Influence of host plants on sexual communication in the herbivorous bug *Lygocoris pabulinus*

Astrid T. Groot and J. Hans Visser

Plant Research International, Wageningen University and Research Center, P.O. Box 16, 6700 AA Wageningen, The Netherlands

Summary. Host plant volatiles may be involved in the sexual communication of insects in several ways. In the pheromone-producing sex, these volatiles may affect pheromone production or release and, in the receptive sex, plant volatiles may have a synergistic effect on the attraction to sex pheromone. We conducted three types of experiments to determine if and how plant volatiles are involved in the sexual communication of *Lygocoris pabulinus* (L.) (Heteroptera: Miridae), the females of which attract males. In a one-choice cylinder bioassay, females were offered to males on two different plants, belonging to different plant families, *i.e.* potato leaves and goosefoot leaves, to determine if specific plant volatiles were involved in the attraction of males towards females. Females on potato leaves were as attractive as females on goosefoot leaves, but significantly more attractive than females without plant material. The latter result suggests an interaction between females and potato leaves. However, in two-choice flying and walking bioassays, using delta traps in a wind tunnel and a vertical Y-track olfactometer, males were attracted to females irrespective of the presence of potato leaves. This difference in result is probably due to the fact that in the latter assays females were confined with pollen as an alternative food source, while females in the one-choice assay had access to water only, so that they may have suffered from malnutrition. Males in the one-choice assay were also attracted to potato leaves from which females had been removed, indicating that attractive components from females are deposited and adsorbed to the substrate. Plants are probably only indirectly involved in sexual communication, their surface merely functioning as a substrate from which pheromone is released. Males may subsequently be attracted to such plants or substrates. Clean plant material was not attractive to *L. pabulinus* males, hence plant volatiles alone do not seem to be used by these males as possible mate location cues.

Key words. Heteroptera – Miridae – sex pheromone production – pheromone release – male receptivity – host plant volatiles – adsorption

Correspondence to: Astrid T. Groot,
e-mail: astrid.groot@users.ento.wau.nl
Present address: Wageningen University, Dept. Entomology, P.O. Box 8031, 6700 EH Wageningen, The Netherlands

Introduction

Host plant volatiles may be involved in the production, the release, or the perception of sex pheromones by insects (reviewed by McNeil & Delisle 1989; Landolt & Philips 1997). Direct use of plant compounds as precursors for the biosynthesis of sex pheromone compounds has been found mainly in male insects (Wood 1982; Eisner & Meinwald 1987; Vanderwel & Oehlschlager 1987; Baker 1989; Landolt *et al.* 1992a). When females produce sex pheromone, plant volatiles have been found to initiate pheromone production in a more indirect way: females start producing pheromone when in the odor of a host plant (McNeil 1991; Raina *et al.* 1989, 1992; Raina *et al.* 1997). Not only pheromone production, but also pheromone release may be affected by plant odors (Hendrikse & Vos-Bünnemeyer 1987; McNeil & Delisle 1989; Landolt *et al.* 1994). The ability of females to stop pheromone production or release until a suitable host is located, coordinates their reproductive behavior with the availability of food for the offspring (Raina *et al.* 1992). At the receiver side, the attracted sex may be more attracted to a combination of pheromone and plant volatiles than to pheromone alone (Landolt *et al.* 1992b; Dickens *et al.* 1990; Dickens *et al.* 1993; Light *et al.* 1993; Hardie *et al.* 1994).

Distinction between the role of host plants in sex pheromone production and pheromone release can be made when the sex pheromone has been identified, and when a pheromone gland has been recognized. The content of this gland can then be analysed under specified conditions. Pheromone release can be observed in insects that exhibit a specific calling behavior (*e.g.* King 1973; Cardé & Taschenberg 1984). A synergistic effect of pheromone with plant compounds in the receiving insect can be determined by differences in trap catches between pheromone traps with or without the addition of plant compounds (Dickens *et al.* 1990, 1993; Light *et al.* 1993; Hardie *et al.* 1994; Lilley & Hardie 1996).

