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Limited intersex mimicry of floral odour in *Ficus carica*

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Summary

1. The mutualism between figs and pollinators is strict and pollination of female flowers occurs by deceit. Hence the chemical signal responsible for the encounter of the partners is expected to have limited variability. However, since male and female trees bloom at different times, sexual mimicry may not be necessary. The variability of floral odour blends of *Ficus carica* was studied between sexes, among trees and over time, as were the quantity and identity of the released compounds.

2. Male and female figs emitted the same compounds, but the quantities and proportions among the compounds differed.

3. The composition of the fig blend and the temporal pattern of emission were similar among trees of the same sex, and emission was synchronized with pollinator presence.

4. Composition of the blend and quantity released changed considerably over time, but at the time of maximal emission, all three compounds known to be essential to attract pollinators were released by male and female figs.

5. In a seasonal environment in which male and female flowers have different phenologies, selection for a strict sexual mimicry of the volatile attractants is weak. The identity of the compounds is the same for male and female figs, but their relative abundance in the blend differ.

Key-words: Figs, headspace, pollination mutualism, variability, volatile compounds

Introduction

Volatile compounds emitted by plants often mediate interspecific interactions between plants and animals (Dodson *et al.* 1969; Whittaker & Feeny 1971; Pellmyr & Thien 1986; Visser 1986; Bergström 1987; Dobson 1994; Loughrin *et al.* 1994; Turlings *et al.* 1995; Röse *et al.* 1996). Among these, plant–pollinator relationships have been extensively studied, and the role of chemical compounds as pollinator attractants is known for a variety of species (Williams & Dodson 1972; Pellmyr *et al.* 1991; Bergström *et al.* 1992; Knudsen, Tollsten & Bergström 1993; Dobson *et al.* 1997; Gibernau *et al.* 1998; Ervik *et al.* 1999; Schiestl *et al.* 1999; Tollsten & Knudsen 1992). In several cases, volatiles involved in the attraction have been identified. However, few of these studies consider the possible variability in the chemical signals emitted by a given species, in the composition of the scent and in the quantities released.

Floral fragrance variability exists among individual plants (Bergström *et al.* 1992; Moya & Ackerman 1993; Tang 1993), among flowers of the same plant (Schiestl *et al.* 1997; Moya & Ackerman 1993) and for a flower at different dates (Altenburger & Matile 1988; Moya & Ackerman 1993; Shaver, Lingren & Marshall 1997). In most studies, pollination was not ensured by only one species of pollinator (Moya & Ackerman 1993; Bergström *et al.* 1992; Miyake, Yamaoka & Yahara 1998; Ervik *et al.* 1999). In a truly specific plant–pollinator interaction (i.e. one species of plant to one species of pollinator), one can expect the chemical signal to show little variation in the relative amounts of each compound. This should apply especially when the interaction is obligate for both partners, as is the case for *Ficus*–pollinator mutualisms. Generally, one species of insect (Hymenoptera, Agaonidae) pollinates and reproduces in figs of one species of *Ficus* (Moraceae) (Berg 1989; Janzen 1979; Compton 1990). When the fig (an urn-shaped inflorescence) is receptive, it emits a blend of volatiles that has been shown for several species to be a pollinator attractant (Barker 1985; Gibernau *et al.* 1998; Grison, Edwards & Hossaert-McKey 1999; Van Noort, Ware & Compton 1989; Ware & Compton 1994). Half of the *Ficus* species are monoecious, while the other half are gynodioecious but functionally dioecious.

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In monoecious species, female pollinators enter the fig, pollinate and lay eggs, and generally die within the fig (Gibernau *et al.* 1996).

In dioecious species, 'male' figs contain both male and female flowers. In these figs, male flowers produce pollen and female flowers do not produce seeds, but are instead the place where pollinators lay eggs. Female figs contain only female flowers, in which the pollinating wasps are not able to lay eggs due to the length of the style. Female figs therefore only produce seeds (and no pollinator). There is thus a conflict of interests between the female fig tree, which needs to be pollinated, and the insect, which should avoid female figs (where it dies without laying eggs). In a non-seasonal environment, where flowering is synchronous within the tree but asynchronous among trees, pollinators emerging from a fig have to fly away from their natal tree to find a male fig to reproduce. A selective pressure for the capacity to discriminate between male and female figs is therefore expected on the wasp's side. But on the other side, male and female figs should be selected to emit exactly the same signal to attract the pollinator, ensuring that the wasps also enter female figs and pollinate their flowers. If this signal is indeed chemical, there should be chemical mimicry between sexes, as hypothesized by Grafen & Godfray (1991) and Patel *et al.* (1995). In a seasonal environment, where there is a phenological delay between male and female tree flowering, pollinators cannot choose between the two kinds of figs (Kjellberg *et al.* 1987). There is therefore no selective pressure for a strict chemical mimicry among sexes.

