Olfactory response of two aphid parasitoids, *Lysiphlebus testaceipes* and *Aphidius colemani*, to aphid-infested plants from a distance

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Abstract

The role of volatile stimuli in the host-searching behaviour of the two parasitoid species *Lysiphlebus testaceipes* Cresson and *Aphidius colemani* Viereck (Hymenoptera: Braconidae) was studied in relation to the host *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumber plants, *Cucumis sativa* L. (Cucurbitaceae). Experiments were carried out in the laboratory in a wind tunnel, exposing individual parasitoids to signals from three sources simultaneously: (1) a complex of cucumber plants, *Cucumis sativa*, and *A. gossypii*; (2) uninfested cucumber plants; and (3) dummy cardboard plants. The flight response of the female parasitoids was considered oriented when they landed on plants and non-oriented when the females landed elsewhere (tunnel floor, sides, or top). Results showed that the proportion of oriented flights was significantly higher than non-oriented flights. A comparison between the two wasp species suggested that *A. colemani* females may be better able to locate plants than *L. testaceipes*, as the proportion of females that made an oriented flight was higher in this species. For females of both wasp species which made an oriented flight, landing was more often observed on real plants (i.e., with no difference between infested and uninfested plants), than on dummy plants. A description of the flight behaviour of the two parasitoid species is presented. One difference between the species was that flight duration was higher in *L. testaceipes* than in *A. colemani*. This work shows that the two parasitoid species respond to stimuli from the host-plants of *A. gossypii* in a similar way to parasitoids of aphid pests in other crops.

Introduction

Most female parasitoids search for their hosts using chemical or visual cues from their herbivorous hosts, the plants on which their hosts feed, or their habitat (Vinson, 1976; Vet & Dicke, 1992; Powell et al., 1998; Dicke, 1999; Guerrieri et al., 2002). In the host selection behavior of insect parasitoids, the volatile cues derived from plants can have a similar influence to that exerted by signals emanating directly from the host (Vinson, 1976; Nordlund et al., 1988; Tumlinson et al., 1992; Vet & Dicke, 1992), but those plant-derived cues are assumed to be more detectable from a distance because of the plant's relatively large biomass (Vet et al., 1991; Vet & Dicke, 1992). Parasitoids, while searching for the hosts' habitat, may exploit volatile cues derived from uninfested plants as well as from infested plants (Nordlund et al., 1988). The plant often provides the first cue in the chain of events that leads to host location, regardless of the nature of the orienting factor (Vinson, 1976).

It is assumed that the release of plant volatiles due to herbivore-feeding damage serves as a mechanism that first evolved as a direct defence against herbivores and pathogens, and the function of attracting natural enemies evolved secondarily (Dicke & Sabelis, 1988; Dicke & van Loon, 2000). This attraction of natural enemies by odours

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derived from plants has been widely studied in the laboratory using wind tunnel experiments showing that parasitoid females are able to locate their hosts and discriminate between uninfested and infested plants by flying upwind toward odours emitted by the host or plant–host complex (Vinson, 1981). Besides volatile cues, other stimuli such as colours, plant architecture, canopy stratification and height, and leaf surface area may also elicit a flight response in parasitoid females (Whitman & Eller, 1990; Guerrieri, 1996; Cloyd & Sadof, 2000; Jang et al., 2000).

