

Is the (E)- β -farnesene only volatile terpenoid in aphids?

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Abstract

Herbivore insects use a broad range of chemical cues to locate their host to feed or to oviposit. Whether several plant volatiles are effective allelochemicals for insects, the latter also emit molecules which have infochemical role. The (E)- β -farnesene (EBF) is a well-known aphid alarm pheromone commonly found in all previous tested species. Analysis of the released molecules from twenty three aphid species, mainly collected on their natural host plant from May to July, were performed by GC-MS. While EBF was identified as the main volatile substance in 16 species, alone or associated with other molecules, the alarm pheromone was only a minor component of the volatile molecule pattern of five other species. Moreover, two species, *Euceraphis punctipennis* and *Drepanosiphum platanoides*, did not release EBF at all but other terpenes were identified. This original observation raised the question on the utility and the source of the non EBF volatiles. Are these potential infochemical substances produced by the aphid or only absorbed from the host plant? Here we determined that terpenes released by insects were not only provided by the host plants. Indeed, *Megoura viciae* emitted additional molecules than the ones from several aphid species reared on the same host plant. Moreover, no systematic relation between the feeding behaviour of the aphid species and the volatile releases was observed. Aphid terpene composition and proportion would provide reliable cues to identify the emitting organism, plant or insect. The next step of this work will be to determine the infochemical role of terpenes found in the range of tested aphid samples to better understand the relations between the different tritrophic levels.

Key-words : terpenes, aphid, (E)- β -farnesene, infochemicals, insect-plant interactions

Introduction

Aphids are major pests throughout the world. They are responsible of several damages on crop plant species due to their sap taking but also as virus vector. More than 300 species were identified recently in Belgium (Nieto Nafria et al., 1999). In the Aphididae family, large differences are observed on the feeding behaviour, from very polyphagous to monophagous specialist species. Type of life cycle also varies in an important way : certain aphids generally remain on the same host plant species throughout the year (autoecious), while others may alternate between different species of host plant during the annual life cycle (heteroecious). Alternations between primary host, which is often a tree or a shrub, and a secondary herbaceous host are generally observed (Blackman and Eastop, 1985).

The understanding of the chemical ecology of aphids is a key factor to know how the insect can locate their host amongst the plant diversity. If semiochemicals from plants are important to explain the aphid distribution, intraspecific infochemicals are also of first importance in the aphid migration in the field. When disturbed, many aphids release volatile substances including alarm pheromone. Important variation was observed among aphid species in their sensitivity to the latter kind of pheromone, in the speed and the form, which can be related to the ecology of the species (Nault and Montgomery, 1977).

The aim of the present study was the investigation of the volatile release of several aphid species, trying to have insect species corresponding to a broad range of ecological habitats and behaviours. We used mainly wild species found on several biotypes (herbaceous, shrub or tree) but also added well-known economically pests

of crop species which are commonly reared under laboratory conditions. In this work, we determined the potential variations of aphid volatile releases, including alarm pheromone, depending on the tested species and in regard to the so huge diversity of these sucking insects.

Material and methods

Insects

Some aphid species (*Acyrtosiphon pisum* Harris, *Myzus persicae* Sultzer, *Aphis fabae* Scopoli and *Megoura viciae* L.) were collected from the mass insect rearing of our laboratory. They were reared on bean (*Vicia faba* L.) at $20 \pm 2^{\circ}\text{C}$ temperature, with 16 hours of light period, in separated rooms in the laboratory, for several years. Most of the aphid species (Table 1) were collected on their host plant in the fields around Gembloux, Belgium, from May to July 2000. Aphid samples were composed by both alate and apterous forms, adults and larvae instars. Using this sample composition, the volatile fractions, released by the aphids, corresponded to the production of aphid colony in nature.

