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Fig volatile compounds—a first comparative study

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Abstract

We analysed the compounds of volatile blends released by receptive figs of twenty *Ficus* species to attract their specific pollinating wasps. In all, 99 different compounds were identified. The compounds are mainly terpenoids, aliphatic compounds and products from the shikimic acid pathway. In each species blend, there are few major compounds, which are generally common among floral fragrances. Most species blends also include rare compounds, but generally their proportion in the blend is low. A possible basis for species-specificity of *Ficus*-wasp interactions is discussed in relation to the patterns of volatiles found in this interspecies comparison.

Keywords: *Ficus*; Moraceae; Fig wasps; Specificity; Headspace; Terpenoids; Compounds from the shikimic pathway; Simple aliphatic compounds

1. Introduction

The genus *Ficus* (Moraceae) comprises about 750 species, most of them living in the tropics. The pollination of *Ficus* inflorescences (the fig or syconium) is intimately linked to agaonid wasps (Hymenoptera: Chalcidoidea), which reproduce inside them. The relationship between *Ficus* and agaonid species is obligate for both partners and generally species-specific: one fig species is pollinated by one species of wasp (Janzen, 1979; Wiebes, 1979). In such a close-knit mutualism, the encounter between partners is a crucial step for the continuity of the life cycle of each partner. Efficient mechanisms for ensuring encounter are particularly important in these systems in which the tiny (1–2 mm in length) and short lived (3–5 h; Hossaert-McKey, personal observation) pollinating wasps have to travel as much as 14 km to locate receptive trees (Nason et al., 1998). It has been shown for numerous fig species that the attractant signal is chemical (Van Noort et al., 1989; Hossaert-McKey et al., 1994; Ware and Compton, 1994; Gibernau et al., 1998). In tropical forests, where several *Ficus* species can live in sympatry (for example, Borneo rainforests contain more than one hundred fig species (Corner, 1965), with often ca. 40 species sympatric at one site, the encounter is especially problematic and requires specific chemical signals for each species pair. Is this specificity due to very peculiar compounds, rare among floral volatiles, or is it due to unique proportions of common compounds in the blend of each species? A previous study suggested that both cases occur in tropical species (Grison et al., 1999), but the volatile compounds in that study were collected under unusual climatic conditions, during an El Niño drought. Further studies were needed to confirm these results or to detect differences in the blends collected during years without such strong climatic constraints.

In this study, we characterized the chemistry of the blends of volatile compounds emitted by receptive figs of 20 *Ficus* species in order to identify the compounds in the bouquet of receptive figs and to obtain insights into the basis for specific attraction of pollinating wasps by their host species.

2. Results and discussion

We identified a total number of 99 compounds in head space collections of the 20 receptive fig species. In each species blend, two (*F. uncinata*) to forty-seven (*F. deltoidea*) compounds were identified, with one or a few major compounds, representing up to 90% of the total

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Table 1
(Part 1)—Relative abundance of the compounds identified in the blends of volatile compounds emitted by receptive figs of 20 *Ficus* species[a]

Compound	N1	N2	*F. condensa*	*F. fulva*	*F. deltoidea*	*F. microcarpa*	*F. xyllophylla*	*F. uncinata*	*F. spathulifolia*
Shikimic pathway									
Benzaldehyde	44	5	0.3	0	0	0	0	0	0
Benzyl alcohol	43	1	0	0	0	0	0	0	0
4-Methylbenzaldehyde	0	3	0.2	0	0.1	1.3	0	0	0
Methyl benzoate	34	1	0	0	0.1	0	0	0	0
1-Phenylpropan-2-ol	3	1	0	0	0	0	0	0	0
1-Phenylpropan-2-one	1	1	0	0	0	0	0	0	0
Methyl salicylate	47	2	0	0	0	1.7	0	0	0
4-Ethylacetophenone	0	1	0	0	0	0	0	0	0
(*Z*)-3-Hexenyl benzoate	6	1	0	0	0	0	0	0	0
Indole	0	2	0	0	0.1	0	0	0	0
Simple aliphatics									
Decane	7	1	0	0	0	0	0	0	0
Undecane	8	1	0	0	0	0	0	0	0
Dodecane	8	1	0	0	0	0	0	0	0
Tridecane	10	7	0	0	0	0	0	0	0
Tetradecane	10	8	0	0	0	0	0	0	0
Pentadecane	14	5	0	0	0	0	0	0	0
Heptanal	4	1	0	0	0	0	0	0	0
Octanal	6	1	0	0	0	0	0	0	0
Decanal	10	4	0.7	0	0.1	0	0	0	0
Undecanal	3	1	0	0	0	0	0	0	0
(*Z*)-3-Hexenol	6	5	1.3	0	0	0	0	0	0
2-Heptanone	5	1	0	0	0	0	0	0	0
1-Hexanol	15	7	0	0	0	0	0	0	0
γ-Butyrolactone	1	2	0	0	0	0	0	0	0
(*Z*)-3-Hexenyl acetate	22	3	0	0	0	0	0	0	0
Nonanol	1	1	0	0	0	0	0	0	0
Octanoic acid	2	1	0	0	0	0	0	0	0
Lauric acid	0	1	0	0	0	0	0	0	0
Acyclic monoterpenes									
6-Methyl-5-hepten-2-One	0	2	0	0	0.1	0	0	0	0
2-Methyl-6-methylene-1,7-octadien-3-one	0	1	0	4.6	0	0	0	0	0
2-Methyl-6-methylene-1,7-octadien-3-ol	0	1	0	0	0	0	0	0	0
3.7-Dimethyl-1.7-octadien-3.6-diol	0	1	0	0	0	0	0	0	0
Myrcene	68	7	0	0.4	0.1	0.4	0	0	0
(*Z*)-β-Ocimene	48	11	0.1	0.3	0.1	0	0	0	0
(*E*)-β-Ocimene	26	17	2.4	8.7	0.7	5.4	0.3	0	0
cis-Furanoid linalool oxide	15	2	0	0	1.0	0	0	0	0
trans-Furanoid Linalool oxide	15	3	0	0	1.5	0	0	0	0
Linalool	66	10	0.4	4.9	20.6	3.1	0	0	0
cis-Pyranoid linalool oxide	11	2	0	0	0.2	0	0	0	0
trans-Pyranoid linalool oxide	11	2	0	0	0.1	0	0	0	0
Hotrienol	3	1	0	0	0	0	0	0	0
Perillene	3	2	0	0	0	0	0	0	0
Cyclic monoterpenes									
α-Thujene	7	2	0	0	0	0	0	0	0
α-Pinene	63	8	0.1	1.3	0	1.9	0	50.3	0
Camphene	14	4	0	0.1	0	0	0	0	0
Sabinene	24	5	0.5	0.3	0	9.4	0	0	0
β-Pinen	51	8	0	0.6	0	0.4	0	0	0
δ-2-Carene	0	3	0	0	0	0	0	0	0
α-Phellandrene	7	2	0	0	0	0	0	0	0
α-Terpinene	0	4	0	0	0	0	0	0	0
p-Cymene	18	5	0	0	0	0	0	0	0
Limonene	75	11	0	0.5	0.1	0.8	0	0	0
1,8-Cineole	44	3	1.8	0.2	0	0	0	0	0
γ-Terpinene	10	3	0	0	0	0	0	0	0
8,9-Dehydro-*p*-cymene	0	4	0	0	0	0	0	0	0
Terpinolene	13	3	0	0	0	0	0	0	0
α-Terpineol	21	1	0	0	0	0	0	0	0