Ficus carica, the edible fig, is a dioecious species growing in a seasonal environment. The pollinating wasp, *Blastophaga psenes* (Hymenoptera, Chalcidoidea, Agaonidae), is attracted by the fig fragrance (Hossaert-McKey *et al.* 1994; Gibernau *et al.* 1998). In this paper, we study the chemical variability of odours emitted by receptive figs of this species. The seasonality of the environment suggests that selection for a chemical mimicry between male and female trees should be limited. To test this hypothesis, odours of male and female figs were compared. Changes in the compounds emitted over the season by the trees were also investigated, as well as intertree variability. At each level, we analysed the total quantity released and the composition of the volatile blend.

Materials and methods

SPECIES AND SITE

Ficus carica is dioecious, like half of all *Ficus* species. 'Male' trees flower in April–May and August–September (last period not studied here) and female trees in June–July (see Kjellberg *et al.* 1987 for more details on the cycle). We studied the volatile emissions of 12 trees (six males and six females, called M_i for male tree i and F_j for female tree j) growing on the CNRS campus in Montpellier, France. This orchard was about 33 years old and planted with the offspring of wild fig trees grown previously on the campus. These trees were associated in pairs of one male and one female, the trees in a pair being located close to each other (less than 10 m apart) and of similar appearance and size. They might have one or two parents in common.

COLLECTION OF VOLATILES

Volatile compounds were collected by headspace sorption (Heath & Manukian 1994; Turlings *et al.* 1991), as detailed in Grison *et al.* (1999). For each tree, four branches bearing figs and one branch without figs (control branch) were enclosed briefly in a polyethylene terephtalate (Nalophan®) bag. An airflow was maintained through the bag by two pumps, one pushing the air into the bag (flow rate: 400 mL min^{-1}), the other pulling it from the bag (flow rate: 300 mL min^{-1}). This difference in flow rates prevented contamination from external air. The air pulled out of the bag was drawn over a Porapak Q® filter, in which the compounds were trapped. They were then eluted by 150 µL of dichloromethane. Each collection lasted 4 h (morning: 0900–1300 h, or afternoon: 1300–1700 h) or 16 h (night: 1700–0900 h). For the trees of pairs 1, 4, 5 and 6, one collection of 4 h (morning or afternoon) was carried out every week. For the trees of pairs 7 and 8, the weekly collection lasted 24 h. The sampling began at 0900 h and the filters were changed at 1300, 1700 and 0900 h the following day. The ratio of the quantity released in the morning or in the afternoon compared with that released in 24 h was calculated with data from trees of pairs 7 and 8. The quantity released per fig and per day was then obtained for every tree at every date of collection using this ratio (average value per sex was used).

IDENTIFICATION AND QUANTIFICATION OF CHEMICALS

Twenty microlitres of a 200 ng μL^{-1} solution of internal standards (nonane and dodecane) were added to each sample. The solution was then analysed by gas chromatography, using a CP-9003 chromatograph (column EC-1, length 30 m, internal diameter 0·25 mm, film thickness 0·25 µm, carrier gas: helium, on-column injector, oven temperature program: 50–250 °C, 5 °C min^{-1}) (Chrompack, Middleburg, The Netherlands). For the identification of compounds, concentrated solutions were analysed by a gas chromatograph-mass spectrometer (GC) (Hewlett-Packard MS: HP 5870; Hewlett-Packard, Palo Alto, CA, USA) (column 30 m, internal diameter 0·25 mm, film thickness 0·25 µm, carrier gas: helium, oven temperature program: 50–180 °C, 3 °C min^{-1}). Compound identity was also verified by comparing the retention indices with those from the literature.

To determine what proportion of the compounds released by the figs was trapped on a Porapak Q® filter, the following preliminary experiment was carried out. One or a few micropipettes were filled with linalool, the main component of the fig blend. They were weighed and placed inside a Nalophan® bag. Air was drawn out of the bag by a pump, at a flow rate of 300 mL min^{-1}, the exiting air passing through a Porapak Q® filter. The entrance of the bag was opened just enough to prevent it from deflation. After 3–4 h of collection, the micropipettes were weighed and the filter eluted with dichloromethane. Internal standards were added and the solutions analysed by GC as described above. This experiment was repeated 45 times with different numbers of micropipettes to provide different rates of evaporation. We compared the quantity of compounds in the solution with the amount evaporated in the bag. The log-transformed data were fitted to the best function (least square method). The same experiment was performed three times with limonene, another constituent of the natural blend. We also corrected for the difference between entrance and exit airflows (400 and 300 mL min^{-1}, respectively; this avoids air contamination from outside the bag). Only 75% of the compounds released by figs in the bag was assumed to be trapped by the Porapak Q® filters.

