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Interspecies variation in floral fragrances emitted by tropical *Ficus* species

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Abstract

In this paper we examine if fig species emit specific compounds in order to attract pollinating wasps. Volatile compounds released by receptive figs from 13 tropical *Ficus* species were identified. They are mainly terpenoids, but also include benzenoids and non-terpenoid oxygenated aliphatic compounds. The blend of volatiles of each species is unique. Seven of the 13 species studied emit some compounds that are uncommon among floral volatiles. Ten of the species studied were dioecious. In three of these species we examined the potential differences in odour blends between male and female inflorescences. In all three, both sexes share compounds, even if one sex has some additional volatiles.

Keywords: *Ficus* sp; Moraceae; Inflorescence volatiles; Specificity; Pollinator attraction; Headspace; Terpenoids; Benzenoids; Non-terpenoid oxygenated aliphatic compounds

1. Introduction

In plant–pollinator interactions, olfactory signals are often necessary to facilitate the encounter of the two partners. Fig–fig wasp interactions are a set of highly specialized and diversified mutualisms, with over 700 replications of a species-specific interaction (Berg, 1989). In this system, the encounter of the two partners is a crucial phase for each of them and necessitates specific signals (Bronstein, 1987; Anstett, Hossaert-McKey & Kjellberg, 1997). It has been shown in several cases that fig pollinating wasps are attracted by olfactory signals (van Noort, 1989; Ware, Kaye, Compton & van Noort, 1993; Hossaert-McKey, Gibernau & Frey, 1994; Harrison, 1996; Gibernau, Hossaert-McKey, Frey & Kjellberg, 1998).

In the fig–fig wasp mutualism, each partner needs the other for its reproduction. Figs are closed receptacles containing flowers (Berg, 1989). When the figs are receptive (female phase), their odour attracts female wasps (Hossaert-McKey et al., 1994; Gibernau, Buser, Frey & Hossaert-McKey, 1997). Once they arrive at the fig surface, wasps will be stimulated and enter within the fig to lay eggs, and in so doing transfer pollen to female flowers. Larvae and seeds develop within the fig. Then newly emerged female wasps, loaded with pollen, leave their natal fig and search for another receptive fig of the same species. As fig development in each individual fig tree is synchronous over the entire crown, newly emerged wasps will have to fly over long distances to find a new receptive tree.

Gibernau et al. (1997) showed that receptive figs of *F. carica*, the common fig tree, emit ten volatile compounds to attract their specific pollinating wasps. Only receptive figs emit compounds. Behavioural tests with synthetic mixtures have shown that only three of these ten compounds (linalool, linalool oxides and benzyl alcohol) are essential for distance attraction of pollinating wasps and their chemostimulation once they have landed on the fig surface. The volatile attractants produced by *F. carica* are compounds that are widespread in floral fragrances of angiosperms (Knudsen, Tollsten & Bergström, 1993). Surprisingly, olfactory