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Table 1 (*continued*)

Compound	N1	N2	*F. condensa*	*F. fulva*	*F. deltoidea*	*F. microcarpa*	*F. xyllophylla*	*F. uncinata*	*F. spathulifolia*
Sesquiterpenes									
Dendrolasine	1	2	0	8.4	0.5	0	0	0	0
α-Cubebene	1	9	0	0.3	0.3	1.9	0	0	0
Cyclosativene	1	1	0	0	0.4	0	0	0	0
Junipene	0	1	0	0	0	9.3	0	0	0
α-Ylangene	0	6	0	0	0.4	0	0	0	0
α-Copaene	7	18	1.3	6.2	6.4	38.2	1.2	49.7	0.2
β-Bourbonene	1	7	0	0	0.7	0	0.1	0	0
1,5-Diepi-β-bourbonene	0	1	0	0	0.1	0	0	0	0
β-Cubebene	2	3	0	0	1.9	0.3	0.1	0	0
β-Elemene	3	5	0.1	0.5	0.7	0.5	0.2	0	0
α-Gurjunene	0	3	0.4	0	0.7	0	0.8	0	0
α-*cis*-Bergamotene	0	1	0	0	0.2	0	0	0	0
Isocaryophyllene	1	1	0	0	0	0	0	0	0
β-caryophyllene	30	18	5.5	46.7	13.1	3.3	5.6	0	30.8
α-santalene	2	1	0	0	0.4	0	0	0	0
Selina-3,6-diene	0	1	0	0	0.2	0	0	0	0
β-Copaene	1	2	0	0	0	6.8	0	0	0
cda-*trans* Bergamotene	8	6	0	0	1.9	0	0	0	0
Aromadendrene	1	9	0.2	0.4	0	5.3	0	0	0
α-Humulene	9	14	0.8	5.6	5.8	0.9	1.1	0	6.2
Alloaromadendrene	3	7	0.5	0.6	1.2	0	0.8	0	0
(*E*)-β-Farnesene	5	1	0	0	0	0	0	0	0
Aciphyllene	0	3	0.1	0	0.1	0	0.1	0	0
Germacrene D	6	17	75.6	2.3	31.0	0.5	80.9	0	53.8
β-Selinene	1	1	0	0	0.9	0	0	0	0
δd-Selinene	0	2	0	0	0.3	0	0.4	0	0
α-Selinene	0	1	0	0	0.1	0	0	0	0
α-Curcumene	1	1	0	0	0	0	0	0	0
Bicyclogermacrene	1	14	5.2	1.1	0.1	3.5	6.7	0	9.0
α-muurolene	1	7	0.3	0	0.2	1.1	0.2	0	0
Germacrene A	0	5	0.5	3.6	2.4	2.6	0.5	0	0
δ-Amorphene	0	1	0	0	0.3	0	0	0	0
(*Z,E*)-α-Farnesene	2	4	0	0	0	0	0	0	0
δ-Cadinene	4	9	0	0	0.5	0.3	0.2	0	0
(*E,E*)-α-Farnesene	1	8	1.2	0	1.6	0	0	0	0
β-Bisabolene	6	3	0	0	0	0	0	0	0
2-*epi*-α-Selinene	0	1	0	0	0.1	0	0	0	0
δ-Cadinene	2	10	0.7	2.2	2.0	1.1	0.8	0	0
Cadina-1,4-diene	1	1	0	0	0.1	0	0	0	0
Germacrene B	0	1	0	0	0.4	0	0	0	0
Nerolidol	8	1	0	0.2	0	0	0	0	0
Caryophyllene oxide	4	2	0	0	0.1	0	0	0	0