The insect of our present interest is the green capsid bug, *Lygocoris pabulinus* (L.) (Heteroptera, Miridae), a pest in Northern European fruit orchards. In this species, as in mirids in general, males are attracted by females, which has been confirmed in the field and in the laboratory (Blommers *et al.* 1988; Groot *et al.*

1996). Chemical identification of the sex pheromone has not been successful so far. Overall, of only three mirids the sex pheromone has been identified (Smith *et al.* 1991; Millar *et al.* 1997; Millar & Rice 1998; reviewed by McBrien & Millar 1999). Plant volatiles may be involved in the sexual attraction of *L. pabulinus*, as virgin females that attracted males were confined with plant material as a feeding source. Also, *L. pabulinus* is a host alternating species, migrating from fruit trees to herbaceous plants in the summer, where a summer generation develops. The summer hosts on which *L. pabulinus* may develop, are potentially numerous, as *L. pabulinus* is a highly polyphagous species (Petherbridge & Thorpe 1928; Kullenberg 1946; Blommers *et al.* 1997). To locate females after their migration, males may use plant volatiles that are released when females are feeding on plants, in addition to sex pheromone.

In this study, we determined if and how host plants may be involved in the sexual communication of *L. pabulinus*. When plant compounds are directly involved in sex pheromone production, a difference in attraction is expected when virgin females are confined with different host plants or with no host plant at all. A possible distinction of indirect involvement of plant volatiles between pheromone production and pheromone release will be hampered in this species, since a sex pheromone gland has not been recognized in Miridae so far, and a specific calling behavior in *L. pabulinus* females has not been observed (Groot *et al.* 1998). Whether host plants are involved at either the producer or the receiver side, *i.e. L. pabulinus* females or males respectively, is determined by placing females either upwind or downwind from the host plant. Attraction may be different when flying or walking towards an odor source (Hardie *et al.* 1992), therefore both flight and walking bioassays were conducted.

Material and methods

Insects

Lygocoris pabulinus was reared on potted potato plants, cultivar Bintje, in wooden cages in a greenhouse at $22 \pm 2°C$, $65 \pm 5\%$ R.H., L18:D6, following the procedure of Blommers *et al.* (1997). Every 2–3 days newly emerged adults were collected from the rearing cages, after which the sexes were placed in separate rearing cages. In this way, virgin males and females (see Groot *et al.* 1998) of known age were continuously available for the experiments.

One-choice bioassay

To determine whether males are attracted to females with or without plant material, and whether this attraction differs between females on two potential summer hosts, one-choice bioassays were conducted using glass cylinders (length 50 cm, diam. 11 cm, see Groot *et al.* 1996). The cylinders were placed horizontally on the floor in a wind tunnel of 3.0 (l) × 1.3 (w) × 0.8 (h) m with adjustable wind speed, light, temperature and R.H. (see Griepink (1997) for further details on the wind tunnel). At the downwind side of each cylinder we placed a plastic dish with gauze bottom and screen cone, containing 8–15 males of 5–8 days old. Against the upwind side a plastic dish with gauze lid and bottom was placed, in which an odor source was offered. In this way, each cylinder was a closed system, so that males from the downwind dish could only walk or fly towards the upwind

dish that was offered in the specific cylinder. Two-three h before a test, the downwind dishes were filled with males, the upwind dishes with odor sources, and all dishes were placed in the wind tunnel.

Leaves of two different plants were used to determine possible attraction differences between females on two potential summer hosts: potato leaves and goosefoot leaves (*Chenopodium quinoa* L.). Potato leaves were chosen, because *L. pabulinus* is reared on potato. Goosefoot leaves were arbitrarily chosen as the alternative, as this plant belongs to a different family (Chenopodiaceae) and hence is likely to differ in composition or release of plant volatiles. Chenopodiaceae have been recorded as summer hosts of *L. pabulinus* (Petherbridge & Thorpe 1928). Eight different odor sources were tested: (1) empty dish, (2) five females on a fresh potato leaf, (3) five females with a small glass tube containing water, closed with oasis, (4) a potato leaf that had been in a dish with five females for 2–3 h prior to the experiment (females removed during the experiment), (5) a clean potato leaf, (6) five females on a fresh goosefoot leaf, (7) a goosefoot leaf that had been in a dish with five females for 2–3 h prior to the experiment (females removed during the experiment), and (8) a clean goosefoot leaf. The wind speed through the cylinders was set at 0.20 m/s. After one hour the number of males sitting or walking on the upwind lid were counted as positive responders. All odor sources were tested 5–20 times. Differences in responses between the sources were compared with a Generalized Linear Model (GLM) for binomial data, using the the logit-link function in computer programme Genstat 5 (release 4.1, PC/Windows NT, 1997). In the model, the variance was assumed to be proportional to binomial variance. Overall effect of treatments was determined by performing an F-test for the ratio of the mean deviance for treatment and the mean deviance of the rest. If the overall test was significant ($P < 0.05$), pairwise comparisons between treatment means on the logit scale were conducted, using the t-test.