Several braconid aphid parasitoid species have been reported as responding to a variety of both contact and olfactory cues associated with the host or with the host's habitat (Powell & Zhang, 1983; Guerrieri et al., 1997; Jang et al., 2000; Carver & Franzmann, 2001). Among these species, *Lysiphlebus testaceipes* Cresson and *Aphidius colemani* Viereck (Hymenoptera: Braconidae), are two polyphagous parasitoids of aphids which have been studied previously. *Lysiphlebus testaceipes* is a generalist parasitoid which has an extremely broad range of hosts (Mackauer & Stary, 1967) with different preferences for different aphid hosts on various plants (Knight, 1944; Sekhar, 1960). *Aphidius colemani* is also a polyphagous aphid parasitoid, originating in Northern India or Pakistan, which is now also found in North and South America, Australia, and Europe (Stary, 1975). These parasitoid species are known to contribute to aphid control in two ways, by causing both a direct mortality of the host, and a decrease in its reproductive rate. They are often used for the biological control of aphid species. *Aphidius colemani* is used in many biological control programmes of various aphid pests (Wellings et al., 1994), but often shows an innate preference for *Aphis gossypii* Glover (Homoptera: Aphididae) (Wellings et al., 1994; Messing & Rabasse, 1995). The influence of learning by these two parasitoid species on the location of aphid-infested and uninfested plants has previously been reported (Grasswitz & Paine, 1993; Grasswitz, 1998; Storeck et al., 2000).

The objective of this study was to determine the effects of the plant's volatiles on the host-searching behaviour of *L. testaceipes* and *A. colemani*, by examining the olfactory response of these parasitoid species to *A. gossypii* on cucumber *Cucumis sativa* L. (Cucurbitaceae) plants. Observations were carried out in the laboratory by means of wind tunnel experiments using signals derived from aphid-infested and uninfested plants.

Materials and methods

The experiment consisted of exposing individual females of *L. testaceipes* and *A. colemani* to stimuli derived from three simultaneous sources: (1) plant-host complex, (2) uninfested plants, and (3) dummy cardboard plants, in a wind tunnel.

Insects

Parasitoids were mass-reared on *A. gossypii* on cucumber plants, *C. sativa*, in controlled environment chambers at 21 ± 1 °C, L16:D8 photoperiod, and 60–70% r.h. In order to obtain standardised young adults, parasitised aphids were isolated at the mummy stage, before parasitoid emergence, in corked glass vials (8 × 60 mm). Emerging females used for the experiment were kept isolated after emergence, fed with a honey-water solution, mated, and experienced for oviposition. The latter condition was used because oviposition experience is known to enhance responsiveness to long-range host-location cues in *L. testaceipes* and *A. colemani* (Grasswitz & Paine, 1993; Grasswitz, 1998). Experienced females were obtained by exposing them after mating to a pre-flight treatment, and each was allowed to forage for about 20 min on a cucumber plant infested with 50 aphids. Females which attacked aphids were then recaptured, and tested in the wind tunnel within 2 h of this initial foraging experience. Mated females were obtained by enclosing single naive pairs (one male and one female) in glass vials until copulation was observed. All females tested in the experiment were less than 12 h old, mated, and experienced solely with *A. gossypii* on cucumber.

Plants

The cucumber plants (var. Serit) used in experiments were reared in an environmental room at 21 ± 1 °C, 60–70% r.h., and under a L16:D8 photoperiod provided by four F58W/33 (standard + UV) neon tubes plugged into 220 V/ 50 Hz transformers producing a light intensity of about 2500 lux. At 32 days of age, these plants were 15–20 cm high and had three to four real leaves. At this stage they were infested with eight parthenogenetic females of *A. gossypii* and these females were allowed to reproduce for 9 days before the test. All plants tested were thus 41 days old and were infested with about 1500 aphids. Dummy plants were constructed using a wooden stick for the stem and dummy cardboard green leaves with a colour hue very similar to those of actual cucumber leaves. All architectural characters of plant size, height, leaf number, leaf surface area, and branch number were designed to resemble real ones, and given a spatial arrangement similar to the architecture of real plants.

