© 2007 The Authors *Insect Science* (2007) 14, 57–63
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Role of terpenes from aphid-infested potato on searching and oviposition behavior of *Episyrphus balteatus*

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Abstract To cope with pathogen and insect attacks, plants develop different mechanisms of defence, in both direct (physical and chemical) and indirect ways (attractive volatiles to entomophagous beneficials). Plants are then able to express traits that facilitate "top-down" control of pests by attracting herbivore predators. Here we investigate the indirect defence mechanism of potato plants by analyzing the volatile patterns of both healthy and aphid-infested plants. Important changes in the emitted terpene pattern by the *Myzus persicae* infested host plant were observed. Using Solid Phase MicroExtraction (SPME) and GC-MS, the (*E*)-β-farnesene (EBF) appeared to be emitted by aphid-infested potato and not by healthy plants. To assess the infochemical role of these volatile releases after aphid damage on the aphidophagous predators *Episyrphus balteatus*, the hoverfly foraging behavior was assessed using the Observer 5.0 software (Noldus, Wageningen, The Netherlands). Aphid-free potato plants were also used as a control volatile source in the predator behavioral study. While aphid-infested plants induced efficient searching and acceptation behaviors leading to egg-laying, no kairomonal effect of healthy potato plants was observed, leading to longer immobility durations and shorter searching periods in the net cage. High oviposition rate of *E. balteatus* was observed when aphid-infested potato was used (mean of 48.9 eggs per laying and per female). On the other hand, no egg was produced by the hoverfly on healthy aphid-free plants. The *E. balteatus* foraging and reproductive behaviors according to the volatile emission from aphid-infested plants are discussed in relation to the potential use of active infochemical molecules in integrated aphid pest management.

Key words aphid infested, behavior, *Episyrphus balteatus*, potato, terpenes
DOI 10.1111/j.1744-7917.2007.00126.x

Introduction

Plant-insect relations are mainly regulated by the evolution of the plant defence mechanisms and the ways herbivorous insects adapt themselves to these defensive systems (Berenbaum, 1995). A broad range of insect pests is efficiently controlled by the production of defensive molecules. Beside the induction of several direct defence molecule productions, such as secondary compounds and pathogenesis related proteins (PRP), the emission of particular volatile organic compounds (VOCs) constitutes an efficient indirect system of plant defence by influencing the third trophic level, namely the entomophagous beneficials. In tritrophic interactions studies investigating plant-hervivore-entomophagous insect relations, the plant response to herbivore damage has already been shown to affect the biological parameters of beneficial species (Kessler & Baldwin, 2001). In particular, the aphid host-

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plant species was shown to significantly affect ladybird and hoverfly development and reproduction (Francis *et al*., 2001; Vanhaelen *et al*., 2002).