Two-choice flight bioassay

To determine if females attract males when on a plant or in the odor of a plant, PVC-cages with two compartments were constructed. The compartments, each 7.5 cm long and 7 cm diam., were divided by gauze and closed at both sides with gauze lids (Fig. 1). The cages were hung in delta traps (30 (l) × 20 (w) × 20 (h) cm) with replacable bottoms treated with Tangle Trap®, and placed in the wind tunnel, hanging from metal clamps 10–15 cm above the wind tunnel floor. Five different combinations were tested: (A) three females with wet oasis and pollen, and a small potato sprout in the downwind compartment, leaving the upwind compartment empty, (B) a small potato sprout in the upwind compartment, and three females with wet oasis and pollen in the downwind compartment, (C) three females with wet oasis and pollen in the upwind compartment, and a small potato sprout in the downwind compartment, (D) three females with wet oasis and pollen in the downwind compartment, leaving the upwind compartment empty, and (E) three *males* with wet oasis and pollen, and a small potato sprout in the downwind compartment, leaving the upwind compartment empty. The pollen was a mixture of different plant species, bought at a commercial bee-station (Bijenhuis, Wageningen, the Netherlands). To offer males a choice, a control trap was placed about 90 cm next to each test cage (so that both cages were about 20 cm from the sides of the wind tunnel), consisting of a similar cage with the two compartments containing the same as the test cage, only without bugs. Both traps were placed in the upwind part of the wind tunnel, about 1 m downwind from which 8–10 potato plants were placed. After arranging the cages and the plants in the wind tunnel, 35–40 virgin males of 5–8 days old were introduced at the downwind side of the wind tunnel. After 3–4 days the males caught in the Tangle Trap® in both traps were counted, and all males were recaptured. Percentage of the males trapped was calculated from the number of males recaptured.

Two-choice walking bioassay

To determine the influence of host plants on sexual attraction when males would walk towards an odor source, vertical Y-track olfactometer assays were conducted as described by Visser & Piron (1998). To suppress flight intention of males, the Y-track was placed in a
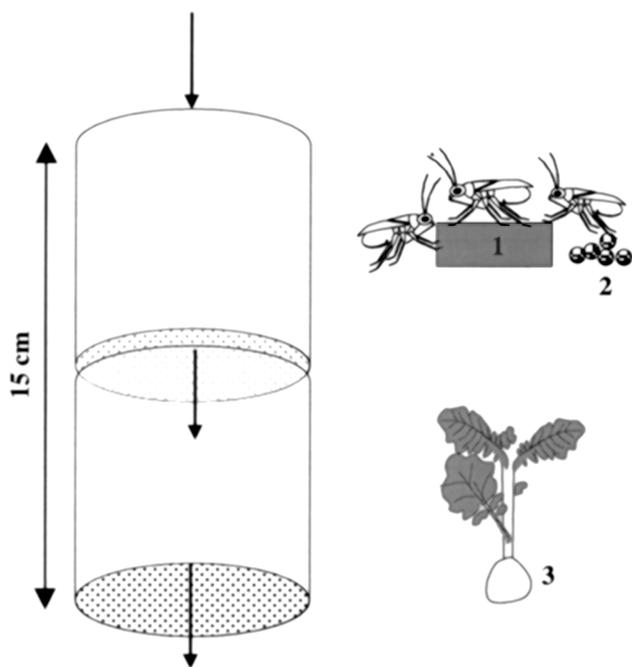
Fig. 1 Cage with two compartments, each 7.5 cm long, diam. 7 cm. Bugs were always confined with wet oasis (1) and pollen (2). A small potato sprout (3; roots wrapped in wet cotton and aluminium foil to avoid dessication) was: (A) added to three females, (B) placed upwind from females, (C) placed downwind from females, (D) not added, (E) added to three *males*. See text for further explanation