Wind-tunnel

The bioassays were conducted in a 150 × 70 × 60 cm wind tunnel made of Plexiglas sheets for the sides, and a glass sheet on the top. The airflow was produced by a fan controlled by a rheostat. Before entering the tunnel, the air was filtered by a 5-cm thick layer of activated charcoal contained between two stainless steel pieces of mesh. The purified flow was then rendered laminar by passing the air through two additional sheets of stainless steel (0.5 mm and 0.3 mm mesh, respectively) and one sheet of polyester organdy. The air speed in the tunnel was about 12 cm s^{-1}. Light was provided by four 58 W neon tubes placed 10 cm above the tunnel, which produced an intensity of about 4600 lux at the takeoff point. A layer of translucent paper placed between the neon tubes and the top of the tunnel provided diffused light. Yellow strips (2 × 5 cm) were placed at random on the floor of the tunnel to provide visual cues (David, 1982).

Bioassay

Tested plants were placed on the tunnel floor, at about 15 cm downwind from the last organdy filter, and at 100 cm from the parasitoid release point. They were aligned crosswind and spaced so that the nearest leaves between two plants were 5 cm from one another. Experiments were conducted between 11:00 h and 16:00 h at 26–27 °C and 50–60% r.h. For acclimatisation to the abiotic conditions in the tunnel, each parasitoid female was enclosed for 5 min in a Petri dish (5 cm diameter) placed in the tunnel before being released. Then, each female was released into the tunnel by placing the Petri dish on a takeoff platform at 15 cm above the tunnel floor and removing the dish cover. From this moment on, the female was observed until she took off and landed. Females that did not take off within 2 min were discarded (17 out of 133 *L. testaceipes* females and 9 out of 111 *A. colemani* females). Measurement of flight duration was made from the moment the females left the take-off platform to the moment they landed. The flight responses of the *L. testaceipes* and *A. colemani* females to the three targets were analysed and compared. A flight response was considered oriented when the female landed on one of the plants, and non-oriented when the female landed elsewhere (tunnel floor, sides, or top). Each individual of the two parasitoid species was tested only once. A choice between dummy, infested, and uninfested plant was given to each parasitoid female and, for each replicate, their locations in the tunnel were randomly exchanged. In all, 244 females (133 *L. testaceipes* and 111 *A. colemani*) were tested.

Data analysis

The percentage of females showing oriented and non-oriented flight responses towards the experimental target, and the mean duration of flight were calculated. Comparisons between landing locations for the two species were made by building 'landing location' × species contingency tables and by computing standard χ^2-tests. Preplanned tests were also performed by building subtables and an overall significance level of 5% was maintained using a modified Bonferroni procedure (Hochberg, 1988). The flight duration of the two species in the wind tunnel was compared with standard log-rank tests (Collett, 1994). All calculations were made using the SAS/STAT package (SAS Institute Inc., 1999).

Results

Overall, 89.3% of females (218) showed flight behaviour in the wind tunnel. Among females that flew, the proportion performing an oriented flight was significantly greater than the proportion which did not (64.2% (140/218) vs. 35.8% (78/218), respectively; $\chi^2 = 8.99$, d.f. = 1, $P < 0.05$). Among females which performed an oriented flight response, a significant difference was found in the landing location between dummy and real plants (5.0% [7/140]) vs. 95.0% (133/140; $\chi^2 = 71.09$, d.f. = 1, $P < 0.05$). Among females which landed on real plants, no significant difference was found between infested and uninfested plants (59.4% [79/133]) vs. 40.6% (54/133); $\chi^2 = 2.37$, d.f. = 1 (ns), even though a trend towards landings on infested plants was noted.

There was a significant difference in the rate of oriented flights between the two species ($\chi^2 = 14.60$, d.f. = 1, $P < 0.05$), with *A. colemani* females showing oriented flights more frequently than *L. testaceipes* females (Figure 1). On the other hand, the preference for real plants over dummy plants was the same for both species ($\chi^2 = 0.67$, d.f. = 1, ns), and both species showed the same landing rate on both infested and uninfested plants ($\chi^2 = 0.001$, d.f. = 1, ns) (Figure 1).

