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LETTER

Alarm pheromone mediates production of winged dispersal morphs in aphids

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Abstract

The aphid alarm pheromone (*E*)-β-farnesene (EBF) is the major example of defence communication in the insect world. Released when aphids are attacked by predators such as ladybirds or lacewing larvae, aphid alarm pheromone causes behavioural reactions such as walking or dropping off the host plant. In this paper, we show that the exposure to alarm pheromone also induces aphids to give birth to winged dispersal morphs that leave their host plants. We first demonstrate that the alarm pheromone is the only volatile compound emitted from aphid colonies under predator attack and that emission is proportional to predator activity. We then show that artificial alarm pheromone induces groups of aphids but not single individuals to produce a higher proportion of winged morphs among their offspring. Furthermore, aphids react more strongly to the frequency of pheromone release than the amount of pheromone delivered. We suggest that EBF leads to a 'pseudo crowding' effect whereby alarm pheromone perception causes increased walking behaviour in aphids resulting in an increase in the number of physical contacts between individuals, similar to what happens when aphids are crowded. As many plants also produce EBF, our finding suggests that aphids could be manipulated by plants into leaving their hosts, but they also show that the context-dependence of EBF-induced wing formation may hinder such an exploitation of intraspecific signalling by plants.

Keywords

Alarm pheromone, (*E*)-β-farnesene, multitrophic interaction, pea aphid, wing induction.

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INTRODUCTION

In recent years, a large number of induced defences in plant-herbivore and predator-prey systems has been described, along with chemical signals that mediate these interactions (e.g. Karban & Baldwin 1997; Tollrian & Harvell 1998; Kessler & Baldwin 2001). Inducible defences are produced in response to stimuli from natural enemies and either deter further predator attack or increase an organism's tolerance to damage (e.g. Karban & Baldwin 1997; Tollrian & Harvell 1998). An important and often as yet unanswered question for many of the newly found induced defences is the question of whether or not the chemical communication involved in induced defences is honest and therefore potentially stable, or whether the signalling pathway can be exploited by illicit signallers (e.g. Godfray 1995; Johnstone 1995; van der Meijden & Klinkhamer 2000). For example, when plants attacked by herbivores release volatiles to attract predators or parasitoids, it is not clear that natural enemies should always respond to such cues, because these cues might be unreliable (van der Meijden & Klinkhamer 2000; Dicke & Hilker 2003). There is also the danger that not only natural enemies but also herbivores respond to the plant signal, such that the signal would be exploited (Godfray 1995). Similarly, in alarm communication between prey attacked by predators the benefits to the signaller are not necessarily clear if the signaller and the receiver are not related (e.g. Kobayashi & Yamamura 2003). For many of the examples of chemical signalling in induced defences, the multitrophic context of the interaction has to be considered to fully understand the evolution and stability of the signalling system (Dicke & van Loon 2000).

Aphids are important pest insects in the temperate region, damaging plants by sucking nutrients from the phloem and by transmitting plant viruses (Minks & Harrewijn 1987). Because of their high abundance, aphids are attacked by a wide range of specialized predators such as ladybirds, lacewings and hoverfly larvae which have been shown to

strongly influence the growth and persistence of aphid colonies (Dixon 1998). Under predator attack, aphids secrete droplets from the siphunculi, a pair of tube-like structures on the back of their bodies. In addition to having direct defensive function by gluing predator mouthparts together, the droplets contain an alarm pheromone whose main and sometimes only component is the sesquiterpene (*E*)-β-farnesene (EBF) (Bowers *et al.* 1972; Kislow & Edwards 1972; Edwards *et al.* 1973; Nault *et al.* 1973; Pickett & Griffiths 1980). EBF triggers various behavioural reactions in other aphids such as increased alertness, withdrawal of the stylets from the plant, walking behaviour and dropping off the host plant (Montgomery & Nault 1977; Wohlers 1980). Although the quantities of EBF potentially released by individuals are known (Mondor *et al.* 2000), little information exists about dose–response curves under natural conditions as the emission of EBF or other volatiles from aphid colonies has not been quantified so far.