black box under a halogen lamp (4–12 V DC, 10 VA), which was placed in a black socket sealed with a red filter, so that the light intensity at the base of the Y-track was 6.3–6.5 lux only. Two 250 ml glass bottles (h. 14 cm, diam. 6.5 cm) were placed outside the black box, one on each side, under a desk-lamp with a 25 W light bulb. One bottle contained the odor source to be tested, the other was the control bottle. Three odor sources were tested: (a) five *L. pabulinus* females with two small potato sprouts in wet oasis and pollen, (b) five females with two strips of green paper, wet oasis and pollen, (c) five *males* with two small potato sprouts in wet oasis and pollen. In all tests the control bottles contained wet oasis and pollen. The bottles were filled and placed in the setup 1 h before each test. All experiments were conducted in three replicates. One replicate consisted of 20 males walking towards one of the sources. After every 5 males the bottles, glass tubes and connecting tubes were exchanged to correct for unforeseen asymmetry in the setup.

Results

One-choice bioassay

In total 1 out of 171 males responded to the empty control dish. Significantly more males responded to females on potato leaves than to clean potato or goosefoot leaves, goosefoot leaves from which females were removed, or to females with water only (Fig. 2). Females on goosefoot leaves were similarly attractive as females on potato leaves, but also as attractive as all other odor sources tested, except for clean goosefoot leaves. Potato leaves from which females had been removed, *i.e.* leaves on which females had walked for 2–3 h prior to the experiment, elicited a similar response as females on potato leaves and females on
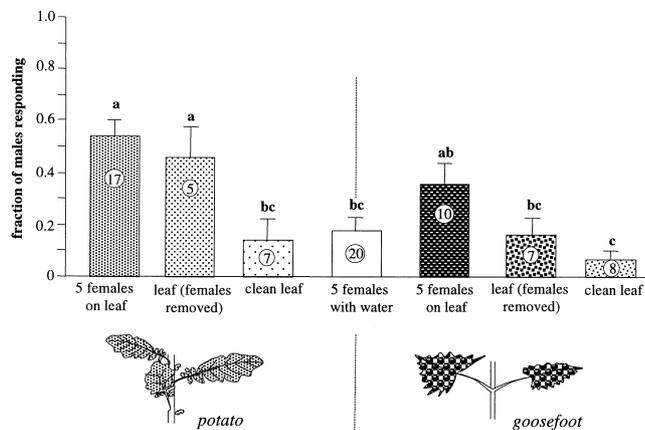
Fig. 2 Mean fraction (+s.e.) of males responding in cylinder bioassay. Numbers in bars: number of replicates. Each replicate consisted of 8–15 males. Letters above the bars indicate significant differences at the 5% level on the logit scale, using GLM. See text for further explanation

goosefoot leaves. Females without plant material elicited a response in only 0.18 ± 0.05 (mean $\pm$ s.e.) of the males tested.

### Two-choice flight bioassay

When females were confined with a potato sprout (combination A), the first time 9 males were trapped in the Tangle Trap® versus one male in the control trap, and the second time 11 males were trapped versus one male in the control trap (Fig. 3). Females compartmentalized downwind (B) or upwind (C) from a potato sprout, caught similar amounts of males, and significantly more than the control traps. Traps without plant material and only females in the downwind compartment (D), caught slightly lower amounts of males, but in total 23 males versus 2 males in the control traps were caught. In the traps with *males* and potato sprouts, in total only three males were caught versus two males in the control traps.