Not only the biological parameters were affected by aphid and host plant associations but the behavior of beneficials also. Recently, reports of electroantennogram (EAG) recordings from three predatory insect species, namely *Coleomegilla maculata* (Coleoptera, Coccinellidae), *Chrysoperla carnea* (Nevroptera, Chrysopidae) (Zhu *et al*., 1999), and *Coccinella septempunctata* (Coleoptera, Coccinellidae; Al Abassi *et al*., 2000) showed significant EAG responses to semiochemicals released from potential preys and host plants (Zhu & Park, 2005). These predators possibly use such chemicals to locate their prey. Ninkovic *et al*. (2001) also demonstrated that the seven-spot ladybird, *C. septempunctata*, responded positively to volatiles from the aphid, *Rhopalosiphum padi*, and *Hordeum vulgare* infested plants. Two molecules, namely (*E*)-β-farnesene (EBF) and β-caryophyllene, were found to be a kairomone and an informative inhibitor respectively, for the seven-spot ladybird by electroantennography and olfactometry methods (Al Abassi *et al*., 2000). The release of plant VOCs, notably the terpenoids, specifically after herbivory, are known to attract parasitoids and predators. These herbivore-induced VOCs actively increased the feeding activity of entomophagous larvae and global predation pressure on the herbivores (De Moraes *et al*., 1998). Particularly, (*Z*)-3-hexen-1-ol, linalool and (*Z*)-α-bergamotene from herbivore-damaged plants were found to attract predators and to increase the predation rate by generalist predators (Kessler & Baldwin, 2001). Particularly, the *Episyrphus balteatus* hoverfly positively responded to semiochemical cues from preys, from host plants and aphid-host-plant associations: *E. balteatus* was attracted by EBF, the well known aphid alarm pheromone (Francis *et al*., 2005b). The latter molecule was identified as the main volatile substance in 16 species, alone or associated with other molecules (Francis *et al*., 2004). Also, the alarm pheromone was only a minor component of the volatile molecule patterns from five other aphid species. Only two of the 23 tested species, *Euceraphis punctipennis* and *Drepanosiphum platanoides*, did not release EBF at all but other terpenes were identified (Francis *et al*., 2004). Terpene molecules were found to be released by aphids but also by plants, mainly under different stress situations such as after pest damage (Francis *et al*., 2001). Particular volatile emissions from aphid-plant associations could be then used as reliable cues by aphidophagous beneficials to locate potential preys. Investigation of the volatile pattern variations of aphid-infested plants and the assessment of their infochemical role is necessary to better understand the relations between plants, aphids and the aphidophagous beneficials.

The objective of this work was to understand mechanisms of indirect defence of aphid-infested potato plants toward a predatory beneficial, namely the *E. balteatus* hoverfly, by: (i) collecting the volatile pattern of healthy and *Myzus persicae* infested plants by SPME and analysing them by GC-MS; and (ii) by assessing the infochemical role of the aphid-infested plant volatiles on the aphidophagous predator *E. balteatus* foraging behavior by using the Observer 5.0 software (Noldus).

Materials and methods

Insect and plant rearing

Potatoes (*Solanum tuberosum* L.) were grown in 30 cm × 20 cm × 5 cm plastic trays including a mixture of vermiculite and perlite (1/1) and were used as host plants for *Myzus persicae* Sultzer. Aphids were reared in a condition-controlled room (16 : 8 L : D and 20 ± 2°C).

Adults of *Episyrphus balteatus* were reared in net cages (75 cm ×60 cm ×90 cm). The latter were fed with pollen and sugar in separate Petri dishes. Water was also supplied. The rearing was realised at 20 ± 2°C and 16 : 8 L : D. Two-to-three-week-old hoverflies were used in the following experiments.

At hatching, *E. balteatus* larvae were placed in aerated plastic boxes (11 cm × 10 cm × 4 cm) to be fed with *M. persicae ad libidum*. Hoverflies were mass-reared in a condition-controlled room under identical environmental conditions as previously described.

Volatile collection

The last leaf (composed of 5 leaflets) was picked from 36-day-old potato plants *S. tuberosum* c.v. Bintjes and immediately used for volatile emission analysis. Three different samples were prepared:

Sample 1. Intact leaf was cut and introduced in a 10 mL septum-cap vial and allowed to equilibrate for 10 min at 40°C.

Sample 2. Leaves were individually pricked with 9 entomological pins and were then placed in a vial and allowed to equilibrate as above.

Sample 3. Leaf was infested for 7 days with 50 *M. persicae* aphids before cutting and preparing as above.

Each condition was analyzed in triplicate.

Volatiles from each sample were collected by SPME technique. Supelco SPME devices coated with divinylbenzene/carboxen/polydimethylsiloxane (DVB/CAR/PDMS, 50/30 μm) were used to sample the potato leaf headspace. After the equilibration time, the fiber was exposed to the headspace for 50 min at 40°C.