The attacked aphids that emit EBF are mostly killed, but other aphid colony members may escape from predator attack in time and therefore benefit from the release of the alarm pheromone. The evolution of this altruistic alarm communication has only been possible because of the peculiarities of the life cycle of many aphid species. Sexual reproduction in aphids takes place only in autumn, when males and females mate and produce a diapausing egg. From spring to autumn, aphids reproduce asexually such that all aphids descending from a female that hatches in spring are genetically identical. This clonal structure of aphid colonies makes the evolution of alarm pheromone an extreme case of kin selection. Because most receivers are genetically identical to the signaller, the benefit of an early escape accrues to the same genotype that is killed by the predator (McAllister & Roitberg 1987). Aphids exhibit a polyphenism whereby individual aphids are either winged or wingless (Dixon 1998). The winged dispersal morphs mostly leave the plants on which they were born to colonize new plants and, in many species, are only produced in response to adverse environmental conditions such as crowding or poor plant quality. The wingless morphs mostly stay on the plant on which they are born. In the case of crowding, the proximate mechanism for wing induction is the increased number of physical contacts between individuals because of increasing aphid density on the plant (Sutherland 1969).

Recently, it was found that in the presence of natural enemies pea aphids (*Acyrthosiphon pisum*) increase the proportion of winged morphs among their offspring (Dixon & Agarwala 1999; Weisser *et al.* 1999; Sloggett & Weisser 2002; Kunert & Weisser 2003). While this reaction is one of the first cases of a predator-induced morphological shift in a terrestrial predator-prey system, the mechanism underlying this response has remained unclear. For this paper, we carried out a series of experiments to test for the involvement of EBF in aphid wing induction and the relation of EBF emission to attack by predators. First, to test if a volatile chemical cue could be involved in predator-induced aphid wing production, we sampled the head space of a pea aphid colony exposed to predation by lacewing larvae, *Chrysoperla carnea*, in a volatile collection chamber. Second, to test for the involvement of EBF in the formation of winged morphs, we exposed pea aphids either singly or in small groups to artificial EBF several times during the day using different dosages.

MATERIALS AND METHODS

General experimental conditions

Clones of pea aphids were reared and the experiments were conducted on 3-week-old broad beans, *Vicia faba* L. The plants were grown in 10-cm-diameter pots. To avoid escape of the aphids, the plants were covered with air-permeable cellophane bags (18.8 × 39 cm). Rearing of aphids and plants and experiments took place at 20 °C, with a photoperiod of 16 : 8 L : D and *c.* 75% relative humidity.

Rearing of experimental aphids

Several different lines of aphids were established. To initiate an aphid line one single foundress aphid was placed on a bean plant. This foundress was left to reproduce over a 2-day period and then removed from the plant. When the progeny reached the fourth larval or young adult stage, they were transferred separately to new plants to avoid crowding. The progeny were then allowed to give birth to several offspring (5–10) and were removed after a 2-day period. This procedure was repeated until enough offspring from a line were available for an experiment. Offspring were split across the different treatments and each line was thus used as one replicate and consisted of genetically identical aphids.

Experiment 1: collection of volatiles from the headspace of aphid colonies

This experiment was conducted with eight lines of a red clone (BP) of the pea aphid, originally collected in Bayreuth, Germany. Plants used for this experiment were potted in beakers of glass to prevent volatile emission from plastic flowerpots. Fifty adults from a line were transferred to two new plants (25 adults per plant) and allowed to reproduce for $2\frac{1}{2}$ days. Immediately prior to collecting volatiles 10 1^{st}-instar predatory lacewing larvae were transferred to one of the replicates. Volatile samples were collected for both the predator and the control treatments simultaneously during two successive intervals during the light period

(6:00–22:00 hours) and during the dark (22:00–6:00 hours) for a total of 24 h. Immediately after the volatile collection, aphids and predators were removed from the plants and frozen for later counting. To estimate the number of consumed aphids, the number of surviving aphids in the predator treatment was subtracted from the number of aphids in the control.

Volatile collection

Volatiles were collected using an apparatus which consisted of two 3-L glass chambers, one containing the control and one the treatment plant. Purified air at a rate of 4 L min^{-1} entered the chambers at the top through tubes that reached the bottom of the chambers to ensure exchange of air. Volatiles were collected on a solid-phase adsorbent trap containing Super-Q (80/100 mesh; Alltech, Deerfield, IL, USA). The trap was inserted in a port at the top of the chamber through which air was pumped at a rate of 2 L min^{-1}. Thus 50% of the air passed through the collection trap, with the remainder exiting the chamber through a small hole on the top.