Two-choice walking bioassay

In total 72% of the 60 males tested walked towards females on potato leaves, versus 28% (17 males) walking towards the control (Fig. 4, I). 70% Of a total of 57 males walked towards females without plant material, while 30% (17 males) walked towards the control (II). When the test bottle contained males with potato leaves (III), 54% of all tested males walked towards the test bottle versus 46% (27 males) walking towards the control.
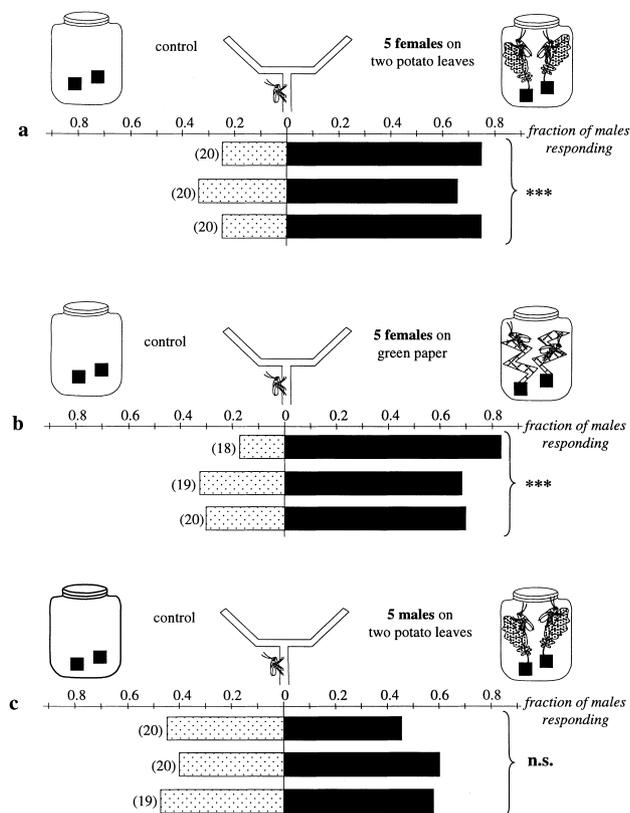
Discussion

Since attraction towards females on potato leaves was not significantly different from attraction towards females on goosefoot leaves, specific plant compounds do not seem to be involved in sex pheromone production
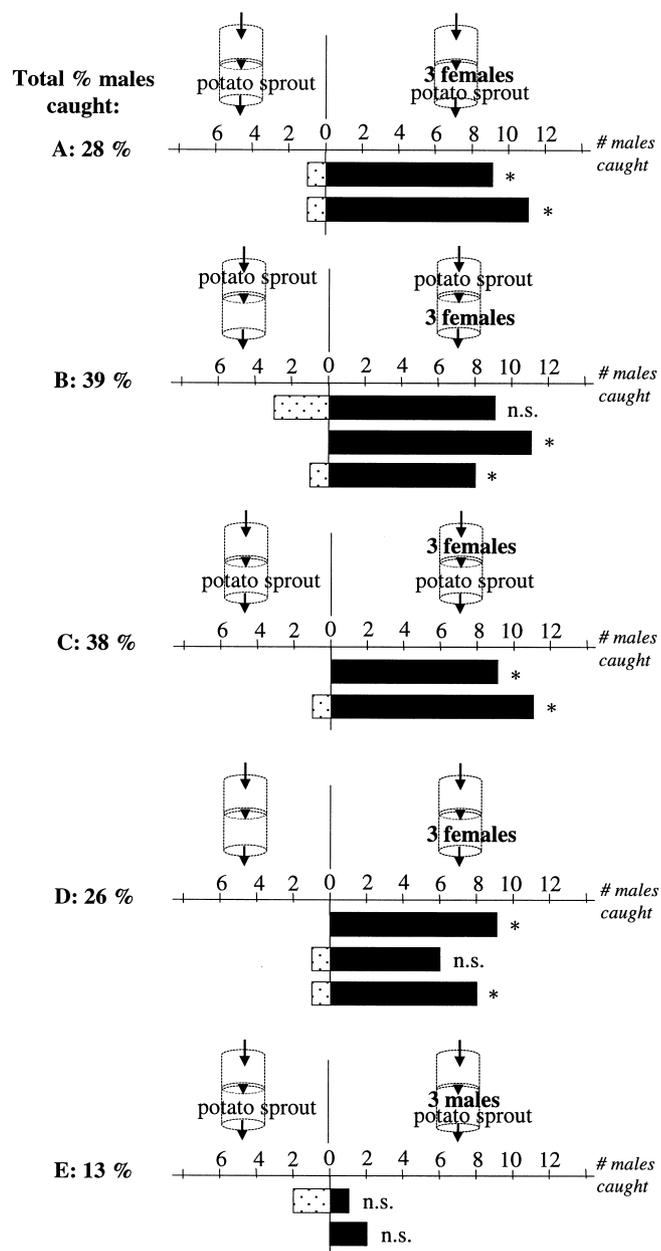
Fig. 3 Numbers of males caught in traps. Per replicate 35–40 males had been released. Bugs were always confined with pollen grains and wet oasis. Significant differences were determined per test, using the two-sided binomial test. *$P < 0.05$, n.s.: $P > 0.05$