Compound	N1	N2	*F. grossularioides*	*F. subgelderi*	*F. punctata*	*F. carica*	*F. salicifolia*	*F. abutilifolia*	*F. sur*
Shikimic pathway									
Benzaldehyde	44	5	0	0	0	0.1	0	15.3	0
Benzyl alcohol	43	1	0	0	0	7.8	0	0	0
4-Methylbenzaldehyde	0	3	0	0	0	0	0	0	0
Methyl benzoate	34	1	0	0	0	0	0	0	0
1-Phenylpropan-2-ol	3	1	0	0	10.0	0	0	0	0
1-Phenylpropan-2-one	1	1	0	0	4.9	0	0	0	0
Methyl salicylate	47	2	0	0	0	0.4	0	0	0
4-Ethylacetophenone	0	1	0	0	0	0.2	0	0	0
(*Z*)-3-Hexenyl benzoate	6	1	0	0	0	0.2	0	0	0
Indole	0	2	0	0	0	0.1	0	0	0
Simple aliphatics									
Decane	7	1	0	0	0.3	0	0	0	0
Undecane	8	1	0	0	0	0	0	0	0
Dodecane	8	1	0	0	5.4	0	0	0	0

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Table 1 (*continued*)

Compound	N1	N2	*F. grossularioides*	*F. subgelderi*	*F. punctata*	*F. carica*	*F. salicifolia*	*F. abutilifolia*	*F. sur*
Tridecane	10	7	0	0	0	0	0.1	2.2	1.8
Tetradecane	10	8	0	0	0.1	0	0	1.0	0
Pentadecane	14	5	0	0	0.4	1.1	0	0	0
Heptanal	4	1	0	0	0	0.1	0	0	0
Octanal	6	1	0	0	0	0.4	0	0	0
Decanal	10	4	0	0	0.2	1.2	0	0	0
Undecanal	3	1	0	0	0	0.2	0	0	0
(*Z*)-3-Hexenol	6	5	0	0	0	0.2	0	0	3.8
2-Heptanone	5	1	0	0	0.1	0	0	0	0
1-Hexanol	15	7	0	0	0.3	0.1	0.1	0.3	0
γ-butyrolactone	1	2	0	0	0	0	0	0	0
(*Z*)-3-Hexenyl acetate	22	3	0	0	0	0.2	0	2.7	0
Nonanol	1	1	0	0	0	0.2	0	0	0
Octanoic acid	2	1	0	0	0	0.2	0	0	0
Lauric acid	0	1	0	0	0.4	0	0	0	0
Acyclic monoterpenes									
6-Methyl-5-hepten-2-one	0	2	0	0	0	0.1	0	0	0
2-Methyl-6-methylene-1,7-octadien-3-one	0	1	0	0	0	0	0	0	0
2-Methyl-6-methylene-1,7-octadien-3-ol	0	1	0	0	0	1.8	0	0	0
3.7-Dimethyl-1.7-octadien-3.6-diol	0	1	0	0	0	1.7	0	0	0
Myrcene	68	7	0	0	0.3	0	1.6	0	0
(*Z*)-β-ocimene	48	11	0	0.2	0	0.2	0.5	1.5	0
(*E*)-β-ocimene	26	17	0	71.3	0.1	0.2	0.6	10.4	40.8
cis-Furanoid linalool oxide	15	2	0	0	0	17.0	0	0	0
trans-Furanoid Linalool oxide	15	3	0	0	0.1	10.8	0	0	0
linalool	66	10	65.6	0	0	36.7	0.3	0.5	0
cis-Pyranoid linalool oxide	11	2	0	0	0	1.1	0	0	0
trans-Pyranoid Linalool oxide	11	2	0	0	0	0.3	0	0	0
Hotrienol	3	1	0	0	0	7.3	0	0	0
Perillene	3	2	0	0	0	0	0	0	7.5
Cyclic monoterpenes									
α-Thujene	7	2	0	0	0	0	0.7	0	0
α-Pinene	63	8	0	0	0.6	0	50.1	0	1.6
Camphene	14	4	0	0	0	0	1.1	0	0
Sabinene	24	5	0	0	16.2	0	0	0	0
β-Pinene	51	8	0	0	0.2	0	5.4	2.0	0
δ-2-Carene	0	3	0	0	0	0	0	1.0	0
α-Phellandrene	7	2	0	0	0	0	0.4	0	0
α-Terpinene	0	4	0	0	0	0	0.1	0.3	0
p-Cymene	18	5	0	0	1.4	0	5.5	8.1	0
Limonene	75	11	9.6	0	0	0	19.9	18.2	1.5
1,8-Cineole	44	3	0	0	42.0	0	0	0	0
γ-Terpinene	10	3	0	0	0	0	6.3	5.2	0
8,9-Dehydro-*p*-cymene	0	4	0	0	0	0	0.7	1.8	0
Terpinolene	13	3	0	0	0	0	3.5	3.1	0
α-Terpineol	21	1	0	0	0.3	0	0	0	0
Sesquiterpenes									
Dendrolasine	1	2	0	0	0	0	0	0	0
α-Cubebene	1	9	0	0	0	0	0.1	0	0
Cyclosativene	1	1	0	0	0	0	0	0	0
Junipene	0	1	0	0	0	0	0	0	0
α-Ylangene	0	6	0	0	0	0	0.1	0	0
α-Copaene	7	18	0	19.3	0.1	0	0.2	4.1	4.9
β-Bourbonene	1	7	0	0	0	4.3	0.1	0	0
1,5-Diepi-β-bourbonene	0	1	0	0	0	0	0	0	0
β-Cubebene	2	3	0	0	0	0	0	0	0
β-Elemene	3	5	0	0	0	0	0	0	0
α-Gurjunene	0	3	0	0	0	0	0	0	0
α-*cis*-Bergamotene	0	1	0	0	0	0	0	0	0
Isocaryophyllene	1	1	0	0	0	0.1	0	0	0
β-Caryophyllene	30	18	0	5.5	0.3	3.5	1.3	3.0	9.5