Analysis of volatiles

Volatiles were extracted from the traps by washing with 170 μL methylene chloride. An internal standard was added to the extract (600 ng nonyl acetate in 30 μL of hexane). Of each collection sample 1 μL was analysed on a Hewlett–Packard 6890 (Hewlett–Packard, Palo Alto, CA, USA) gas chromatograph equipped with a splitless injector (temperature 220 °C) and a flame ionization detector (temperature 250 °C). H_2 was used as a carrier gas at a linear flow rate of 2 mL min^{-1}. All samples were analysed on a DB-5MS column (J & W, Folsom, CA, USA), 30 m × 0.25 mm i.d. × 0.25-μm thick film of bonded methyl silicone with 5% phenyl. The column oven was maintained at 40 °C for 3 min than increased at a rate of 5 °C min^{-1} to 220 °C followed by 220 °C for 3 min.

To identify compounds, samples were analysed by GC–MS with a Hewlett–Packard 6890 equipped with a Hewlett–Packard 7683 auto sampler and a Hewlett–Packard 5973 quadrupole-type mass selective detector operated in electron impact mode. The mass detector had a transfer line temperature of 230 °C, a source temperature of 230 °C, a quadrupole temperature of 150 °C, an electron energy of 70 eV, and a scan range of 50–400 amu. Helium was used as a carrier gas at a linear flow rate of 1 mL min^{-1}. All samples were analysed on a DB-5MS (J & W) column as specified above. The column oven temperature programme was set as described above. GC retention times of EBF were compared with those of an authentic EBF standard (Bedoukian, Danbury, CT, USA). In addition the mass spectra were compared with those of the National Institute of Standards and Technology library and the Wiley library (Hewlett–Packard).

Experiments 2–4: application of alarm pheromone and control solvent

Aphids were exposed to either 3 μL of a solution of EBF dissolved in *n*-hexane or to 3 μL of the solvent. The solutions were applied with a micropipette through a small hole in the cellophane bag to a piece of filter paper fixed by a wooden toothpick at the base of the pot. The amounts of EBF used are approximate amounts found naturally in pea aphids (Mondor *et al.* 2000, result of experiment 1).

Experiment 2: exposure of aphid groups to alarm pheromone

A red clone (JP1) of pea aphid, originally collected in Jena, Germany, was used for this experiment. Ten lines of aphids were established. A line consisted of 12 groups of 15 third or fourth instar aphids, placed on 12 different plants. Aphids of six groups were exposed to the alarm pheromone solution containing 50, 300 or 1000 ng EBF, applied either twice (8:00 and 18:00 hours) or five times (9:00, 11:30, 14:00, 16:30 and 19:00 hours) per day, and aphids of the other six control groups received hexane at the corresponding frequency and times. After 5 days of application, the aphids, by now adults, were removed from the plants and all offspring produced during the experiment were reared until they reached the fourth instar or early adult stage, then taken off the plant and frozen for later counting and determination of the morph type.

Experiment 3: exposure of single aphids to alarm pheromone

This experiment was similar to experiment 2, but 20 lines of aphids were established and each line consisted of two plants (treatment and control) with one single adult aphid each. Alarm pheromone solution containing 50 ng EBF in *n*-hexane or a solvent control were applied five times a day. Each day the adult aphids were transferred to new plants. The offspring were reared until adulthood, then taken off the plant and frozen for later counting and determination of the phenotype.

Experiment 4: quantification of behavioural responses

For this experiment, a red clone (BP) of pea aphid was used. Offspring from 10 lines were reared to third or fourth instar and divided into six groups of 15 individuals each. Three groups of aphids were exposed to 50 ng EBF one, three or five times a day. The other three groups served as controls.

At each application, the behavioural reactions of the aphids, including kicking, dropping, walking, body and antennal movement, were observed for 1 min and documented separately for adults and juvenile aphids. For each behaviour the extent of reaction in the aphid group was classified in the following categories: 0 = no reaction, 1 = one aphid reacted, 2 = few (2–3) aphids reacted, 3 = some (4–8) aphids reacted, 4 = more than eight aphids reacted. For walking, the strength of aphid walking responses was calculated by summation of the category numbers over the time-course of the experiment. After 5 days of treatment the adult aphids were removed and the progeny reared to maturity when they were frozen and their morphology scored.

Statistical analysis

Results are presented as mean ± SE. The influence of the EBF application treatment on wing production was tested with a generalized linear model (GLM, Crawley 2002). To investigate the importance of the number of applications and the amount of EBF on wing induction, only the EBF treatments were included in the GLM. To analyse the influence of the number of consumed aphids on the amount of EBF released and the dependence of the percentage of winged morphs produced on behavioural patterns linear regressions were used. The software package SIGMASTAT for Windows version 2.03 (SPSS Inc. 1997) was used for regressions and the program R version 1.6.2 (Venables *et al.* 2002) was used for generalized linear models.