Fig. 4 Y-track olfactometer tests with (I) 5 females on two potato leaves, (II) 5 females on green paper, (III) 5 *males* on two potato leaves. All bottles contained wet oasis and pollen grains. Significant differences between test source and control were determined using the two-sided binomial test after summation of male responses in the three experiments per test source. ***$P < 0.001$, n.s.: $P > 0.05$

in *L. pabulinus* females. However, the fact that females on potato leaves were significantly more attractive than females without plant material, does suggest an interaction between females and potato leaves. On the other hand, the results of both two-choice assays do not confirm such interaction, because females without plant material attracted similar amounts of males as females with potato sprout, containing potato leaves. The significant difference in the one-choice assay is probably due to malnutrition of the females without plant material, as they were confined with water only. In the two-choice assays pollen was added

as a food source. We frequently observed *L. pabulinus* actively feeding on the pollen. Pollen is a highly nutritious food source, which is verified in *L. pabulinus* by a higher production of eggs by females reared with pollen than by females reared without it (Groot *et al.* 1998). Malnutrition is likely to stop pheromone production or release, as energy is needed for somatic maintenance.

Summarizing all results, we conclude that plant volatiles are not directly involved in pheromone production in *L. pabulinus* females. Female bugs do not need plant volatiles to attract males, as evidenced by females upwind from a potato sprout attracting similar numbers of males as did females downwind from a potato sprout. As a consequence, *L. pabulinus* females do not seem to coordinate their reproductive behavior with the availability of food for offspring. For *L. pabulinus* males, all females with pollen were attractive in the flight and walking bioassays, irrespective of the presence of plant material. Hence, the perception of sex pheromone in *L. pabulinus* males does not seem to be influenced by plant volatiles either.

Our findings may not apply to field bugs, as laboratory-reared insects may respond differently to host odors in relation to sex pheromone than field insects,

which has been demonstrated for *Heliothis virescens* (Raina *et al.* 1997). However, *H. virescens* was reared continuously on an artificial diet. When plant material is lacking completely for a number of generations, it is likely that life-history aspects, such as reproduction, are not associated with plant volatiles anymore. *Lygocoris pabulinus* has been reared continuously on potato plants, which reduces the chance that possible associations with plant volatiles have disappeared.

There are more examples that plant volatiles do not affect sex pheromone production, release or perception (Cardé & Taschenberg 1984; Guldemont *et al.* 1993; Den Otter *et al.* 1996). Cardé & Taschenberg (1984) suggest that such kairomonal interactions are less likely to occur in polyphagous species. *L. pabulinus* is polyphagous and host-alternating, laying overwintering eggs in woody plants, such as fruit trees, while the summer generation feeds on herbaceous plants (Petherbridge & Thorpe 1928; Kullenberg 1946; Southwood & Leston 1959). Also, plant volatiles probably do not influence sexual communication when eggs are not deposited near the site where females call. Such spatial discontinuity between calling activity and oviposition has been described for some insects (Showers *et al.* 1976; Noldus *et al.* 1991), and should be studied more closely in *L. pabulinus*.

One result of the one-choice assay needs further attention, *i.e.* the fact that *L. pabulinus* males were similarly attracted towards females on potato leaves as towards potato leaves, from which females had been removed. This is probably due to deposition of attractive components from females on the substrate on which they walked (Groot *et al.* 2000). Most likely these components are female-specific cuticular hydrocarbons. In a similar assay used for *Mamestra brassicae*, males were attracted to leaves on which female sex pheromone was adsorbed as well (Noldus *et al.* 1991). In our assay wind was blown over the potato leaves for 1 h, which may enhance evaporation of low-volatile compounds. Adsorption of pheromone to a substrate increases the surface area from which pheromone evaporates, thereby increasing both the rate of volatilization and the possible communication distance (Colwell *et al.* 1978).

In conclusion, plants seem to be involved only indirectly in sexual communication, their surface merely functioning as a substrate from which pheromone is released. Males may subsequently be attracted to such plants or substrates. Since clean plant material is not attractive to *L. pabulinus* males, plant volatiles alone do not seem to be used by these males as possible mate location cues.