In the wind tunnel, females of both species showed different behavioural responses depending on whether they were in pre-flight, flight, or landing phases. During the pre-flight phase, the females walked on the edge of the Petri dish and, after about 10 s, stopped for a few seconds, holding their body at an approximate angle of 45 degrees relative to the substrate, with antennae facing the airflow. At this point, they took off or continued walking and stopped once or twice before starting to fly. During the flight phase, females that showed non-oriented flight jumped or zigzagged with upwind movements from side to side or showed a downwind flight following the airflow. Females in oriented flight showed straight upwind flights hovering towards sources and moving from side to side before landing. During such behaviour, flight duration appeared to be longer than for other flight types. During the landing phase, females landed on either the sources (in

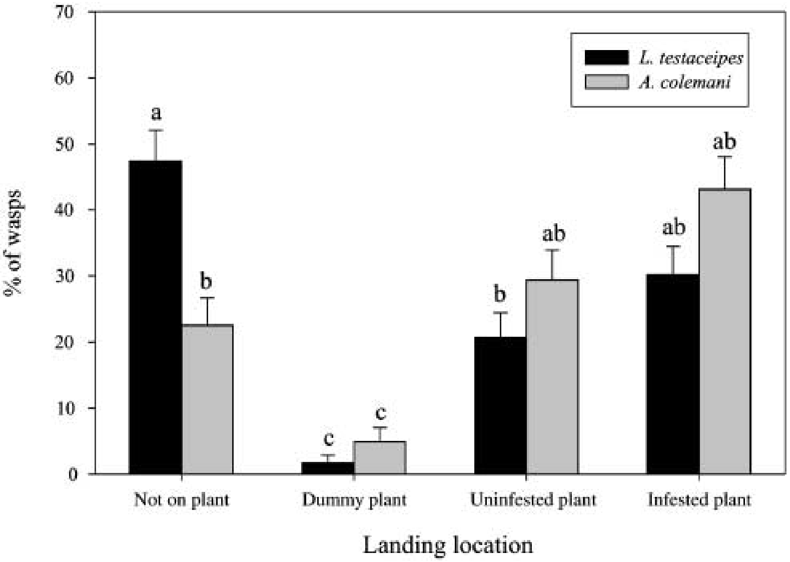

Figure 1 Flight response of *L. testaceipes* and *A. colemani* to different landing locations in choice-tests. Bars having no letters in common indicate significantly different mean values ($P < 0.05$).

oriented flights) or on the tunnel floor, sides, and top (in non-oriented flights). Overall, *L. testaceipes* showed an oriented flight duration significantly longer than *A. colemani* (18.4 ± 2.09 s and 13.2 ± 1.22 s, respectively; log-rank test: $\chi^2 = 4.22$, d.f. = 1, P = 0.04). However, no significant difference was found in the oriented mean flight duration according to the landing locations ($\chi^2 = 2.09$, d.f. = 2, ns).

Discussion

It has been shown that plant volatiles attract phytophagous insects (Visser, 1986) and their natural enemies (Tumlinson et al., 1992; Guerrieri et al., 1997; Powell et al., 1998; Guerrieri et al., 2002). In parasitoids this attraction can also occur when the hosts are no longer on the plant (Vinson, 1981; Elzen et al., 1986). Thus, parasitoids in the process of host habitat location move progressively towards areas that are likely to harbour potential hosts, and may be attracted to these areas by cues which are not directly produced by the hosts (Elzen et al., 1986). In our experiments, both *L. testaceipes* and *A. colemani* showed a strongly significant response to real plants compared to cardboard dummy plants, despite the latter bearing a physical appearance to real plants. Thus, it appears that the chemical stimuli contributed significantly to their attractiveness.