RESULTS

Experiment 1: collection of volatiles from the headspace of aphid colonies

Compared with control colonies without predators, the only new peak appearing in the gas chromatograms of headspace volatiles was that of EBF (Fig. 1a). Moreover, the amount of EBF released correlated closely with the rate of predation of the lacewing larvae (Fig. 1b).

Experiment 2: exposure of aphids groups to alarm pheromone

The number of offspring produced during the experiment did not differ between the groups ($F = 0.828$, $P = 0.567$). Aphids exposed to alarm pheromone produced a significantly higher proportion of winged morphs among their offspring compared with a control ($t = 7.733$, $P < 0.001$).

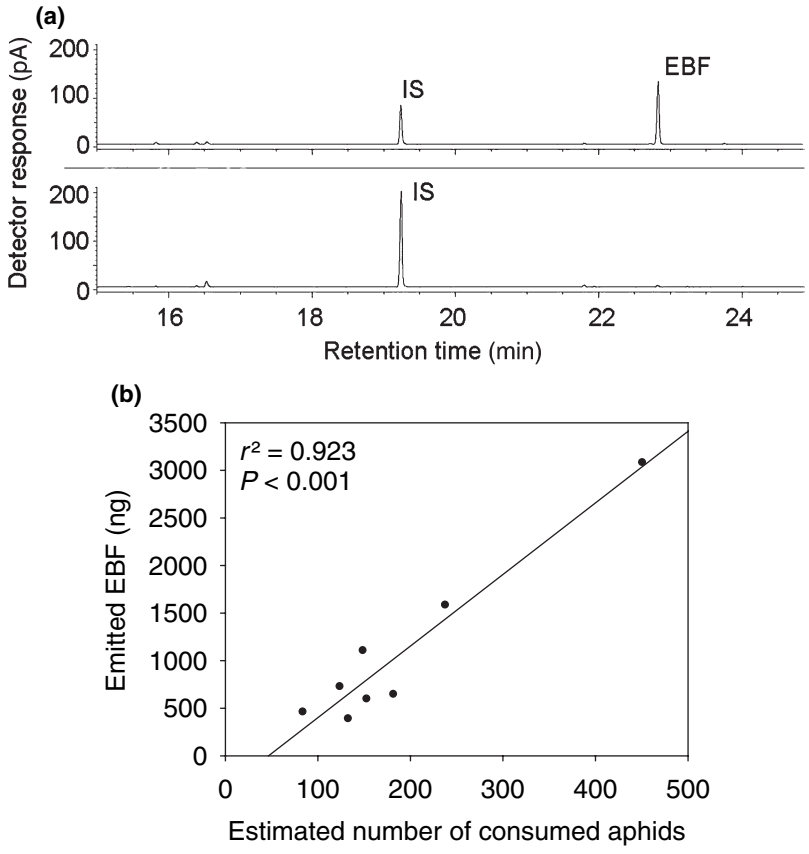

Figure 1 Volatile chemicals collected from the headspace of pea aphid colonies on bean plants. Twenty-five adult aphids and their offspring born during a period of 2.5 days were placed in a volatile collection chamber for 24 h. (a) Chromatographic profiles after analysis of volatiles from treatments during light period with (above) and without (below) predatory lacewing larvae released in the aphid colony. IS, internal standard (nonyl acetate); EBF, (*E*)-β-farnesene. (b) The relationship between the amount of EBF released and the predation rate of the lacewing larvae, calculated as the difference in aphid numbers between control and predator treatment at the end of the experiment. Regression line: amount of farnesene released (ng) = −350.5 + 7.5 × estimated number of consumed aphids ($P < 0.001$, $r^2 = 0.923$, $n = 8$).

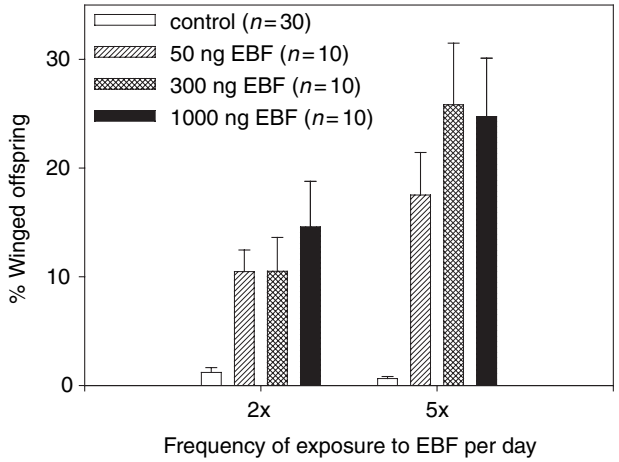

Figure 2 Percentage of winged morphs among offspring born by mothers of the clone JP1 exposed to various quantities of EBF with a different frequency. The bars show the mean values ± SE.