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Table 1 (*continued*)

Compound	N1	N2	*F. grossularioides*	*F. subgelderi*	*F. punctata*	*F. carica*	*F. salicifolia*	*F. abutilifolia*	*F. sur*
α-Santalene	2	1	0	0	0	0	0	0	0
Selina-3,6-diene	0	1	0	0	0	0	0	0	0
β-Copaene	1	2	0	0	0	0.1	0	0	0
α-*trans* Bergamotene	8	6	0	0	1.1	0	0	4.5	1.9
Aromadendrene	1	9	0	3.7	0	0	0.1	0	0
α-Humulene	9	14	0	0	0	0.1	0.1	0.8	0
Alloaromadendrene	3	7	0	0	0	0	0	0	0
(E)-β-Farnesene	5	1	0	0	1.01	0	0	0	0
Aciphyllene	0	3	0	0	0	0	0	0	0
Germacrene D	6	17	0.2	0	0	0.3	0.3	12.1	15.4
β-Selinene	1	1	0	0	0	0	0	0	0
δ-Selinene	0	2	0	0	0	0	0	0	0
α-Selinene	0	1	0	0	0	0	0	0	0
α-Curcumene	1	1	0	0	0.2	0	0	0	0
Bicyclogermacrene	1	14	24.6	0	0	0	1.1	0.5	0
α-Muurolene	1	7	0	0	0	0	0	0	0
Germacrene A	0	5	0	0	0	0	0	0	0
δ-Amorphene	0	1	0	0	0	0	0	0	0
(*Z,E*)-α-Farnesene	2	4	0	0	0.5	0	0.1	0	0
γ-Cadinene	4	9	0	0	0	0	0	1.3	0
(*E,E*)-α-Farnesene	1	8	0	0	0.6	0.2	0	0	11.4
β-Bisabolene	6	3	0	0	0	0	0	0	0
2-*epi*-α-Selinene	0	1	0	0	0	0	0	0	0
δ-Cadinene	2	10	0	0.1	0	0	0.1	0	0
Cadina-1,4-diene	1	1	0	0	0	0	0	0	0
germacrene B	0	1	0	0	0	0	0	0	0
Nerolidol	8	1	0	0	0	0	0	0	0
Caryophyllene oxide	4	2	0	0	0	1.6	0	0	0

Compound	N1	N2	*F. tettensis*	*F. thonningii*	*F. polita*	*F. religiosa*	*F. macrophylla*	*F. glumosa*
Shikimic pathway								
Benzaldehyde	44	5	0.4	0	0	0	5.5	0
Benzyl alcohol	43	1	0	0	0	0	0	0
4-Methylbenzaldehyde	0	3	0	0	0	0	0	0
Methyl benzoate	34	1	0	0	0	0	0	0
1-Phenylpropan-2-ol	3	1	0	0	0	0	0	0
1-Phenylpropan-2-one	1	1	0	0	0	0	0	0
Methyl salicylate	47	2	0	0	0	0	0	0
4-Ethylacetophenone	0	1	0	0	0	0	0	0
(*Z*)-3-Hexenyl benzoate	6	1	0	0	0	0	0	0
Indole	0	2	0	0	0	0	0	0
Simple aliphatics								
Decane	7	1	0	0	0	0	0	0
Undecane	8	1	0	0	0	1.9	0	0
Dodecane	8	1	0	0	0	0	0	0
Tridecane	10	7	0.2	0.5	0	1.4	0	0.6
Tetradecane	10	8	1.1	1.4	2.5	8.1	0.5	1.3
Pentadecane	14	5	0.7	0.6	0	0	0	0.4
Heptanal	4	1	0	0	0	0	0	0
Octanal	6	1	0	0	0	0	0	0
Decanal	10	4	0	0	0	0	0	0
Undecanal	3	1	0	0	0	0	0	0
(*Z*)-3-Hexenol	6	5	0	0	0	0.3	0.1	0
2-Heptanone	5	1	0	0	0	0	0	0
1-Hexanol	15	7	0	0.6	0	1.1	0.2	0
γ-butyrolactone	1	2	0	0	0	0	0.4	38.1
(*Z*)-3-Hexenyl acetate	22	3	0	0	0	1.1	0	0
Nonanol	1	1	0	0	0	0	0	0
Octanoic acid	2	1	0	0	0	0	0	0
Lauric acid	0	1	0	0	0	0	0	0

(*continued on next page*)

Table 1 (*continued*)