Volatile analysis by GC-MS

The volatiles sampled by SPME were analyzed after equilibration time by GC-MS on an Agilent 5973 mass selective detector (MS), scanning from m/z 35-350, coupled with an Agilent 6890N gas chromatograph. The following analytical conditions were used: splitless injection at 250°C, HP5-MS (5% phenyl-dimethylpolysiloxane) column (30 m × 0.25 mm, df = 1 μm). The temperature program was from 35°C (2 min hold) to 150°C at 5°C/min then to 260°C at 20°C/min. Injector temperature was 270°C. The MS spectra were obtained in the EI mode at 70eV. The analytes were identified on the basis of their retention times and by interpretation of MS fragmentation patterns. The recorded spectra were finally compared to: (i) those of the Wiley238.L spectral library; and (ii) those related to previous analysis of our pure terpene references.

Behavioral assays

Free or aphid-infested *S. tuberosum* plants (6 true leaves, 20 cm high, 36-day-old plants) were presented to *E. balteatus* gravid female (10 replicates per assay) in a no-choice experiment (one free or one aphid-infested plant at a time in a net cage [25 × 25 × 50 cm]). A single mated hoverfly female (21 days old) was introduced in the net cage in the presence of either healthy or aphid-infested plants and was observed for 10 min. The behaviors that were visually observed and simultaneously encoded using the Observer 5.0 software (Noldus) were grouped as described below:

1. Immobility: when the hoverfly stayed on the net cage without moving;
2. Searching: when the syrphid flew in the cage around the infested plant, either in an extensive or intensive way;
3. Acceptation: when the hoverfly landed on the plant, stayed immobile or walked on it, made proboscis extension on the plant surface;
4. Oviposition: when the syrphid had abdomen-bending and laid eggs.

Reproduction efficacy study

Hoverfly oviposition efficacy was observed by providing either aphid-infested or healthy plants in the net cage (similar to the ones previously described). A single *E. balteatus* female was introduced in the cage including one (aphid-infested or healthy) plant for 3 hours. The eggs on plants were counted after this period.

Statistical analysis

The hoverfly behavior in the net cage was analyzed by pairwise mean comparison tests using Minitab software (12.2 version). Predator reproductive efficacies were analyzed using mean comparison tests according to the Tukey method.

Results

Even if β-caryophyllene was the main volatile compound emitted by both healthy and mechanically damaged potato plants (71.6% ± 6.7% and 68.8% ± 4.9% of the total volatile emission respectively), this relative abundance decreased to 48.2% ± 5.3% when the potato plants were infested with *M. persicae* aphids. Proportions of other volatile compounds according to the different plant states are presented in Figure 1. Healthy plants emitted nine volatiles as did mechanically damaged ones. The volatile pattern from aphid-infested plants was more diversified, including five supplementary volatiles, namely the β-sesquiphellandrene, the EBF, the α-zingiberene, the β-bisabolene and the germacrene D-4-ol.

Due to the similar volatile patterns emitting from both healthy and mechanically damaged plants, only healthy plants were compared to aphid-infested ones. The infochemical role of aphid-infested plants was observed on the different behavioral groups (Fig. 2). First, *E. balteatus* was significantly less immobile in the net cage in the presence of aphid-infested plants ($t = 2.93$, $P = 0.011$). Second, the searching frequencies related to the *M. persicae* infested potato was twice as high as the ones observed with healthy plants ($t = 2.00$, $P = 0.05$). The following step in the host-plant-prey selection, namely the acceptation, was significantly higher for the syrphid female in contact with aphid-infested than for healthy plants ($t = 4.05$, $P = 0.002$). Finally, the predator oviposition was significantly higher when *M. persicae* infested rather than healthy plants were used in the net cage ($t = 3.23$, $P = 0.010$). Hoverfly was shown to be receptive to the indirect defence cues from aphid-infested potato plants. While the female hoverfly mobility already increased in the first few minutes in the net cage, oviposition, acceptation and research frequencies were obviously induced in the presence of aphid-infested potatoes. To quantify the *E. balteatus* reproductive efficiency, a last parameter was observed to complete the predatory hoverfly foraging assessment; reproductive behavior was investigated, that is, the predator egg number laid on the plants. As a mean of 48.9 ± 21.2 eggs per laying and per female was observed on aphid-infested plants, and no egg was produced by the hoverfly on healthy aphid-free plants (Fig. 3), a highly significant difference was observed according to the presence of *M. persicae* on plants ($t = 6.87$, $P < 0.001$).