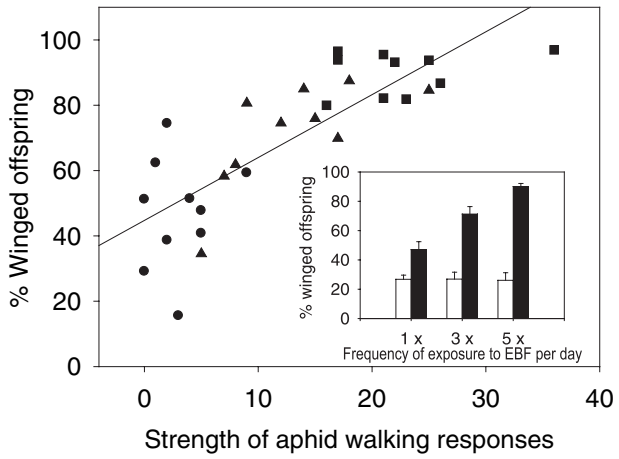

Figure 3 Percentage of winged morphs among offspring related to the number of aphids walking away from their feeding site when exposed to EBF (see Materials and methods). Aphid mothers of the clone BP were exposed to 50 ng EBF once a day (circles), three times a day (triangles), and five times a day (squares). A linear regression over all 30 data points shows a significant influence of the walking behaviour on wing induction ($r^2 = 0.655$, $F = 53.054$, $P < 0.001$). Walking behaviour was assessed by classifying the reaction of the aphid group as follows: 0 = no reaction, 1 = one aphid reacted, 2 = few (2–3) aphids reacted, 3 = some (4–8) aphids reacted, 4 = more than eight aphids reacted. The strength of aphid walking responses was calculated by summation of the category numbers over the time-course of the experiment. The inset shows the percentage of winged morphs among the offspring born in this experiment depending on the frequency of EBF exposure. The bars show the mean values ± SE. Open bars indicate the control groups, filled bars the EBF treatment groups.

The frequency of exposure was more important for wing induction than the amount of EBF applied or aphid density (frequency of exposure: $t = 3.312$, $P = 0.002$; amount of EBF: $t = 1.294$, $P = 0.201$; aphid density: $t = 1.481$, $P = 0.144$; Fig. 2).

Experiment 3: exposure of single aphids to alarm pheromone

Aphids that were kept singly on plants did not produce any winged offspring when exposed to EBF even though they showed typical behavioural responses such as withdrawal of the stylet from the plant, walking behaviour and dropping off the host plant.

Experiment 4: quantification of behavioural responses

The percentage of winged morphs among offspring was significantly related to the number of aphids walking from their feeding site when exposed to EBF. A linear regression over all 30 data points show a significant influence of the walking behaviour on the wing induction ($r^2 = 0.655$, $F = 53.054$, $P < 0.001$), the higher the number of aphids that were observed walking after pheromone exposure, the higher the resulting proportion of offspring that developed into a winged phenotype (Fig. 3).

DISCUSSION

Our results clearly show that the alarm pheromone EBF can mediate the production of winged dispersal morphs in pea aphids. As aphids in groups produced a significantly higher proportion of winged morphs among their offspring when exposed to EBF compared with a control but aphids that were kept singly on plants did not produce any winged offspring when exposed to EBF, the perception of alarm pheromone alone is not sufficient to trigger wing production in aphids. As the strength of the behavioural responses of aphids to alarm pheromone exposure closely corresponded to the observed increase in wing induction, we suggest that perception of EBF results in a 'pseudo-crowding' effect whereby the alarm pheromone perception causes increased walking behaviour resulting in an increase in the number of physical contacts between individuals, similar to what happens when aphids are crowded (Sutherland 1969; Sloggett & Weisser 2004). In wing induction caused by crowding Sutherland (1969) found that the tactile cue is the important one. The more often the release of alarm pheromone, representing a high-predator activity, the higher the movement activity in the aphid colony, which is consistent with the close correlation between predator activity and the percentage of winged offspring observed in earlier studies (Kunert & Weisser 2003). Thus, although