Previous wind tunnel studies on *L. testaceipes* have used *Schizaphis graminum* (Rondani) as an insect host, and wheat as a host plant (Schuster & Starks, 1974; Grasswitz & Paine, 1993). As in our study, *L. testaceipes* did not land more frequently on aphid-infested than on uninfested plants. For this species, the attraction to food plants of their hosts has also been reported (Schuster & Starks, 1974). Such a response could likely be involved in the establishment of host location in the field where parasitoids must first search for plants and then locate aphids on them (Schuster & Starks, 1974). In contrast, similar studies on *A. colemani* using *Myzus persicae* Sulzer as an insect host, and the bell pepper (*Capsicum annuum* L.) as a host plant, showed that experienced females responded significantly more to infested plants than to uninfested ones (Grasswitz, 1998). The ability of parasitoids to locate their host is expected to vary with different host and plant species, because they release different blends of volatiles. It is likely that the difference between our results and the results of previous work on *A. colemani* was due to the different attraction levels of the plants used in experiments. In addition, it may be possible that cucumber plants do not release specific volatiles in response to feeding by *A. gossypii*. Udayagiri & Jones (1993) reported that *Macrocentrus grandii* Goidanich was not attracted to the volatiles of pepper, the same plant that Grasswitz (1998) used with *A. colemani*, but was attracted to odours from other plant species (potato and snap bean).

In addition, the use of different rearing systems and experimental set-up could affect female responsiveness (Drost et al., 1988; Storeck et al., 2000). Regarding experimental set-up, the distance between plants placed in the wind tunnel could affect the point at which a wasp could make a decision concerning landing location (Kitt & Keller, 1998). One particularity of our bioassay was that females were exposed simultaneously to three types of plants (infested, uninfested, and dummy) so that the response to one type was not independent of the presence of the others. In other studies on *L. testaceipes* and *A. colemani*, each parasitoid was only exposed to a single plant type. Nonetheless, this difference in experimental design cannot totally explain the difference in results, at least for *L. testaceipes.* Indeed, a previous no-choice experiment carried out with the same treatments (infested, non-infested, and dummy plants) showed that *L. testaceipes* females displayed a similar response. They landed more often on real plants than on dummy plants, but with real plants, they did not land more frequently on infested plants rather than on uninfested ones (X. Fauvergue, unpubl. obs.). This similarity in results between choice and no-choice conditions reinforces our findings, that females are no more attracted to infested plants than to uninfested ones.

This study gives surprising results, in that experienced females are not more attracted to plants infested with their hosts. This behaviour is different from the behaviour of many other parasitoid species, which were shown to be more attracted to infested plants (Drost et al., 1986; McAuslane et al., 1991; Grasswitz & Paine, 1993). It appears to be counterproductive for females, with a short life-span (2 days), to spend time searching for uninfested plants in a habitat. However, the attraction of aphidiid parasitoids to their host plants has been reported for several species (Schuster & Starks, 1974; Powell & Zhang, 1983; Williams et al., 1988; Wickremasinghe & Van Emden, 1992; Udayagiri & Jones, 1993; Kitt & Keller, 1998). Some authors suggested that learning to respond to uninfested plants may serve to prolong parasitoid foraging within a local habitat during periods of low host density, when host-induced volatiles would be scarce or absent (Guerrieri et al., 1997; Powell et al., 1998). Another hypothesis is that plants may produce, even if in low quantities, the same odours as those produced by host insects. This has been demonstrated, for example, with the alarm pheromone of *S. graminum* which is detectable in the volatile profile of undamaged wheat plants (Grasswitz & Paine, 1993).

Finally, the two parasitoids studied showed a flight behaviour similar to other parasitoid species (Drost et al., 1986; Kaiser & Cardé, 1992; Guerrieri, 1996). It is likely that the difference in the flight duration observed between *A. colemani* and *L. testaceipes* was dependent on the attractiveness of the odour source and female responsiveness, as observed in other parasitoid species (McAuslane et al., 1991).

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References

Carver M & Franzmann B (2001) *Lysiphlebus* Forster (Hymenoptera: Braconidae: Aphidiinae) in Australia. Australian Journal of Entomology 40: 198–201.