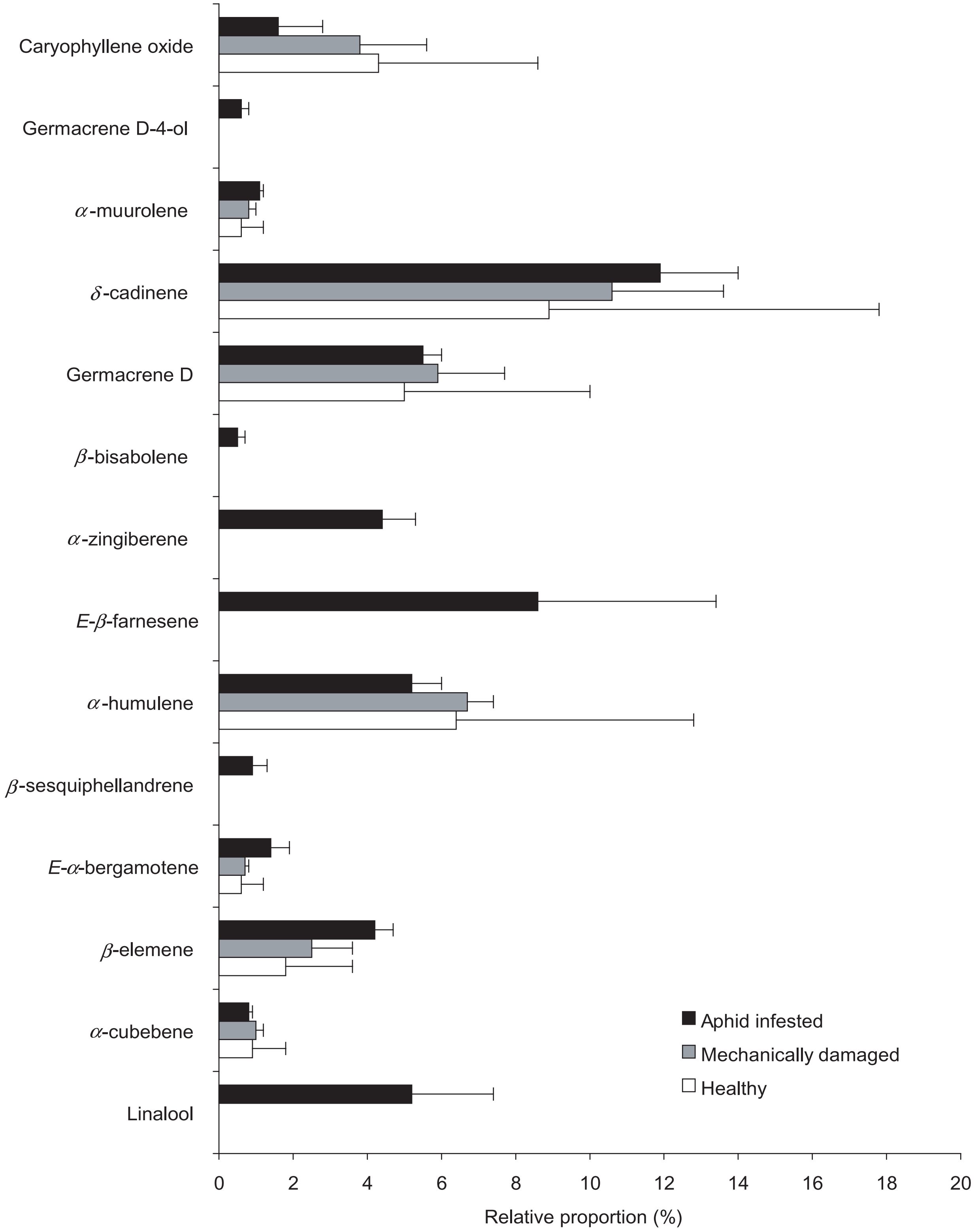

Fig. 1 Changes of volatile emission (in relative %) from healthy compared to aphid-infested and mechanically damaged potato host plant. Data points show the mean ± SE of three independent assays.