Compound	N1	N2	*F. tettensis*	*F. thonningii*	*F. polita*	*F. religiosa*	*F. macrophylla*	*F. glumosa*
Acyclic monoterpenes								
6-Methyl-5-hepten-2-one	0	2	0	0	0	0	0	0
2-Methyl-6-methylene-1,7-octadien-3-one	0	1	0	0	0	0	0	0
2-Methyl-6-methylene-1,7-octadien-3-ol	0	1	0	0	0	0	0	0
3.7-Dimethyl-1.7-octadien-3.6-diol	0	1	0	0	0	0	0	0
myrcene	68	7	0.1	0	0	0	1.3	0
(*Z*)-cdb-Ocimene	48	11	0.4	0	0	0.8	0.6	0.3
(*E*)-β-Ocimene	26	17	6.5	5.3	11.1	14.2	11.9	0.6
cis-Furanoid linalool oxide	15	2	0	0	0	0	0	0
trans-Furanoid Linalool oxide	15	3	0	0	0	0	0	0
Linalool	66	10	3.5	0	0	0	7.2	0
cis-Pyranoid linalool oxide	11	2	0	0	0	0	0	0
trans-Pyranoid linalool oxide	11	2	0	0	0	0	0	0
Hotrienol	3	1	0	0	0	0	0	0
Perillene	3	2	0	0	0	0.8	0	0
Cyclic monoterpenes								
α-Thujene	7	2	0	0	0	0	0.2	0
α-Pinene	63	8	0	0	0	28.7	0	0
Camphene	14	4	0	0	0	3.8	0.1	0
Sabinene	24	5	0	0	0	0	0.7	0
β-Pinene	51	8	0.7	0	0	2.6	0.8	0
δ-2-Carene	0	3	1.0	0	0	0	0.5	0
α-Phellandrene	7	2	0	0	0	0	0.1	0
α-Terpinene	0	4	0.2	0	0	3.1	0	0
ρ-Cymene	18	5	0	0	0	0	0.5	1.0
Limonene	75	11	0.5	0	0	1.8	0.9	1.5
1,8-Cineole	44	3	0	0	0	0	0	0
γ-Terpinene	10	3	0	0	0	0	0.3	0
8,9-Dehydro-*p*-cymene	0	4	0.7	0	0	0	0.3	0
Terpinolene	13	3	0.7	0	0	0	0	0
α-Terpineol	21	1	0	0	0	0	0	0
Sesquiterpenes								
Dendrolasine	1	2	0	0	0	0	0	0
α-cubebene	1	9	0.2	0.5	0	0.9	0.2	0.4
Cyclosativene	1	1	0	0	0	0	0	0
Junipene	0	1	0	0	0	0	0	0
α-Ylangene	0	6	0	0.9	2.6	1.4	0	0.5
α-Copaene	7	18	7.5	8.8	30.5	4.0	1.1	1.4
β-Bourbonene	1	7	0.3	0	0	1.7	0	0.3
1,5-Diepi-β-bourbonene	0	1	0	0	0	0	0	0
β-Cubebene	2	3	0	0	0	0	0	0
β-Elemene	3	5	0	0	0	0	0	0
α-Gurjunene	0	3	0	0	0	0	0	0
α-*cis*-Bergamotene	0	1	0	0	0	0	0	0
Isocaryophyllene	1	1	0	0	0	0	0	0
β-Caryophyllene	30	18	33.1	17.3	30	4.4	43.3	18.0
α-Santalene	2	1	0	0	0	0	0	0
Selina-3,6-diene	0	1	0	0	0	0	0	0
β-Copaene	1	2	0	0	0	0	0	0
α-*trans* Bergamotene	8	6	0.8	0	0	1.6	0	2.0
Aromadendrene	1	9	0	3.4	0	1.8	1.0	0.6
α-Humulene	9	14	2.5	2.0	0	1.3	4.0	4.0
Alloaromadendrene	3	7	2.1	0	0	1.0	0	3.3
(*E*)-β-Farnesene	5	1	0	0	0	0	0	0
Aciphyllene	0	3	0	0	0	0	0	0
Germacrene D	6	17	28.0	41.7	18.1	3.2	7.6	4.9
β-Selinene	1	1	0	0	0	0	0	0
δ-Selinene	0	2	0	0	0	0	0	0
α-Selinene	0	1	0	0	0	0	0	0
α-Curcumene	1	1	0	0	0	0	0	0
Bicyclogermacrene	1	14	1.7	6.8	0	0.8	9.5	0.8
α-Muurolene	1	7	2.4	1.8	0	0	0	1.1

(*continued on next page*)

Table 1 (*continued*)

Compound	N1	N2	*F. tettensis*	*F. thonningii*	*F. polita*	*F. religiosa*	*F. macrophylla*	*F. glumosa*
Germacrene A	0	5	0	0	0	0	0	0
δ-Amorphene	0	1	0	0	0	0	0	0
(*Z,E*)-α-Farnesene	2	4	0	0	0	0	0.7	1.1
γ-Cadinene	4	9	4.1	6.4	3.7	7.2	0	1.3
(*E,E*)-α-Farnesene	1	8	0	1.5	1.4	0	0	2.2
β-Bisabolene	6	3	0.7	0.4	0	0	0	0.9
2-*epi*-α-Selinene	0	1	0	0	0	0	0	0
δ-Cadinene	2	10	0	0	0	1.2	0.3	12.9
Cadina-1,4-diene	1	1	0	0	0	0	0	0
Germacrene B	0	1	0	0	0	0	0	0
Nerolidol	8	1	0	0	0	0	0	0
Caryophyllene oxide	4	2	0	0	0	0	0	0

[a] N1: number of genera emitting this compound among the 174 genera reviewed by Knudsen et al. (1993). N2: number of *Ficus* species releasing this compound in our study.

mass. The bouquets are dominated by terpenes (monoterpenes and sesquiterpenes), aliphatic compounds and compounds from the shikimic acid pathway (Table 1). These chemical classes are well represented among compounds released by plants in floral fragrances (Williams, 1983; Knudsen et al., 1993), as well as among deterrent compounds functioning as defenses against herbivores (Finch, 1980; Gershenzon and Croteau, 1991). These bouquets are probably also responsible for the specificity of the fig/wasp relationship, as suggested by reciprocal tests with blends of volatile compounds of *F. fulva*, *F. condensa* and *F. microcarpa* and their pollinators: the insects were only stimulated by the blend from their host species (Grison-Pigé et al., 2002). Except for *F. carica* (Gibernau, 1997) we have not yet performed bioassays using the different volatiles. Thus, we do not know which chemicals act as specific signals to the wasps. However, examination of the abundance and distribution of compounds between species suggests several reasonable hypotheses.