Volatile Product Analysis

Aphids (250 mg) were crushed with a glass pestle in a glass tube specially adapted to the SPME (Solid Phase Micro Extraction) method. Each aphid species was tested at least in duplicate. The crushed samples were first maintained for 30 min at $30 \pm 0.2^{\circ}\text{C}$ in thermostated glass tubes adapted for SPME device. The volatile metabolites were sampled for 30 min with 100 μm PDMS (polydimethylsiloxane) SPME fibers from Supelco® and directly analyzed by GC-MS on a Hewlett Packard HP5972 Mass spectrometer coupled with a HP5890 series II gas chromatograph. The following analytical conditions were used : split-splitless injection at 250°C , HP5–MS (5% phenyl-dimethylpolysiloxane) column (30m x 0.25mm, $\text{df} = 1\mu\text{m}$). Samples were purged with He at 4 ml min^{-1} for 11 min and the temperature program was from 40°C (1 min hold) to 180°C at $6^{\circ}\text{C.min}^{-1}$ than to 280°C at $15^{\circ}\text{C.min}^{-1}$. The MS spectra were obtained in the EI mode at 70eV (scanned mass range from 30 to 300

amu). 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 those of the Wiley238.L spectral library.

Whenever possible, pure reference molecules were co-injected using the same sampling and analytical procedures to corroborate the identification. (E)- β -farnesene was recovered from *Acyrtosiphon pisum* lipids using micro-column chromatography (40 x 5 mm, 70-230 mesh silicagel E60 column) and hexane as eluent.

The use of the SPME method allowed us to analyse a large number of insect samples and was already confirmed to be reliable and sensible for aphid volatile detection (Francis et al., 2001).

Results

Beside the (E)- β -farnesene, many other volatile substances were detected in analysed aphid samples (Table 2). Whether the well-known alarm pheromone was mainly released from 16 homopteran species, the (E)- β -farnesene was found as a minor constituent of the volatile molecule pattern in five other taxa namely *Aphis idaei*, *Brevicoryne brassicae*, *Chaitophoros populeti*, *Dysaphis plantaginea* and *Megoura viciae*. Two species, *Euceraphis punctipennis* and *Drepanosiphum platanoides* did not release at all the alarm pheromone. Complementary informations on the feeding behaviour and the host plant species are presented in Table 1. Every feeding behaviours, from strictly monophagous to very polyphagous pests, are represented in our screening.

Discussion

From the 23 aphid species, (E)- β -farnesene (EBF) was identified in most of them, either alone (in 12 species) or in combination with other volatile components (in 9 species) but *E. punctipennis* and *D. platanoides* did not release EBF at all. It is the first time that EBF was not detected in the aphid volatiles. This original observation raised some questions on the utility of the identified volatile molecules from aphids, mainly in the absence of EBF. Do some aphid species have no alarm pheromone ? Do other volatiles than EBF play an infochemical role ? Are these molecules produced by the aphid or only taken from the host plant ?

Terpene releases from insects such as aphids could come from their related host plants. Indeed, plant emissions of terpenes was described for several species. Twenty one identified molecules from *Prunus* species fruits originated from terpene metabolism (Krammer et al., 1991; Mattheis et al., 1992). Loughrin and colleagues (1996) reported the β -ocimene, caryophyllene, germacrene-D and α -farnesene emission from apple leaves (*Malus* sp). Not only the tree species emit terpene volatiles, herbaceous plants such as *Solanum tuberosum* (Agelopoulos et al., 1999), carrot and caraway (Nehlin et al., 1996) produced this kind of volatiles. The characteristics of the floral fragrances of several Apiaceae species namely *Heracleum sibiricum*, *Pastinaca sativa*, *Laserpitium latifolium* and *Anthriscus sylvestris*, were found to originate in differences in the proportions of monoterpene hydrocarbons, among which α - and β -pinene, cis- and trans- β -ocimene, limonene, sabinene and myrcene dominated (Borg-Karlson et al., 1994). Even if these molecules were found in the host plant, they must not be considered as the insect volatile source. In regard to our work, the results related to several aphid species