Acknowledgements

References

Baker TC (1989) Origin of courtship and sex pheromones of the oriental fruit moth and a discussion of the role of phytochemicals in the evolution of lepidopteran male scents. Pp 401–418 *in* Cou CH, Waller GR (eds) Phytochemical Ecology: Allelochemicals, Mycotoxins and Insect Pheromones and Allomones. Taipei ROC: Institute of Botany, Academia Sinica Monograph Series No 9

Blommers LHM, Bus V, de Jongh E, Lentjes G (1988) Attraction of males by virgin females of the green capsid bug *Lygocoris pabulinus* (Heteroptera: Miridae). Entomologische Berichten, Amsterdam 48:175–179

Blommers LHM, Vaal FWNM, Helsen HHM (1997) Life history, seasonal adaptations, and monitoring of common green capsid *Lygocoris pabulinus* (L.) (Hemiptera: Miridae). Journal of Applied Entomology 121:389–398

Cardé RT, Taschenberg EF (1984) A reinvestigation of the role of (E)-2-hexenal in female calling behaviour of the polyphemus moth (*Antheraea polyphemus*). Journal of Insect Physiology 30:109–112

Colwell AE, Shorey HH, Baumer P, van Vorhis Key SE (1978) Sex pheromone scent marking by females of *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). Journal of Chemical Ecology 4:717–721

Den Otter CJ, De Cristofaro A, Voskamp KE, Rotundo G (1996) Electrophysiological and behavioural responses of chestnut moths, *Cydia fagiglandana* and *C. splendana* (Lep., Tortricidae), to sex attractants and odors of host plants. Journal of Applied Entomology 120:413–421

Dickens JC, Jang EB, Light DM, Alford AR (1990) Enhancement of insect pheromone responses by green leaf volatiles. Naturwissenschaften 77:29–31

Dickens JC, Smith JW, Light DM (1993) Green leaf volatiles enhance sex attractant pheromone of the tobacco budworm, *Heliothis virescens* (Lep: Noctuidae). Chemoecology 4:175–177

Eisner T, Meinwald J (1987) Alkaloid-derived pheromones and sexual selection in Lepidoptera. Pp 251–269 *in* Prestwich GD, Blomquist GJ (eds) Pheromone Biochemistry. Orlando FL: Academic Press

Griepink FC (1997) Wind tunnel bioassays of the *Symmetrischema tangolias* sex pheromone. Pp 93–101 *in* Griepink FC, Analysis of the sex pheromones of *Symmetrischema tangolias* and *Scrobipalpuloides absoluta*. PhD thesis, Wageningen Agricultural University

Groot AT, Heijboer A, Drijfhout FP, van Beek TA, Visser, JH (2000) Close-range sex pheromone of *Lygocoris pabulinus* (L.) – source of attractant. Pp 71–80 *in* Groot AT, Sexual Behaviour of the Green Capsid Bug. PhD thesis, Wageningen Agricultural University

Groot AT, Schuurman A, Visser JH, Blommers LHM (1996) Laboratory bioassay of sex pheromone activity in *Lygocoris pabulinus* (L.) (Heteroptera: Miridae). Proceedings of the 13th Annual ISCE meeting, Prague: 189

Groot AT, Van der Wal AJ, Schuurman A, Visser JH, Blommers LHM, Van Beek TA (1998) Copulation behavior of *Lygocoris pabulinus* under laboratory conditions. Entomologia Experimentalis et Applicata 88:219–228

Guldemont JA, Dixon AFG, Pickett JA, Wadhams LJ, Woodcock CM (1993) Specificity of sex pheromones, the role of host plant odor in the olfactory attraction of males, and mate recognition in the aphid *Cryptomyzus*. Physiological Entomology 18:137–143

Hardie J, Nottingham SF, Dawson GW, Harrington R, Pickett JA, Wadhams LJ (1992) Attraction of field-flying aphid males to synthetic sex pheromone. Chemoecology 3:113–117

Hardie J, Storer JR, Nottingham SF, Peace L, Harrington R, Merritt LA, Wadhams LJ, Wood DK (1994) The interaction of sex pheromone and plant volatiles for field attraction of male bird-cherry aphid, *Rhopalosiphum padi*. Brighton Crop Protection Conference – Pest and Diseases: 1223–1230

Hendrikse A, Vos-Bünnemeyer E (1987) Role of host-plant stimuli in sexual behaviour of small ermine moths (*Yponomeuta*). Ecological Entomology 12:363–371

King ABS (1973) Studies of sex attraction in the cocoa capsid *Distantiella theobroma* (Heteroptera: Miridae). Entomologia Experimentalis et Applicata 16:243–254