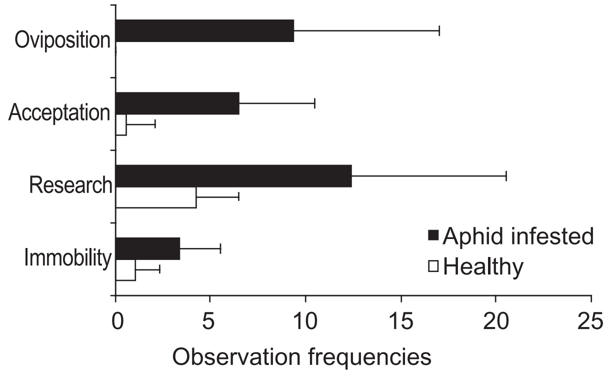

Fig. 2 Behavioral sequences (frequencies) of *Episyrphus balteatus* adults in net cages according to aphid-free or infested host potato plant. Data points show the mean ± SE of 10 independent assays.

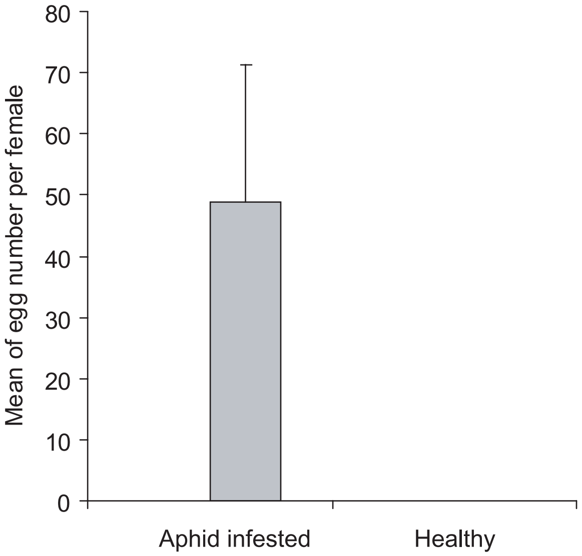

Fig. 3 Reproductive efficiency of *Episyrphus balteatus* in net cages according to aphid-free or infested potato host plant. Egg numbers were observed after 2 hours of egg-laying.

Discussion

Several tritrophic interaction studies on plant-herbivores-natural enemies demonstrated the plant indirect defence mechanisms as an efficient way to cope with pests by the use of volatile infochemicals (Turlings *et al.*, 1990; Turlings & Tumlinson, 1992). When attacked by herbivores, several plant species were shown to emit volatiles that attract natural enemies of the damaging insect pests (Vet & Groenwold, 1990; Vet & Dicke, 1992; Tumlinson *et al.*, 1992). Here we found that the volatile pattern from aphid-infested potatoes was very different from the one from healthy potatoes. Five volatile molecules were emitted by aphid-infested potato plants, while mechanical damage did not have this impact. According to Miles (1999), the salivary proteins injected by the aphid during its feeding on plants seemed to be directly involved in this plant response change when compared to non-aphid damage. In particular, the production of some terpenes was induced by the aphid feeding on plant, including the EBF, a dual active compound towards aphids (as alarm pheromone) and aphidophagous beneficials (i.e. kairomones) (Francis *et al.*, 2004, 2005a, b). Here, the EBF was found to represent 9% of the volatiles related to the *M. persicae* feeding on bean while it did not appear when mechanical damage occurred on plants. Completely different volatile profiles between insect-damaged and mechanically damaged plants were already observed using corn seedlings-beet-armyworm associations. The larvae of the latter pest induced the emission of (*Z*)-3-hexen-1-yl acetate, linalool, (3E)-4,8-dimethyl-1,3,7-nonatriene, indole, 8, α-E-bergamotene, EBF, (*E*)-nerolidol, and (3E, 7E)-4,8,12-trimethyl-1,3,7, 11-tridecatetraene when feeding on corn plants. Artificially damaged corn plants led to far fewer volatile releases, in both abundance and diversity (Turlings *et al.*, 1990). The EBF was again one of the particular volatile molecules related to insect-infested plants. For example, the *E. balteatus* aphidophagous predator and females of the *Cotesia marginiventris* (Cresson) parasitic wasp perceived the difference between mechanically and insect-damaged plants to locate armyworm hosts. Also, cucumber plants infested either with thrips, *Frankliniella occidentalis* (Pergande) or spider mites, *Tetranychus urticae* Koch, attracted the predatory bug *Orius laevigatus* (Fieber) (Venzon *et al.*, 1999). In this work, as well as in the previously cited examples, the beneficial decision was based on the odour pattern and volatile abundance from the plant-herbivore combination. The volatile profiles were specific from the first and second level associations in tritrophic interactions, whereas the third level of entomophagous insects benefit from airborne cues from the first two trophic levels (Paré & Tumlinson, 1999).