collected on *Vicia faba* (Fabaceae) provided a strong evidence that the insects did not take the terpenes from host plants even if the latter could supply precursors of the aphid emitted volatiles. Indeed, while *A. pisum*, *M. persicae* and *A. fabae* only released EBF, several terpenes were identified in *M. viciae* samples. Moreover, this work allows us to conclude that there is no systematic relation between the feeding behaviour of the aphid species and the volatile releases. While most of the polyphagous species (*M. persicae*, *A. fabae* and *B. cardui*) only produced EBF, two sesquiterpenes were detected in the generalist *A. solani*. Considering monophagous aphid species, *B. schartmzi* and *A. urticata* only emitted EBF while the four others *M. lithri*, *M. cerasi*, *A. ideai* and *E. punctipennis* released volatile blends with different terpene compositions. Among the oligophagous species, no significant difference can be observed between genus or family specialist aphids. In each category, we found insects emitting EBF alone or in combination with other volatiles.

Aphid alarm pheromones were studied for several years (Pickett et al., 1992) and EBF was identified in each tested aphid samples. For several years, the latter was considered as the unique alarm pheromone but Pickett and Griffith (1980) detected additionally the presence of other terpene compounds when they studied the vetch bean aphid, *M. viciae*. The five other species they studied only emitted EBF. At that time, *M. viciae* was considered to be a particular case in the Aphididae family. The α -pinene molecule was shown to have a higher alarm activity than EBF for *M. viciae* even if it was found in the same amount than EBF. An other species, the turnip aphid, *Lipaphis erysimi*, also responded weakly to EBF but the response was highly increased by isothiocyanates from its host plant (Dawson et al., 1987). The role of

other than EBF molecule from these previous examples could be extended to many molecules which are reported herein. Indeed, most of terpenes we detected were already demonstrated to be infochemicals for herbivore species when emitted from related host plant. *Diaphania nitidalis* (Stoll.) (Lepidoptera : Pyralidae) is attracted by R-, S-limonene and germacrene D from *Cucurbita pepo* leaves. Even if germacrene was attractive alone, only the terpene mixture was so attractive than the whole leaf volatiles (Peterson et al., 1994). Using electroantennography (EAG) methods, Weissbecker and colleagues (1999) demonstrated that *Leptinotarsa decemlineata* was influenced by caryophyllene and germacrene-D emitted by injured potato plants. Limonene, the most abundant orange emitted volatiles, induced actively the EAG responses of *Ceratitis capitata* (Hernandez et al., 1996). Two aphid species, *Sitobion avenae* and *Metopolophium dirhodum*, also responded positively to β -pinene (Visser et al., 1995).

Whether sesquiterpene hydrocarbons including EBF are commonly produced by plants, the sensibility of aphids towards plant molecule largely depend on the composition of the volatile pattern. The presence of additional terpenes in insect volatile releases in conjunction with EBF (such as β -caryophyllene) allows the animals to differ the emitting organism and enables the aphid to distinguish alarm pheromone from conspecific individuals and plant source. *M. viciae* seems to perceive general plant volatile (butyl-isothiocyanate, pentyl-isothiocyanate) as well as more specific ones associated with the odour blends of non-host plant as Brassicaceae species (Visser and Piron, 1995). The role of aphid released terpenes could be to allow to differ plant and insect emitting organisms. Several species which were studied here could illustrate and explain the occurrence of some volatiles in the

bouquet. *B. brassicae* released isothiocyanates as the crucifer hosts but also EBF. When the aphid plant species do not emit EBF, the presence of the latter, alone, is sufficient to distinguish plant and insect volatile releases. Whether the host plant do not emit terpene volatile, the insect EBF release allows to inform the other aphids in the closed environment. In the opposite side, when the plant emit terpene including or not EBF, the occurrence of complementary volatile molecules or the EBF overproduction could be seen as a way to differ plant and aphid releasing volatiles. Either the composition or the proportion between the potential infochemical substances would be of first importance to recognize the emitting organism, plant or insect.

The molecules named ST204 in the results which were detected at 15.4 to 16.2 min and 20.1 to 21.1 min have a molecular ion at 204 corresponding to sesquiterpene hydrocarbons. Their mass spectra have been compared with those of the Wiley 275.L and Joulain (1998) data bases. None of them correspond with that of the volatile products isolated from different aphid species (*A. solani*, *B. brassicae*, *C. elaeagni*, *D. plantagine*, *E. punctipennis*, *M. lithy*). The recovery of these unknown molecules needs further fractionations to undertake their identification. This work is actually in progress.