Many chemicals (37 of 99) were found only once, and we refer to them as "specific" compounds. The great majority of chemicals were recorded in three or fewer species (Mann–Whitney $U=51$, $P=0.009$, Table 2). Notwithstanding, a number of compounds were very common. For example, (*E*)-β-ocimene and germacrene D were identified in 17 of the 20 species studied, and α-copaene and β-caryophyllene in 18 of them (Table 1). Six species contained at least one "specific" compound, identified only in its floral blend: *F. fulva*, *F. deltoidea*, *F. microcarpa*, *F. punctata*, *F. carica* and *F. religiosa*.

The mean relative abundance of each compound in the blend was recorded, as well as the number of fig species in which it occurred (Fig. 1). The shared compounds were also abundant compounds in the fig blends where they were found, and the greater the degree of restriction of compounds to a few species, the less abundant in the blends they were.

Table 2
Number of chemicals that were recorded in a given number of *Ficus* species[a]

Number of chemicals	Number of species recorded in
37	1
13	2
11	3
5	4
7	5
1	6
8	7
4	8
3	9
2	10
2	11
0	12
0	13
2	14
0	15
0	16
2	17
2	18

[a] The 37 compounds present in only one species of our sample are called "specific" in the text.

The compounds released by receptive figs were compared to those from Knudsen et al.'s checklist (1993), which reviews the floral fragrances (detected by head space techniques) of taxa belonging to 174 genera. Forty of the 99 total compounds identified in our study were listed in none or one of the 174 genera of the checklist (Table 1), and will be called "rare". Eighteen of the 20 *Ficus* species blends contained one or more of these compounds, rare among floral fragrances (Fig. 2). These rare compounds were mainly aliphatic compounds or sesquiterpenoids. In 13 cases these rare compounds represented more than 5% of the total compounds of the bouquet: for example, γ-butyrolactone represented 38% of the total compounds released by *F. glumosa*, bicyclogermacrene

represented 25% of the blend of *F. grossularioides*, and (*E,E*)-α-farnesene 11% of that of *F. sur*.

Most *Ficus* species released compounds that are rare among floral fragrances. Of the 40 compounds "rare" among floral fragrances, 20 were found among the volatiles of only one *Ficus* species (specific compounds). However, only a small number of species accounted for the emission of such compounds and each emitted several rare compounds. The 20 rare and specific compounds were accounted for by only five species: *F. carica* (5 rare and specific compounds), *F. deltoidea* (10), *F. fulva* (1), *F. microcarpa* (1), and *F. punctata* (3).

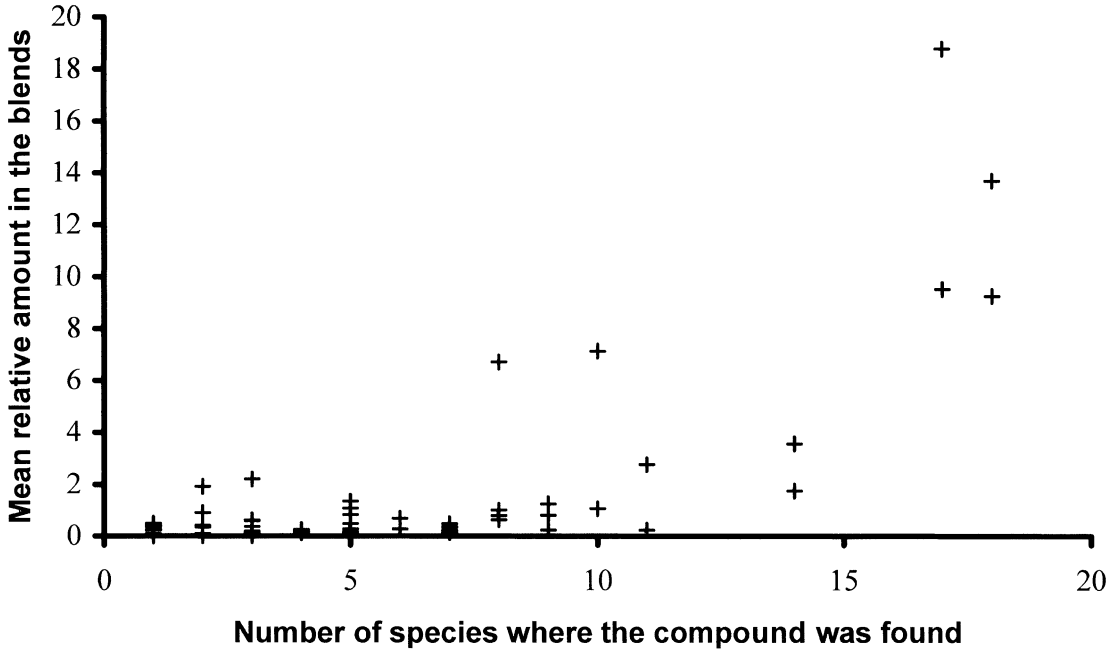

Fig. 1. For each chemical are presented the number of times it was observed in the *Ficus* species sampled and the relative amount it represented in the blends of each (for each compound, average of the relative abundances in all the fig blends where it was identified). The "specific" compounds (37 in number) are those that were present in only one of the fig species sampled.