predation in aphid colonies results in a decrease in aphid numbers on the plant, the increase in movements within the aphid colony results in individuals perceiving an increase in aphid density. Alarm pheromone is perceived by aphids through specialized sensory organs on the aphids' antennae, the primary and, to a lesser extent, the secondary rhinaria (Nault *et al.* 1973; Wohlers & Tjallingii 1983). Therefore aphids with ablated antennae do not show the typical defence reactions such as walking or dropping off the host plant (G. Kunert & W.W. Weisser, unpublished results), and consistent with the 'pseudo-crowding' hypothesis, aphids with ablated antennae do not produce more winged offspring in the presence of predatory lacewing larvae (Kunert & Weisser 2005). Further support for the 'pseudo-crowding' hypothesis comes from experiments with different degrees of predation. When predators reduce the number of aphids on the plants very strongly so that only a few adults are left, the proportion of winged offspring produced is similar to the no-predator control, suggesting that although alarm pheromone emission must have been high, the few aphids left on the plant encountered each other rarely, in contrast to a stronger wing induction in replicates where the predator consumed fewer individuals, leaving more individuals on the plant (Kunert & Weisser 2003).

The change in phenotype because of EBF exposure reported here has consequences for our understanding of plant-aphid-natural enemy interactions and for aphid control. Our findings suggest that natural enemies that trigger alarm pheromone release in aphids also trigger the emigration of individuals from the plant. Thus, plants not only benefit from the reduction of aphid numbers through the feeding activities of the natural enemies, but also from a further reduction through the departure of winged individuals that will deposit their offspring on other plants. Because aphids are highly fecund, often producing five to ten offspring per day, this reduction in future aphid reproduction may well be of even greater advantage to the plant than direct predation on currently feeding aphids. EBF is a compound present in the headspace of many plants, and sesquiterpene synthases involved in EBF production have been isolated from several plant species (Crock *et al.* 1997; Du *et al.* 1998; Schnee *et al.* 2002). The EBF may repel aphids from settling on those plants (Bernasconi *et al.* 1998) and there is some indication that EBF may act as an attractant to aphid natural enemies (Micha & Wyss 1996; Al Abassi *et al.* 2000), which would reduce aphid density. However, our results suggest a direct way in which plants could use alarm pheromone emission to reduce their aphid load that is by using EBF as an allomone to manipulate aphids into the production of winged morphs, which then can leave the plant. Given the huge benefit that would accrue to a plant able to induce winged morph production, it is tempting to speculate about mechanisms that prevent such an exploitation of intraspecific communication by plants. First, there is evidence that aphids compare the ratio of EBF they perceive to that of (*E*)-β-caryophyllene, another sesquiterpene often released by plants, to distinguish between aphid-released and plant-derived EBF (Dawson *et al.* 1984). However, for the wild potato *Solanum berthaultii*, which is resistant against a number of pests of cultivated potatoes, including aphids, it was shown that the plant releases sufficient quantities of EBF from glandular hairs to prevent settlement of the peach potato aphid *Myzus persicae* (Gibson & Pickett 1983), showing that the release of EBF as an aphid defence mechanism may be overcome by plants. Our results suggest a second mechanism by which aphids are able to distinguish between the actual presence of predators and plants trying to mimic the presence of aphid predators. As wing induction depends on the frequency rather than the amount of EBF released, successful manipulation of aphids by plant-released EBF would require a repeated release of aphid alarm pheromone. The stronger response by aphids to pulses rather than a constant or single release of EBF may also explain why attempts to reduce aphid populations by spraying crop fields with alarm pheromone have not been very successful so far. In these field trials the emphasis has been on behavioural responses such as dropping or walking off the plant (Pickett 1989; Pickett *et al.* 1991), rather than production of winged dispersal morphs.

We have shown that aphid alarm pheromone, first described >30 years ago, not only causes a variety of escape behaviours in aphids, but is also involved in the shift from wingless to winged morphs in aphid colonies and thus may result in aphids leaving plants where predators are present. In the coevolutionary arms race between plants and aphids, the most important pest insects in the temperate region, plants may benefit from exploiting this signal. However, our results show that the context-dependence of EBF-induced wing formation may hinder such an exploitation of intraspecific communication by illicit signallers. Thus, EBF is not only an important example of alarm communication within an insect species, but it also exemplifies the multiple functions and various selection pressures that may be involved in intraspecific signalling in a multitrophic context.

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