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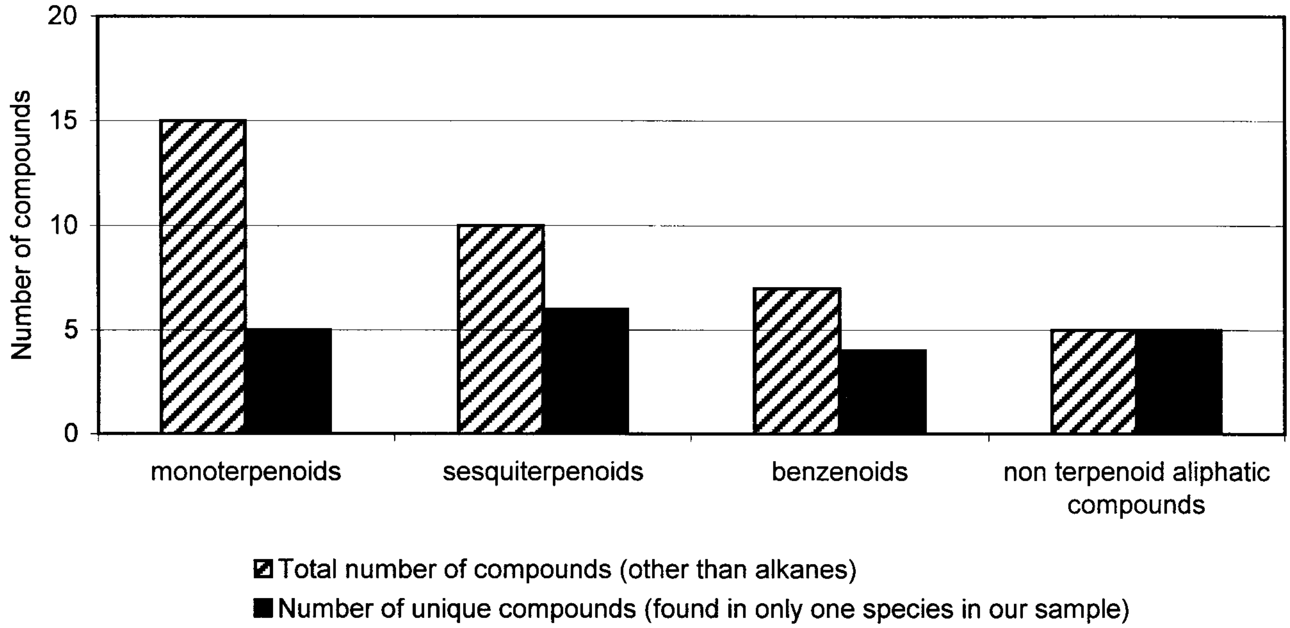

Fig. 1. Chemical classes of volatile compounds emitted by receptive figs of 13 tropical *Ficus* species.

attraction of the specific pollinating wasps in this species-specific system depends on a simple blend of common volatile compounds.

However, *F. carica* is usually the only fig species present in its habitat and hence needs not produce a signal distinct from other figs to ensure specific attraction of its pollinators. But in tropical forests, over 50 fig species may occur together in the same site. In such a situation, is the specific attraction of the wasp pollinator of each species due to quantitative differences in the blend of the olfactory "bouquet", or to qualitatively different compounds in each species? Fig species-rich forests of Brunei, combined with the nearby availability of a laboratory with instruments for analysis, offer a rare opportunity to study this question.

A second question concerns the role of volatile chemicals in the functioning of pollination systems in dioecious species. Half of all fig species are monoecious: each tree produces seeds, pollen and pollinators. The other half of fig species are functionally dioecious. In these species, female trees produce only seeds. "Male" trees produce female flowers, but these function only as development sites for pollinators. Thus "male" trees produce pollen and the pollinating wasps that transport it, and are functionally male (Kjellberg, Gouyon, Ibrahim, Raymond & Valdeyron, 1987). Do figs of male and female trees of dioecious species produce the same odour? This question is important because intersexual mimicry appears to play a role in the functioning of the system (Patel, Anstett, Hossaert-McKey & Kjellberg, 1995; Anstett, Gibernau & Hossaert-McKey, 1997).

In this paper we try to answer these two major questions on specificity of attraction of fig pollinators using adsorption–desorption (headspace) technique and GC–MS analysis. In contrast to a previous study by Gibernau et al. (1997), which involved extraction of entire figs with pentane, headspace adsorption extracts only volatile compounds (Turlings, Tumlinson & Lewis, 1990; Raguso & Pellmyr, 1998).

2. Results and discussion

A wide variety of compounds were found in the odours emitted by receptive figs. They belong to five different chemical classes (Fig. 1): monoterpenoids (acyclic, monocyclic and bicyclic), sesquiterpenoids (bicyclic, tricyclic and tetracyclic), benzenoids, non-terpenoid oxygenated aliphatic compounds (aldehyde, alcohol, ketone and ester) and alkanes. One to 22 compounds (median: 4 compounds) were identified for each species. Table 1 shows that the composition of the floral scent of each fig species is unique and that the volatile blends of male and female figs of the same species are different from each other. Volatiles from *F. condensa* female figs included considerably more types of branched alkanes (C_8–C_{13}) than any other fig studied. Alkanes have sometimes been reported as floral scent constituents (Knudsen et al., 1993) but no biological activity tests have yet been done to establish what role, if any, they play in attracting pollinators. Only *F. condensa* female volatiles included a substantial number of non terpenoid oxygenated aliphatic