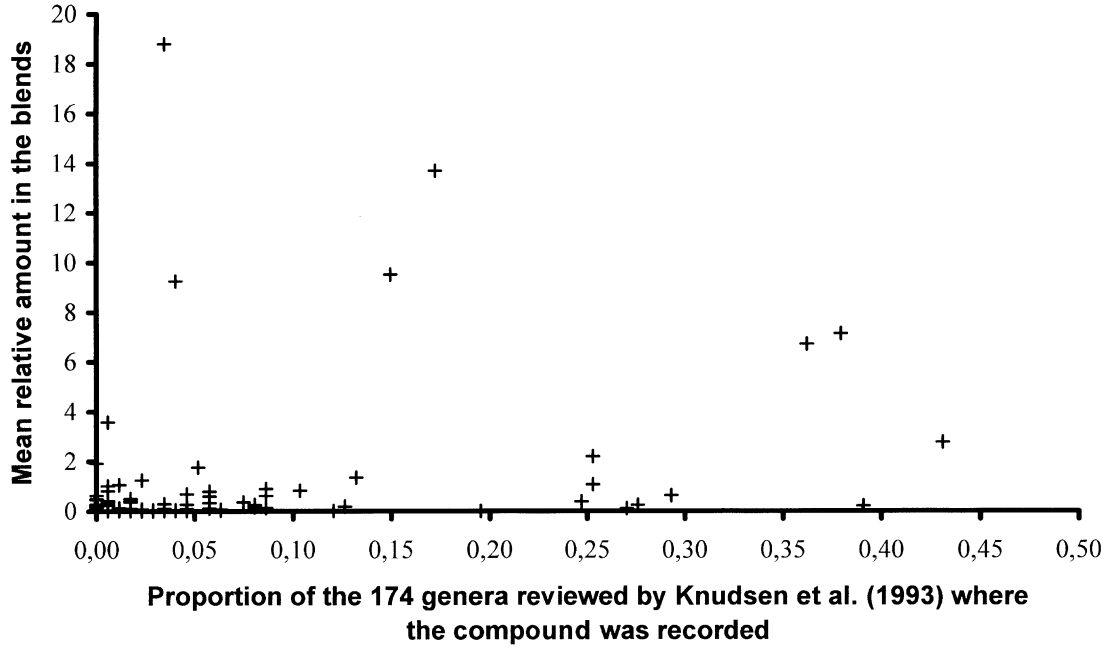

Fig. 2. Relationship between the proportion of the genera in which each compound was identified among the 174 genera reviewed by Knudsen et al. (1993), and the mean relative amount of the compound in the fig blends (for each compound, average of the relative abundances in all the fig blends where it was identified). The "rare" compounds (40 in number) are those present in fewer than 0.6% of the genera reviewed.

Table 3
Systematics and biological characters of the *Ficus* species studied

Species	Subgenus	Section	Place of study	Reproductive system	Biological form	Environment
F. fulva Reinw.	*Ficus*	*Ficus*	Brunei	Dioecy	Small tree	Forest understorey or secondary forests
F. deltoidea Jack.	*Ficus*	*Ficus*	Brunei	Dioecy	Epiphyte or shrub	Forest or open areas
F. grossularioides Burm.	*Ficus*	*Ficus*	Brunei	Dioecy	Shrub	Open areas
F. carica L.	*Ficus*	*Ficus*	France	Dioecy	Small tree	Open areas
F. punctata Thunb.	*Ficus*	*Kalosyce*	Brunei	Dioecy	Climber	forests
F. sur Forssk.	*Sycomorus*	*Sycomorus*	South Africa	Monoecy	Medium-size tree	Along streams
F. condensa King	*Sycomorus*	*Sycocarpus*	Brunei	Dioecy	Small tree	Forest understorey or secondary forests
F. uncinata Becc.	*Sycomorus*	*Sycocarpus*	Brunei	Dioecy	Small tree, geocarpic figs	Forest understorey or secondary forests
F. salicifolia Miq.	*Urostigma*	*Urostigma*	South Africa	Monoecy	Small tree	Woodland, often in rocky places
F. religiosa Linn.	*Urostigma*	*Urostigma*	South Africa[a]	Monoecy	Hemiepiphytic to terrestrial	Forests or secondary forests
F. microcarpa Linn.	*Urostigma*	*Conosycea*	Brunei	Monoecy	Hemiepiphytic to terrestrial	Forests or secondary forests
F. xyllophylla Wall.	*Urostigma*	*Conosycea*	Brunei	Monoecy	Hemiepiphytic to terrestrial	Forests or secondary forests
F. spathulifolia Corner	*Urostigma*	*Conosycea*	Brunei	Monoecy	Hemiepiphytic to terrestrial	Forests or secondary forests
F. subgelderi Corner	*Urostigma*	*Conosycea*	Brunei	Monoecy	Hemiepiphytic to terrestrial	Forests or secondary forests
F. abutilifolia Miq.	*Urostigma*	*Galoglychia*	South Africa	Monoecy	(Hemi-)epilithic	On rocks in savana woodland
F. polita Vahl.	*Urostigma*	*Galoglychia*	South Africa	Monoecy	Hemi-epiphytic/secondarily terrestrial	Evergreen forests
F. tettensis Hutch.	*Urostigma*	*Galoglychia*	Botswana	Monoecy	(Hemi-)epilithic	On rocks in dry areas
F. thonningi Bl.	*Urostigma*	*Galoglychia*	South Africa	Monoecy	Terrestrial to hemi-epiphytic	Wooded grasslands and tickets
F. glumosa Delile	*Urostigma*	*Galoglychia*	South Africa	Monoecy	Trees or shrubs	Savanna woodland, often on rocks
F. macrophylla Des.	*Urostigma*	*Malvanthera*	South Africa[a]	Monoecy	Hemiepiphytic to terrestrial	Forests

[a] Introduced.