Focusing on a particular group of pests such as aphids, indirect defences from plants leading to the aphidophagous beneficial attraction were observed from aphid-infested plants. For example, *C. septempunctata* responded positively to volatiles from *R. padi* L. aphids infesting barley plants in olfactometer assays (Ninkovic *et al.*, 2001). Francis *et al.* (2004) previously showed that both *Adalia bipunctata* predatory larvae and adults were attracted by EBF emitted from crushed *Acyrthosiphon pisum* Harris and *M. persicae* aphids reared on broad beans (*Vicia faba* L.). In that experiment, EBF, the well-known aphid alarm pheromone, was found to be an effective kairomone for the two-spot ladybird. Using another aphidophagous species, namely *E. balteatus* DeGeer, the infochemical role of aphid-volatile releases, particularly EBF, was also demonstrated (Francis *et al.*, 2005b). Working on another parasitoid, Du *et al.* (1998) identified six volatile compounds (linalool, 6-methyl-5-hepten-one, *Z*-3-hexen-1-yl acetate, *E*-β-ocimene, *Z*-3-hexen-1-ol and EBF) involved in the attraction of parasitoid *Aphidius ervi* to *A. pisum* infested broad beans.

Attacks from phloem-feeding aphids elicit weak responses in contrast to tissue-feeding lepidopteran larvae and mesophyl-sucking insects (Voelckel *et al.*, 2004; De Vos *et al.*, 2005; Zhu-Salzman *et al.*, 2005). This is due to their feeding style: stylet penetrates plant epidermal and parenchymal cells to reach phloem sieves, thereby inflicting minimal wounding to the plant (Miles, 1999). Limited plant damage brings aphids closer to parasites than herbivores. However, we showed that volatile response (terpene emission in particular) of *M. persicae* infested *S. tuberosum* was significantly different from the healthy plants and influenced *E. balteatus* foraging and reproductive behavior. Attraction of natural enemies is known as an indirect defence mechanism and is potent for control of harmful agricultural pests like aphids. Aphidophagous predators are widespread in agro-ecosystem and, among these predators, *E. balteatus* were found to be the most common hoverfly species in crop areas in Belgium (Colignon *et al.*, 2001) and temperate regions (Gilbert, 1986). Once identified, volatile attractants for beneficial insects had to be evaluated in field experiments (James, 2003). Semiochemicals can be used with great success as components of integrated pest management strategies. The way from the discovery to commercial production is long and full of pitfalls but represents an opportunity already illustrated by Birkett and Pickett (2003) for aphid sex pheromones.

Acknowledgments

N. Harmel was financially supported by a PhD grant from the Fonds pour la formation à la Recherche dans l'Industrie et l'Agriculture (F.R.I.A.), Belgium.

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Accepted September 21, 2006

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