Table 1
Volatiles identified in the odours emitted by 13 tropical *Ficus* species

Compounds	Species sex	*F. fulva* male	*F. fulva* female	*F. aurata* male	*F. deltoidea* female	*F. punctata* male	*F. punctata* female	*F. obscura* male	*F. condensa* female	*F. condensa* male	*F. megaleia* female	*F. uncinata* female	*F. stolonifera* female	*F. beccarii* female	*F. microcarpa* monoecious	*F. benjamina* monoecious	*F. crassiramea* monoecious	Frequency in our sample (number of species)	Frequency in Knudsen et al., 1993 (number of genera)
Monoterpenoids	1,8-cineole @[a]	+[d]	-[e]	-	-	+ + +[b]	+ + +	-	-	-	-	-	-	+ + +	-	-	-	4	44
	Camphene	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	14
	Limonene @	+	-	+	-	+	-	-	-	-	+	-	-	-	-	-	-	4	75
	Pinene, α-@	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	3	63
	Pinene, β-@	-	-	-	-	+ *[f]	-	-	-	-	-	-	+	-	-	-	-	2	51
	Carene, δ-3-@	-	-	-	-	-	-	-	-	-	-	-	-	-	+ + +	-	-	1	15
	Linalool @	+	+	-	+ +[c]	+	-	+ + +	+ +	+ + +	+ + +	+ + +	+ +	-	-	-	+ + **[g]	11	66
	Linalool oxide (2 forms)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	9
	Myrcene, β-@	+	-	+	-	+ *	-	-	-	-	+	-	-	-	-	-	-	4	68
	Allo-ocimene	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
	Ocimene, β-	+ +	+	+ + +	-	+ +	-	-	-	-	-	-	-	-	-	+ +	-	5	15
	Sabinene @	+	-	-	-	+ +	+	-	-	-	-	-	-	-	-	-	-	3	24
	Terpinene, γ-@	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	3	10
	Thujene, α	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	1	7
	Phellandrene, β	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	1	15
Sesquiterpenoids	Cadinene	-	-	-	-	-	-	-	-	-	-	-	+ +	-	-	-	-	1	1
	Copaene, α-	+	+ +	+ +	+ +	-	-	-	-	-	-	-	-	+ + +	-	+ + +	+ + +	7	7
	Cubebene @	+	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	3	1
	Caryophyllene (β/*trans*) @	+ + +	+ + +	+	-	-	-	-	-	-	-	-	-	-	-	-	+ + +	4	30
	Caryophyllene (γ-/*cis*)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	Cyclosativene	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+ +	-	2	1
	Humulene, α-/ selinene	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	9 or 1
	Elemene, β-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3
	Lepidozene	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
	Clovene	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
Benzenoids	Benzaldehyde @	+	-	-	+ +	+	-	+ +	+	+ +	+ + +	+ +	+	-	-	-	-	9	44
	Benzyl alcohol @	+	-	-	+ + +	+	-	+ + +	+ +	+ + +	+ + +	+ + +	+ + +	-	-	-	-	9	43
	benzyl alcohol, α,α-dimethyl	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	1	0
	(1-methylethenyl)benzene X[h]	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	1	0
	C10 H14 alkylbenzene	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	1	2
	Styrene X	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	1	0
	Cymene	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	2	18
Non terpenoid	2-ethyl-1-hexanol @	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	1	1
Oxygenated	2-ethyl-2-hexenal	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	1	0
Aliphatic compounds	3-octen-2-one, (E)-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	1	0
	3-hexen-1-ol acetate (Z)	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	1	22
	2-heptadecanone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+ +	-	1	2
Alkanes		+	-	-	+ +	+ +	+ +	-	+ + +	+	-	-	-	-	-	-	-	6	> 10

[a] @ — retention time and mass spectrum were compared with those of authentic compounds.
[b] + + + — % area > 20% of total peak area of components detected.
[c] + + — % area = 10–20% of total peak area of components detected.
[d] + — % area < 10% of total peak area of components detected.
[e] - — not detected.
[f] * — β-pinene/β-myrcene mixture.
[g] ** — could be partly or wholly α-terpinolene.
[h] X — could be an artefact.