The most abundant compounds in the blend of a *Ficus* species were never compounds rare across the genera reviewed by Knudsen et al. (1993) (Fig. 2), except for γ-butyrolactone in *F. glumosa*. These compounds were limonene (11 species of the 20 studied), linalool (10 species), (*Z*)-β-ocimene (17 species), β-caryophyllene (18 species), (*E*)-β-ocimene (17 species), α-copaene (18 species), and germacrene D (17 species), which were found in 43, 38, 27, 17, 15, 4 and 3%, respectively, of the 174 genera reviewed by Knudsen et al. (1993).

The patterns we document suggest reasonable hypotheses about the chemical basis of specificity of wasp attraction. First, 37 of the 99 compounds identified were found in only a single species, suggesting that in some cases specificity of attraction could theoretically be based on a single compound. However, specificity probably seldom has such a simple basis, because these "speific" compounds were accounted for by only 6 of the 20 species. In the majority of species studied here, the specificity of the signal is thus unlikely to be due to a single compound and must instead be based on a unique mixture of several compounds. For *F. carica*, Gibernau (1997) showed that a mixture of linalool, benzyl alcohol and linalool oxides was responsible for the attraction of the pollinating wasp. These three compounds are common among floral fragrances, and linalool is the main compound in the *F. carica* blend (Gibernau et al., 1997). In this case the efficiency of the attraction is, therefore, not generated by rare compounds, but depends on the relative proportions of the compounds in the mixture.

3. Concluding remarks

This study showed that the major compounds produced by most *Ficus* species are generally not rare among floral fragrances and that in our sample, the specificity is not likely to be the result of one specific signal. Our results point to the need for biological tests in species pairs other than *F. carica* and its specific pollinator and suggest hypotheses to guide the design of such tests. Further work should also include determination of the enantiomeric composition of compounds in fig odours and investigations on the role of enantiomeric compositions of chiral volatiles in attraction and specificity.

4. Experimental

4.1. Plant material

This study involved 20 species of figs belonging to three of the four extant subgenera. Within each subgenus several sections were represented (Table 3). These species also represent diverse biological forms. Some of them, such as *F. microcarpa*, are hemi-epiphytes, others are lianas (e.g. *F. punctata*) or small trees (e.g. *F. fulva*). Their natural environment is forest understory (e.g. *F. condensa*), open forests (e.g. *F. fulva*, *F. subgelderi*), mangroves (e.g. *F. microcarpa*), forest canopies (e.g. *F. xyllophylla, F. spathulifolia*) or non-forested areas (e.g. *F. carica*, *F. salicifolia, F. tettensis*...) (Table 3). Herbarium specimens of the species studied in Brunei are

deposited in the Herbarium of the Forestry Department of Brunei Darussalam. The South African fig species studied here are all well known, and specimens can be obtained from J.M.G.

4.2. Collection of volatile compounds

To allow collection from many figs, branches bearing receptive figs were cut. The leaves were removed to prevent transpiration, and the branches were enclosed in humid air inside plastic bags. Collection of the volatile compounds was conducted at the Universiti Brunei Darussalam, where the branches were brought within 1 h, and around Pretoria (South Africa) or in Botswana. The cut branches were placed in receptacles with water during collection of volatile compounds. Volatile compounds were collected by the adsorption–desorption (headspace) technique as described in Grison et al. (1999). The effect of cutting branches on the emission by receptive figs was previously examined in some of the species studied here.

4.3. Chemical analyses

Solutions obtained were combined to form a more concentrated solution (one per species) that was analyzed using a gas chromatograph-mass spectrometer (GC: Hewlett-Packard, MS: HP 5870; FID, column DB5, 30 m, ID 0.25 mm, film thickness 0.25 μm, carrier gas: helium, oven temperature program: 50–180 °C, 3 °C/min). Non-combined solutions were indeed not sufficiently concentrated for GC or GC–MS analysis. Percentages of each compound in the scent are given on the basis of the total chromatogram obtained. Component identification was based on computer matching of the mass spectra. Using Library Search System HP-5872 (Hewlett-Packard), we consulted the following databases: Wiley 138 and NBS 75K libraries (McLafferty, 1988), NIST98 (Stephen, 1998), and the compilation by Adams (1995). If needed we used retention indices reported in the literature (Adams, 1995) and additional libraries (Joualin, Casabianca) for identification of the mass spectra. With the GC and the column used in this study, we were not able to determine the enantiomeric composition of the compounds present in the blend.

4.4. Data analyses

To estimate the abundance in plant taxa of the volatile compounds found in the *Ficus* blends, we used the checklist compiled by Knudsen et al. (1993). These authors reviewed the composition of volatile blends, collected by headspace techniques, of plant taxa belonging to 174 genera.

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