Kullenberg B (1946) Studien über die Biologie der Capsiden. Zoologische Bidrag, Uppsala 23:1–522

Landolt PJ, Philips TW (1997) Host plant influences on sex pheromone behavior of phytophagous insects. Annual Review of Entomology 42:371–391

Landolt PJ, Heath RR, Chambers DL (1992a) Oriented flight responses of female Mediterranean fruit flies to calling males, odor of calling males, and a synthetic pheromone blend. Entomologia Experimentalis et Applicata 65:259–266

Landolt PJ, Reed HC, Heath RR (1992b) Attraction of female papaya fruit fly (Diptera: Tephritidae) to male pheromone and host fruit. Environmental Entomology 21:1154–1159

Landolt PJ, Heath RR, Millar JC, Davis-Hernandez KM, Dueben BD, Ward KE (1994) Effects of host plant, *Gossypium hirsutum* L., on sexual attraction of cabbage looper moths, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae). Journal of Chemical Ecology 20:2959–2974

Light DM, Flath RA, Buttery RG, Zalom FG, Rice RE, Dickens JC, Jang EB (1993) Host-plant green-leaf volatiles synergize the synthetic sex pheromones of the corn earworm and codling moth (Lepidoptera). Chemoecology 4:145–152

Lilley R, Hardie J (1996) Cereal aphid responses to sex pheromones and host-plant odors in the laboratory. Physiological Entomology 21:304–308

McBrien HL, Millar JC (1999) Phytophagous bugs. Pp 277–304 *in* Hardie J, Minks AK (eds) Pheromones of non-lepidopterous insects associated with agricultural plants. Oxon UK: CABI Publishing

McNeil JN (1991) Behavioral ecology of pheromone-mediated communication in moths and its importance in the use of pheromone traps. Annual Review of Entomology 36:407–430

McNeil JN, Delisle J (1989) Are host plants important in pheromone-mediated mating systems of Lepidoptera? Experientia 45:236–240

Millar JG, Rice RE, Wang Q (1997) Sex pheromone of the mirid bug *Phytocoris relativus* Knight. Journal of Chemical Ecology 23:1743–1754

Millar JG, Rice RE (1998) Sex pheromone of the plant bug *Phytocoris californicus* Knight (Heteroptera: Hemiptera: Miridae). Journal of Economic Entomology 91:132–137

Noldus LPJJ, Potting RPJ, Barendregt HE (1991) Moth sex pheromone adsorption to leaf surface: bridge in time for chemical spies. Physiological Entomology 16:329–344

Petherbridge FR, Thorpe WH (1928) The common green capsid bug (*Lygus pabulinus*). Annals of Applied Biology 15:446–472

Raina AK, Stadelbacher EA, Ridgway RL (1989) Comparison of sex pheromone composition and pheromone-mediated male behavior of laboratory-reared and wild *Heliothis zea* (Lepidoptera: Noctuidae). Journal of Chemical Ecology 15:1259–1265

Raina AK, Kingan TG, Mattoo AK (1992) Chemical signals from host plant and sexual behavior in a moth. Science 255:592–594

Raina AK, Jackson DM, Severson RF (1997) Increased pheromone production in wild tobacco budworm (Lepidoptera: Noctuidae) exposed to host plants and host chemicals. Environmental Entomology 26:101–105

Showers WB, Reed GL, Robinson JF, Derozari MB (1976) Flight and sexual activity of the European corn borer. Environmental Entomology 5:1099–1104

Smith RF, Pierce HD, Borden JH (1991) Sex pheromone of the mullein bug, *Campylomma verbasci* (Meyer) (Heteroptera: Miridae). Journal of Chemical Ecology 17:1437–1447

Southwood TRE, Leston D (1959) Land and Water Bugs of the British Isles. London: F Warne

Vanderwel D, Oehlschlager AC (1987) Biosynthesis of pheromones and endocrine regulation of pheromone production in Coleoptera. Pp 175–215 *in* Prestwich GD, Blomquist GJ (eds) Pheromone Biochemistry. Orlando, FL: Academic Press

Visser JH, Piron PGM (1998) An open y-track olfactometer for recording of aphid behavioural responses to plant odors. Proceedings Experimental and Applied Entomology, NEV Amsterdam 9:41–45

Wood DL (1982) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology 27:411–446