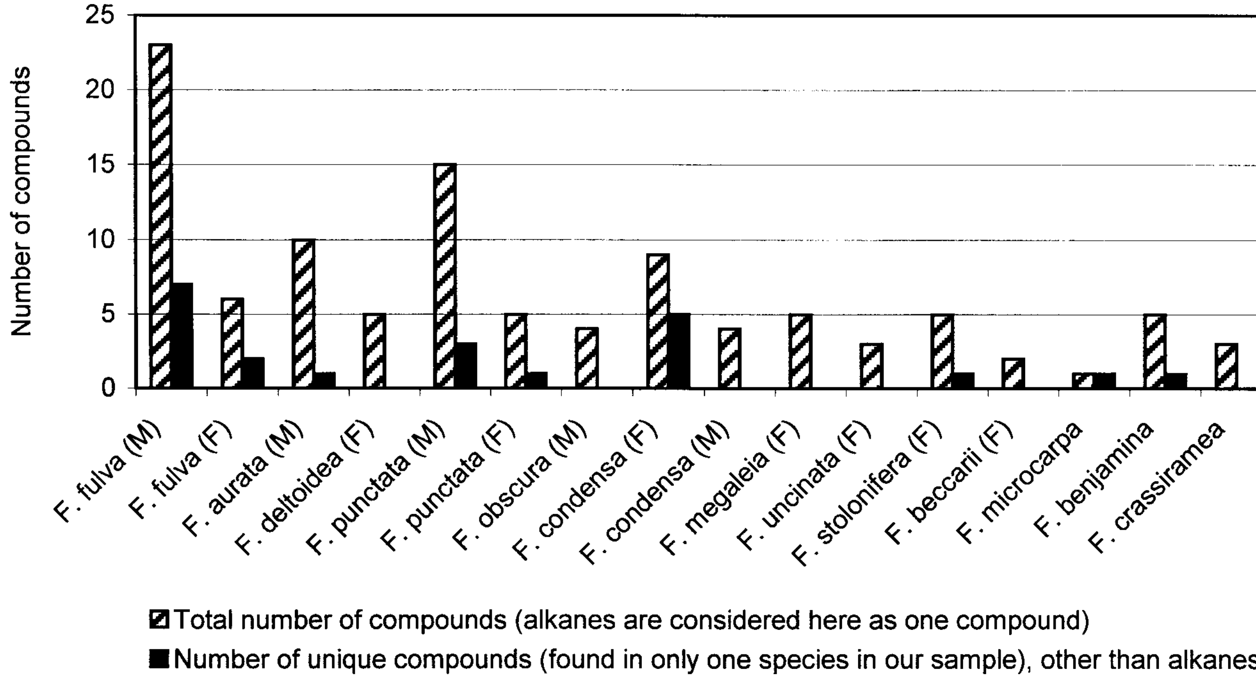

Fig. 2. Specific compounds emitted by receptive figs of the 13 tropical *Ficus* species studied (M: male figs, F: female figs).

compounds. Only *F. aurata* male figs had an ester constituent. This ester, (Z)-3-hexenyl acetate, has been reported for many plants (22 genera of the 174 studied by Knudsen et al. (1993)), and is often characteristic of wounded foliage, as a product of the lipoxygenase pathway.

The range of boiling points of these constituents (150–270°C) suggests that they may be responsible for both long-distance attraction and contact stimulation of pollinators. Studies to determine the biological activities of these volatiles are underway.

Some of the compounds, namely benzaldehyde, benzyl alcohol, linalool, limonene, the pinenes, β-myrcene, 1,8-cineole, sabinene and β-caryophyllene are common constituents of floral scents previously reported, since each was found in at least 24 of the 174 genera studied by Knudsen et al. (1993). Others, however, have been reported for only one to three genera. Several of these compounds have been found in only one species in our sample, and hence could be specific volatiles. Seven of the 13 species studied contained at least one "specific" compound (Fig. 2). Among these are allo-ocimene, β-elemene, β-selinene and β-cubebene. Styrene and 1-methylethenyl-benzene are well-known monomers; the former is also a known natural product and other alkenylbenzenes such as 4-ethylstyrene and styrene dimer have been reported as floral scent constituents (Knudsen et al., 1993).