Cloyd RA & Sadof CS (2000) Effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), a parasitoid of the citrus mealybug (Homoptera: Pseudococcidae). Environmental Entomology 29: 535–541.

Collett D (1994) Modelling Survival Data in Medical Research. Chapman & Hall, London.

David CT (1982) Competition between fixed and moving stripes in the control of orientation by flying *Drosophila*. Physiological Entomology 7: 151–156.

Dicke M (1999) Evolution of induced indirect defence of plants. The Ecology and Evolution of Inducible Defenses (ed. by R Tollrian & CD Harvell), pp. 62–88. Princeton University Press, NJ.

Dicke M & Sabelis MW (1988) How plants obtain predatory mites as bodyguards. Netherlands Journal of Zoology 38: 148–165.

Dicke M & van Loon JJA (2000) Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. Entomologia Experimentalis et Applicata 97: 237–249.

Drost YC, Lewis WJ & Tumlinson JH (1988) Beneficial arthropod behaviour mediated by airborne semiochemicals. V. Influence of rearing method, host plant, and adult experience on host-searching behaviour of *Micropletis croceipes* (Cresson), a larval parasitoid of *Heliothis*. Journal of Chemical Ecology 14: 1607–1616.

Drost YC, Lewis WJ, Zanen PO & Keller MA (1986) Beneficial arthropod behaviour mediated by air-borne semiochemicals. I. Flight behaviour and influence of preflight handling of *Microplitis croceipes* Cresson. Journal of Chemical Ecology 12: 1247–1262.

Elzen GW, Williams HJ & Vinson SB (1986) Wind tunnel flight responses by hymenopterous parasitoid *Campoletis sonorensis* to cotton cultivars and lines. Entomologia Experimentalis et Applicata 42: 285–289.

Grasswitz TR (1998) Effect of adult experience on the host-location behaviour of the aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). Biological Control 12: 177–181.

Grasswitz TR & Paine TD (1993) Effect of experiences on in-flight orientation to host-associated cues in the generalist parasitoid *Lysiphlebus testaceipes*. Entomologia Experimentalis et Applicata 68: 219–229.

Guerrieri E (1996) Flight behaviour of *Encarsia formosa* in response to plant and host stimuli. Entomologia Experimentalis et Applicata 82: 129–133.

Guerrieri E, Pennacchio F & Tremblay E (1997) Effect of adult experience on in-flight orientation to plant and plant-host complex volatiles in *Aphidius ervi* Haliday (Hymenoptera: Braconidae). Biological Control 10: 159–165.

Guerrieri E, Poppy GM, Powell W, Rao R & Pennacchio F (2002) Plant-to-plant communication mediating in-flight orientation of *Aphidius ervi*. Journal of Chemical Ecology 28: 1691–1703.

Hochberg Y (1988) A sharper Bonferroni procedure for multivariate tests of significance. Biometrika 75: 800–802.

Jang EB, Messing RH, Klungness LM & Carvalho LA (2000) Flight tunnel responses of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) to olfactory and visual stimuli. Journal of Insect Behaviour 13: 525–538.

Kaiser L & Cardé RT (1992) In-flight orientation to volatiles from the plant-host complex in *Cotesia rubecula* (Hymenoptera: Braconidae): increased sensitivity through olfactory conditioning. Physiological Entomology 17: 62–67.

Kitt JT & Keller MA (1998) Host selection by *Aphidius rosae* Haliday (Hymenoptera: Braconidae) with respect to assessment of host specificity in biological control. Journal of Applied Entomology 122: 57–63.

Knight P (1944) Insects associated with the palay rubber vine in Haiti. Journal of Economic Entomology 37: 100–102.

Mackauer M & Stary P (1967) Ichneumonoidae, World Aphidiidae. Index of Entomophagous Insects (ed. by V Delucchi & G Rémaudiere). Le François, Paris.

McAuslane HJ, Vinson SB & Williams HJ (1991) Influence of adult experience on host microhabitat location by the generalist parasitoid, *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Journal of Insect Behaviour 4: 101–113.