The next step in our research will be to test the role of the released aphid volatiles using olfactometry methods as infochemical substances toward both aphid and related predators such as ladybirds and hoverflies. Previous works on carabid beetle showed that EBF from *Sitobion avenae* induced higher activity of the polyphagous predators (Kirkland et al., 1998). The use of EBF aphid alarm pheromone as prey-

finding kairomone was determined using two carabid species: *Pterostichus melanarius* and *Harpalus rufipes* (Kielty et al., 1996). A contact kairomone in aphid cornicle secretions stimulated oviposition attack responses by the braconid parasitoids *Lysiphlebus testaceipes* (Cresson) and *Aphidius ervi* Haliday (Grasswitz and Paine, 1992). This response was not elicited by (E)- β -farnesene when presented alone but the kairomonal activity of cornicle secretion may depend upon an interaction between the alarm pheromone and other chemical components. The determination of the infochemical role of volatile compounds found in the range of tested aphid samples will lead towards a better understanding of the relations between insects and plants, insects from the same species and between host preys and natural enemies.

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Aphid species	Host plant collected	Feeding behaviour*
<i>Acyrthosiphon pisum</i> Harris	<i>Vicia faba</i> L	Family specialist (Fabaceae)
<i>Aphis fabae</i> Scop.	<i>Vicia faba</i> L	Polyphagous
<i>Aphis idaei</i> v.d.Goot	<i>Rubus</i> sp	Species specialist (<i>Ribes idaeus</i> L.)
<i>Aphis sambuci</i> L.	<i>Sambucus nigra</i> L.	Genus specific (<i>Sambucus</i> sp) and several herbaceous species
<i>Aphis urticata</i> L.	<i>Urtica dioica</i> L.	Species specialist (<i>U. dioica</i>)
<i>Aulacortum solani</i> Kalt.	<i>Sinapis alba</i> L.	Polyphagous
<i>Brachycaudus cardui</i> L.	<i>Cynara scolymus</i> L.	Polyphagous
<i>Brachycaudus schartmzi</i> Börn	<i>Prunus persica</i> L. (Batsch)	Species specialist (<i>P. persica</i>)
<i>Capitophorus elaeagni</i> d.Guerc.	<i>Inula helenium</i> L.	Family specialist (Asteraceae)
<i>Chaitoporus populeti</i> Panz.	<i>Populus alba</i> L.	Genus specialist (<i>Populus</i> sp)
<i>Dysaphis plantaginea</i> Pass.	<i>Malus sylvestris</i> (L.) Mill	Genus specialist (<i>Malus</i> sp)
<i>Drepanosiphum platanoïdes</i> Schr.	<i>Acer pseudoplatanus</i> L.	Genus specialist (<i>Acer</i> sp)
<i>Euceraphis punctipennis</i> Zett.	<i>Betula pubescens</i> Ehrh.	Species specialist (<i>B. pubescens</i>)
<i>Hyalopterus pruni</i> Geoffr.	<i>Prunus domestica</i> L.	Genus specialist (<i>Prunus</i> sp)
<i>Hyperomyzus lactucae</i> L.	<i>Sonchus arvensis</i> L.	Genus specialist (<i>Sonchus</i> sp) and <i>Ribes</i> sp (2 nd hosts)
<i>Macrosiphoniella tanacetaria</i> Kalt.	<i>Tanacetum</i> sp	Genus specialist (<i>Tanacetum</i> sp, <i>Achillea</i> sp)
<i>Megoura viciae</i> L.	<i>Vicia faba</i> L.	Family specialist (Fabaceae)
<i>Metopolophium dirhodum</i> Wlk.	<i>Triticum aestivum</i> L.	Family specialist (Poaceae)
<i>Myzus cerasi</i> Fabr.	<i>Prunus cerasus</i> L.	Species specialist (<i>P. cerasus</i>) and <i>Galium</i> sp, <i>Euphrasia</i> sp, <i>Veronica</i> sp (2 nd hosts)
<i>Myzus lythri</i> Schr.	<i>Prunus mahaleb</i> L.	Species specialist (<i>P. mahaleb</i>) and <i>Lythrum</i> sp and <i>Epilobium</i> sp (2 nd hosts)
<i>Myzus persicae</i> Sultz.	<i>Vicia faba</i> L.	Polyphagous
<i>Sitobion avenae</i> Fabr.	<i>Triticum aestivum</i> L.	Family specialist (Poaceae)