Specificity of attraction can thus be obtained by emission of very specific compounds, when several fig species are present in the same forest, while *F. carica*, which is the only fig species in its habitat, emits only compounds that are common among floral volatiles.

In the three dioecious species studied, both sexes share compounds, and one sex usually has some additional compounds (Fig. 3). In dioecious fig species, female trees need to attract wasps, so that their flowers will be pollinated. But pollinating wasps can only lay eggs in male figs, not in female ones, where they pollinate and die. There is thus a conflict between dioecious fig trees and pollinating wasps (Patel et al., 1995; Anstett et al., 1997b). When male and female figs are receptive at the same time, it is reasonable to assume that natural selection should favour pollinating wasps that avoid female figs, and should favour female figs that can attract them (Grafen & Godfray, 1991; Anstett et al., 1997a). One way in which female figs may attract pollinating wasps would be to imitate the male odour (pollination by deceit). So far, some differences have been found between odours of male and female figs of the same species, but further studies are needed to examine if pollinating wasps are able to detect these differences.

Compounds found in other, less specific, pollination mutualisms are often terpenoids or aromatic compounds, just like the compounds most frequently represented in our samples. The fragrance of *Clarkia brewerii* (Onagraceae), which attracts nocturnal pollinators (Raguso & Light, 1998), has been shown to contain linalool and its oxides (Wang, Dudareva, Bhakta, Raguso & Pichersky, 1997). Such compounds are also often present in fairly specific interactions

