed larger relative EAGs to hexan-1-ol, heptan-1-ol, 1-octen-3-ol, 2-heptanone, (*R*)-carvone, linalool, geraniol, nerol, and methyl salicylate than male antennae.

DISCUSSION

Responses to Esters. Some of the esters tested were <95% pure, hence the recorded EAGs could in part be responses to the corresponding alcohols or, in the case of (*E*)-2-octenyl acetate, to 1-octenyl acetate, since this comprised ~30% of the solution. Despite these inpurities, the five groups of esters showed similar relative response patterns in both *L. pabulinus* male and female antennae. Larger EAGs to the different ester groups could be due to differences in volatilities, i.e., acetates > propionates > butanoates > pentanoates > hexanoates. Since such correlations were not found for any of the ester analogs, the measured EAGs cannot be explained solely by differences in volatilities.

Esters consist of an alcohol and an acid part. With regard to the alcohol part, both sexes were highly sensitive when (*E*)-2-hexenol was present in the esters, i.e., the (*E*)-2-hexenyl esters, and to a lesser extent the hexyl esters, (*Z*)-3-hexenyl esters, and (*E*)-2-octenyl esters. The octyl esters elicited the lowest EAGs. With regard to the acid part, both sexes responded least when hexanoic acids were part of the esters, i.e., the hexanoates, followed by acetates, with largest EAGs to butanoates. Both sexes were most sensitive to (*E*)-2-hexenyl butanoate, which is one of the main compounds found in *L. lineolaris* (Gueldner and Parrot, 1978; Dickens et al., 1995) and is found in both sexes of *L. pabulinus* (F. P. Drijfhout, unpublished result). These results suggest that butanoates may play a role in the biology of *L. pabulinus*. Whether this role is intra- or interspecific, or attractive or repellent, cannot be concluded from the present data. EAGs only indicate that the insect perceives the volatiles and do not reveal their function in mediating behavior.

Of the esters that elicited larger relative EAGs in male than in female antennae, three are known to play a role in the sexual communication of mirids. Butyl butanoate and (*E*)-2-butenyl butanoate are sex pheromone components in *Campylomma verbasci* (Smith et al., 1991), and (*E*)-2-octenyl butanoate is a sex pheromone component of *Phytocoris relativus* (Millar et al., 1997). In *L. pabulinus*, a possible sexual role of esters was assessed by offering 100 ng of compounds to males in Petri dishes, after which the number of vibrating males was quantified (Groot et al., 1998b). Butyl butanoate elicited male vibration response in 35%, (*E*)-2-butenyl butanoate did not elicit vibration behavior in any, (*E*)-2-hexenyl butanoate elicited a response in 22%, and (*E*)-2-octenyl butanoate elicited a vibration behaviour in 87% (Groot et al., 1998b). Hexyl butanoate was also tested in this assay, since this is the major compound in the metathoracic scent gland of *L. pabulinus*, constituting up to 95% of the total oil (F. P. Drijfhout, unpublished result). When 100 ng of hexyl butanoate was offered, 40% of the males started to vibrate (Groot et al., 1998b). Since this vibration behavior is a specific sexual response of males (Groot et al., 1998a), the compounds that elicited it may play a role in sexual communication in *L. pabulinus*.

Responses to Plant Volatiles. In comparing the relative EAGs, males were less sensitive than females to most of the tested plant volatiles, with the exception of (*E*)-2-hexen-1-ol, to which both sexes showed strong responses. The high response to (*E*)-2-hexen-1-ol may be due to similarity in structure between this fragment and (*E*)-2-hexenyl butyrate, which elicits high EAGs in both sexes as well. On the other hand, (*E*)-2-hexen-1-ol may play a role in general host plant orientation of *L. pabulinus*, as this is a common green leaf volatile (Visser et al., 1979). The nine plant volatiles that showed larger EAGs in female than in male antennae are common plant volatiles (Visser, 1986). 1-Octen-3-ol, linalool, and methyl salicylate are also found in herbivore-infested leaves of several apple cultivars (Takabayashi et al., 1994). Female *L. pabulinus* may use these compounds for host orientation in autumn when they fly back from herbaceous summer hosts to apple orchards to lay winter eggs.

Some common plant volatiles are produced by heteropterans and may play a role in sexual communication (Aldrich, 1988, 1995). In Miridae, these compounds have not been found, but since *L. pabulinus* males are mostly attracted to females on potato leaves (Groot et al., 1996), some plant compounds may be involved indirectly in the attraction between the sexes.

In conclusion, male antennae are relatively more sensitive to a number of insect-produced esters, while female antennae are more sensitive to a number of plant volatiles. The same trend has been seen previously in *L. lineolaris* males and females (Chinta et al., 1994). This sexual difference in response may be due to the fact that in mirids males are attracted to females, while females may use plant compounds for their orientation towards oviposition sites. Since hexyl butanoate, (*E*)-2-hexenyl butanoate, and (*E*)-2-octenyl butanoate elicited a vibration behavior in some males, these or closely related compounds may be involved in sexual communication, at least at short range. Which of the volatiles that elicited large EAGs play a role in the sexual attraction at long range, remains to be studied.

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