Table 1 : List of aphid species analysed for their volatile releases. Related feeding behaviour and host plant species which the insect were collected on are also presented. (*) according to Heie (1992).

Aphid species	Benzy ITC	α -Bergamotene	β -Bourbonene	Camphene	p-Cimene	α -Copaene	(E)- β -farnesene	Germacrene D	α -Gurjunene	Isobornyl acetate	Limonene	Myrcene	α -Phellandrene	β -Phellandrene	α -Pinene	β -Pinene	α -Terpinene	γ -Terpinene	Terpinolene	α -Thujene	ST204 (*)	Unknown (**)
Rt (min)	21.3	18.1	16.8	8.4	9.8	16.6	17.6	18.3	20.1	14.8	9.9	9.0	9.4	8.8	8.0	8.9	9.6	10.5	9.8	7.8	(*)	(**)
<i>Acyrtosiphon pisum</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aphis fabae</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aphis idaei</i>	-	-	-	-	6.4	-	1.3	-	-	-	-	15.0	0.9	16.0	6.0	26.5	18.3	1.2	-	8.4	-	-
<i>Aphis sambuci</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aulacorthum solani</i>	-	-	-	-	-	-	91.8	-	-	-	-	-	-	-	-	3.0	-	-	-	-	5.2	-
<i>Aphis urticae</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachycaudus cardui</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachycaudus schamtzi</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brevicoryne brassicae</i>	70.1	-	-	-	-	-	5.0	-	9.4	-	6.2	-	-	-	-	2.0	-	-	-	-	1.7	5.6
<i>Capitophorus elaeagui</i>	-	1.6	-	-	-	-	73.1	-	-	-	-	-	-	-	-	-	-	-	-	-	23.7	1.6
<i>Chaitoporus populeti</i>	-	-	-	10.8	-	-	5.9	-	-	12.7	0.7	-	-	-	53.3	16.6	-	-	-	-	-	-
<i>Dysaphis plantaginea</i>	-	-	-	-	-	-	15.9	-	-	-	-	-	-	-	-	-	-	-	-	-	84.1	-
<i>Drepanosiphum platanoides</i>	-	-	-	1.2	-	-	-	-	-	1.1	32.8	-	-	8.2	12.8	41.3	-	-	0.7	1.9	-	-
<i>Euceraphis punctipennis</i>	-	-	28.2	-	-	22.2	-	42.0	-	-	-	-	-	-	-	-	-	-	-	-	7.6	-
<i>Hyalopterus pruni</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyperomyzus lactucae</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macrosiphoniella abrotani</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Megoura viciae</i>	-	-	-	-	-	-	8.0	-	-	-	6.2	-	-	-	11.8	74.0	-	-	-	-	-	-
<i>Metopolophium dirrhodum</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myzus cerasi</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myzus lythri</i>	-	-	-	-	-	-	83.3	-	-	-	-	-	-	-	-	-	-	-	-	-	3.9	12.8
<i>Myzus persicae</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sitobion avenae</i>	-	-	-	-	-	-	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 2 : GC-MS identification and relative proportion (in %) of the volatile molecules released from aphid samples. Retention times (Rt) were presented below the name of identified molecules. Bold percentages in the table indicate the main molecule for each aphid species. (*) unidentified sesquiterpene hydrocarbon 4 at 15.4 to 16.2 min and 20.1 to 21.1 min, (**) unknown molecules, (-) not detected.