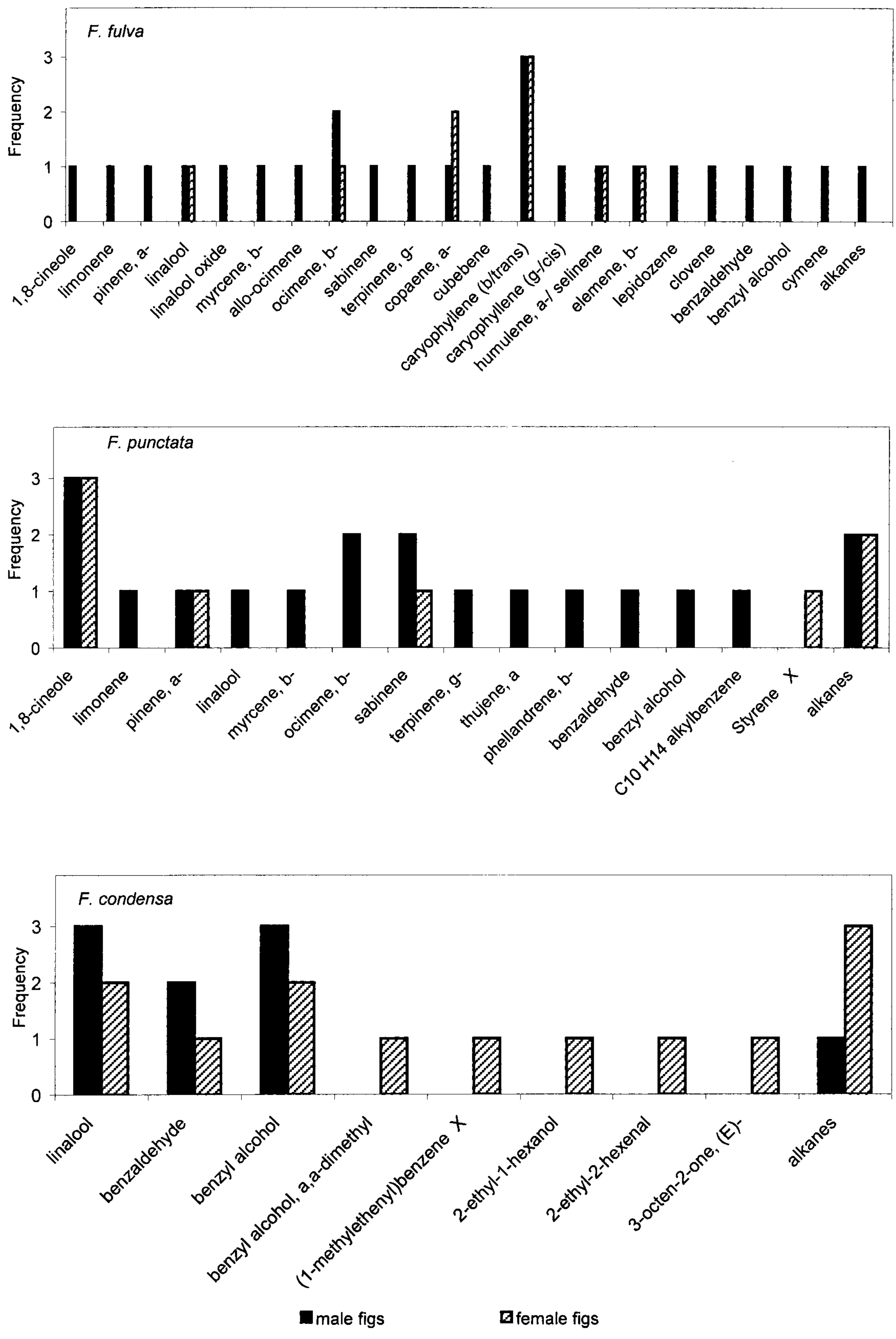

Fig. 3. Compounds released by male and female figs of *F. fulva*, *F. punctata* and *F. condensa*. Frequency 1: < 10% of total peak area of components detected. Frequency 2: between 10% and 20% of total peak area of components detected. Frequency 3: > 20% of total peak area of components detected.

such as in orchid fragrances that attract male euglossine bees, where 11 compounds found by Williams & Dodson (1972) were all terpenoids and aromatic compounds. Among the terpenoids was 1,8-cineole, which has been found in our studies in four fig species. When plants interact with very particular groups of pollinators, in contrast, compounds belonging to other chemical families than terpenoids and aromatic compounds seem to be involved. Pollinating bats, for example, are attracted by sulfur compounds (Bestmann, Winkler & von Helversen, 1997).

We compared the chemical blends emitted by some closely related fig species. In several cases the fragrances were very similar. This suggests that phylogeny is important in the evolution of fig fragrances. This result is further supported by the observation that differences in floral fragrances do not seem to be related to differences in habitat. Thien, Heimermann & Holman (1975) found that a chemical classification of *Magnolia* and *Liriodendron* species fitted only partly with the phylogeny. Beyond phylogenetic constraints, selective pressures or population-level pressures such as isolation and drift may have some influence on the composition of the fragrance. Sometimes chemistry can help to distinguish taxa, as in *Cypripedium calceolus*, which contains several infraspecific taxa, each of which has its own pollinators and geographic area (Bergström, Birgersson, Groth & Nilsson, 1992). This also seems to be the case in *Ficus* sp. with *F. boninsimae* and *F. nishimurae* in the Bonin islands, which were considered by Corner (1965) as the same species, but have distinct odours (Yokoyama, 1995).

3. Experimental

3.1. Plant material

Figs were identified within the scope of a broader project including establishment of a reference herbarium and testing congruence between plant and wasp identification. Voucher specimens were deposited at the herbarium of the Forestry Department of Brunei Darussalam. Determinations were confirmed by Prof. C.C. Berg (University of Bergen, Norway). This study involved 13 *Ficus* species, belonging to three different sub-genera (out of four existing Berg, 1989). Of these species, ten are dioecious and three are monoecious (*F. microcarpa*, *F. crassiramea* and *F. benjamina*). These last three species belong to the same section and are hemi-epiphytes, usually found in the forest canopy. Four of the ten dioecious species (*F. aurata*, *F. fulva*, *F. obscura* and *F. condensa*) are small trees, living in forest understorey or in secondary forests, specially along river banks (*F. condensa*). *F. deltoidea* var. *borneensis* is usually an epiphyte, living in open areas, but can be found as a small tree on poor soils. *F. punctata* is a climber, living in primary forest. The last four species of our sample (*F. uncinata*, *F. beccarii*, *F. stolonifera* and *F. megaleia*) are geocarpic species (they have figs beneath the soil litter layer) and are phylogenetically very closely related to each other. Their natural habitat is the forest understorey. All the species were studied in Brunei, either in Kuala Belalong Field Studies Centre of University Brunei Darussalam or in secondary forests along roads. Due to the difficulty of having all fig trees at the right stage (receptive) during one field season (spring 1998), not all sexes were sampled for all dioecious species. Headspace collections were made on figs that appeared to be morphologically receptive (ostiole opened, flowers within the fig with turgescent stigma). One to six individual trees per species were sampled, but all the collections of volatiles of the same species were finally combined, to allow a better detection of compounds.