Messing RH & Rabasse JM (1995) Oviposition behaviour of the polyphagous aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). Agriculture, Ecosystems and Environment 52: 13–17.

Nordlund DA, Lewis WJ & Altieri MA (1988) Influences of plant-produced allelochemicals on the host-prey selection behaviour of entomophagous insects. Novel Aspects of Insect–Plant Interactions (ed. by P Barbosa & DK Letourneau), pp. 65–90. Wiley, New York.

Powell W, Pennacchio F, Poppy GM & Tremblay E (1998) Strategies involved in the location of hosts by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae: Aphidiinae). Biological Control 11: 104–112.

Powell W & Zhang ZL (1983) The reaction of two cereal aphid parasitoids, *Aphidius uzbeckistanicus* and *A. ervi* to host aphids and their food plants. Physiological Entomology 8: 439–443.

SAS Institute Inc. (1999) SAS/STAT User's Guide, Version 8. SAS Institute Inc, Cary, NC.

Schuster DJ & Starks KJ (1974) Response of *Lysiphlebus testaceipes* in an olfactometer to a host and a non-host insect and to plants. Environmental Entomology 3: 1034–1035.

Sekhar PS (1960) Host relationships of *Aphidius testaceipes* (Cresson) and *Praon aguti* (Smith), primary parasites of aphids. Canadian Journal of Zoology 38: 593–603.

Stary P (1975) *Aphidius colemani* Viereck: Its taxonomy, distribution, and host range. Acta Entomologica Bohemoslovaca 72: 156–163.

Storeck A, Poppy GM, Van Emden HF & Powell W (2000) The role of plant chemical cues in determining host preference in the generalist aphid parasitoid *Aphidius colemani*. Entomologia Experimentalis et Applicata 97: 41–46.

Tumlinson JH, Turlings TCJ & Lewis WJ (1992) The semiochemical complexes that mediate insect parasitoid foraging. Agricultural Zoology Reviews 5: 221–251.

Udayagiri S & Jones RL (1993) Variation in flight response of the specialist parasitoid *Macrocentrus grandii* Goidanich to odours from food plants of its European corn borer host. Entomologia Experimentalis Applicata 69: 183–193.

Vet LEM & Dicke M (1992) Ecology of infochemical use by natural enemies in a trophic context. Annual Review of Entomology 37: 141–172.

Vet LEM, Wackers FL & Dicke M (1991) How to hunt for hiding hosts: the reliability-detectability problem in foraging parasitoids. Netherlands Journal of Zoology 41: 202–213.

Vinson SB (1976) Host selection by insect parasitoids. Annual Review of Entomology 21: 109–134.

Vinson SB (1981) Habitat location. Semiochemicals: Their Role in Pest Control (ed. by DA Nordlund, RL Jones & WJ Lewis), pp. 51–77. Wiley-Interscience, New York.

Visser JH (1986) Host odour perception in phytophagous insects. Annual Review of Entomology 31: 121–144.

Wellings PW, Hart PJ, Morneau DC & Kami V (1994) The introduction and establishment of *Aphidius colemani* Viereck (Hymenoptera: Aphidiinae) in Tonga. Journal of Applied Entomology 118: 419–428.

Whitman DW & Eller FJ (1990) Parasitic wasps orient to green leaf volatiles. Chemo-Ecology 1: 69–75.

Wickremasinghe MGV & Van Emden HF (1992) Reactions of adult female parasitoids, particularly *Aphidius rhopalosiphi*, to volatile cues from the host plants of their aphid prey. Physiological Entomology 17: 297–304.

Williams HJ, Elzen GW & Vinson SB (1988) Parasitoid–host–plant interactions, emphasizing cotton, (*Gossypium*). Novel Aspects of Insect–Plant Interactions (ed. by P Barbosa & DK Letourneau), pp. 171–200. John Wiley & Sons, New York.