3.2. Collection of volatiles

Volatiles released by figs were collected using an adsorption–desorption (headspace) technique (Turlings, Tumlinson, Heath, Proveaux & Doolittle, 1991). Figs (on a cut branch or in situ) were enclosed in a polyethylene terephtalate (Nalophan®) bag. Air was purified by charcoal filters and drawn by a Millipore® pump into the bag (entrance flux: 400 ml/min), through Teflon tubing. It was then drawn out of the bag (exit flux: 300 ml/min) over a Porapak®Q (25 ng, 80–100 mesh) collection trap, and pulled through Tygon tubing. Depending on size, 6 (mean diameter: 65 mm) to 563 (mean diameter: 5.1 mm) figs still on branches were enclosed per bag. Each headspace collection lasted from 3 to 6 h. Controls with ambient air or branches without figs were also performed. The Porapak®Q collection trap was then eluted with 150 μl of dichloromethane. In cases where solutions were too dilute to allow detection of volatiles, two or more extracts from the same species were combined. In most of our headspace collections, fig branches were cut and placed in a vase with water (figs bearing branches are often very high and difficult to enclose while attached to a tree). For two species (*F. condensa* and *F. aurata*), in situ collections of volatiles were also made. Odours emitted in the lab and in situ were quite similar (as during other experiments on *F. carica* in Montpellier), even if there were some differences concerning minor compounds (L. Grison and M. Hossaert, unpublished data).

3.3. Chemical and data analysis

GC–MS analyses were carried out using an HP-5 (5% phenyl methyl siloxane) column (length 50 m, internal diameter 0.22 mm, film thickness 0.33 μm), in an HP 5890 Series II GC with mass-selective detector 5971A MSD under the following conditions: carrier gas, helium, 5 psi head pressure, split flow ratio 20 : 1; column flow $\leq$ 2 ml/min; injector 280°C, detector 300°C; oven temperature program: 50°C for 1 min then 5°C/min to 200 held for a total run time of 46 min. Injection volumes were 1–3 μl. Data analyses were carried out using HP G1030A MS Chemstation software and a Wiley 138K Spectral Database. In many cases, the retention time and mass spectrum of authentic compounds were determined and compared with those of identical compounds detected in our extracts.

3.4. Limitations

The extent of adsorption of different compounds on any adsorbent including Porapak®Q depends on molecular properties. The presence of functional groups normally enhances adsorption. Our unpublished results of direct solvent extraction of figs showed considerably more abundance of saturated hydrocarbons than the Porapak®Q adsorbed volatiles and it could be that branched and unbranched alkanes are under-represented in the current results.

Another limitation arose with identification of overlapping peaks. These cases and the distinguishing features used for identification, if any, are given below:

1. 1,8-cineole (M^+ 154) with benzyl alcohol (M^+ 108). The prominence of *m/e* 79 and 77 are taken as indicating presence of benzyl alcohol. These two peaks are the base peak and prominent peak, respectively, for benzyl alcohol but are $<20\%$ the abundance of the base peak for 1,8-cineole.
2. β-pinene with β-myrcene. These are constitutional isomers so the molecular ions are of no help in detecting mixtures of the two; they both have the same base peak, *m/e* 93 but the relative intensities of the base peak and *m/e* 69 are quite different for the two compounds, being $>70\%$ for β-myrcene and $<30\%$ for β-pinene. In addition, pure β-myrcene has a more prominent peak at *m/e* 41 ($\approx 80\%$ of its base peak) compared to pure β-pinene ($\approx 26\%$) and its molecular ion is less prominent than that of β-pinene. Mixtures of these two compounds had relative intensities which were intermediate between these values.

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