CLIMATIC PARAMETERS

Temperature, incident global radiation and precipitation were recorded at the Centre d'Ecologie Fonctionnelle et Evolutive meteorological station, 100 m from the fig tree orchard.

DATA ANALYSES

To investigate the effect of time on the quantities of volatiles released and the percentages of the main compounds, a repeated measures analysis of variance was performed within each sex [model: $y_{ijk} = \mu + A_i + B_j + (AB)_{ij} + \varepsilon_{ijk}$, with A the effect of the tree, B the effect of the time, (AB) their interaction, ε the error term and i, j and k the numbers of trees, dates of measurements and branches per tree, respectively]. Since testing normality for this model is delicate, the normality of the residuals of analysis of variance models was tested graphically for each variable and for each date of measurement (Univariate procedure; SAS Institute Inc., Cary, NC, USA). Percentages were transformed by the arcsinus (square-root) function. Because some data from male and female 1 were missing, these trees were omitted from the analyses.

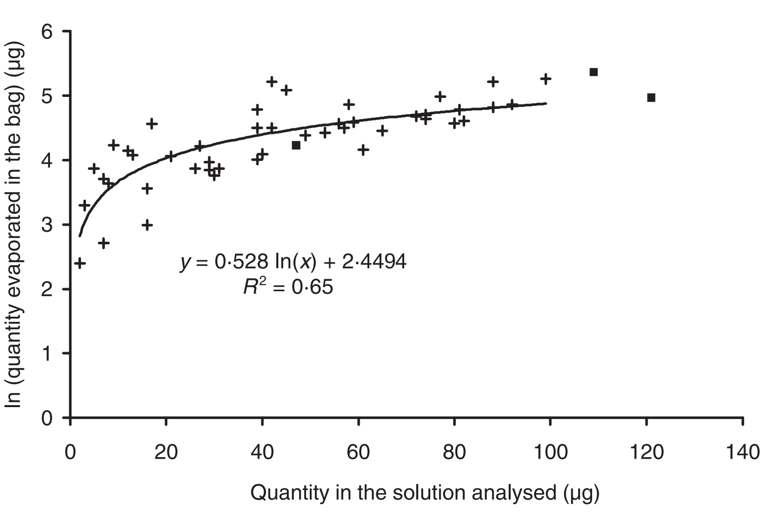

Fig. 1. Relationship between the quantity of linalool (+) and limonene (■) evaporated in a Nalophan® bag and the quantity trapped on Porapak Q®, calculated from the peak area on the chromatogram.

Results

RECOVERY RATE OF VOLATILES

The relationship resulting from the experiment was:

$$\ln Q_i = (0{\cdot}528 \times \ln Q_f) + 2{\cdot}4494,$$

where Q_i = quantity of linalool evaporated in the bag (μg) and Q_f = quantity of linalool in the solution (μg). The amounts of the compounds in fig sample solutions were between 0 and 20 μL, and were in the range of the amounts of linalool in the solutions of this experiment (0–100 μL). The results obtained with limonene were comparable to linalool (Fig. 1). The equation above was therefore applied to all the compounds of the fig blend. For example, for quantities of 2, 10 or 20 μg detected on the chromatogram, quantities of 17, 39 and 56 μg were estimated to have been released in the bag, respectively. This corresponds to recovery percentages of 12, 26 and 36%, respectively. This experiment gives an estimate of the recovery rate of volatile compounds in the fig blend, but the two situations remain quite different (one compound *vs* a blend of compounds, and two emission surfaces probably presenting quite different properties). Hence, recovery rates may differ. Recovery rates are rarely mentioned in the literature. Raguso & Pellmyr (1998) had an average recovery rate of 10%.

CLIMATIC PARAMETERS

During the study, average daily temperature increased steadily from 10 °C at the end of March to 20–25 °C in June (Fig. 2a). Incident radiation also increased in March and April, with maxima of 20 MW m^{-2} d^{-1} at the end of March and 30 MW m^{-2} d^{-1} at the end of May and in June. Two periods of several days with very weak irradiance occurred, the first around 10 May and the second around 12 June. Precipitation was moderate, with maxima of 30–35 mm d^{-1} (Fig. 2a). The influence of climate on the temporal pattern of volatile emission was unclear, but it could explain the low emission rates at the beginning of April (which was cool, cloudy and wet). Furthermore, the end of male emission coincided with a period of several cloudy days, with rain and very low incident radiation.

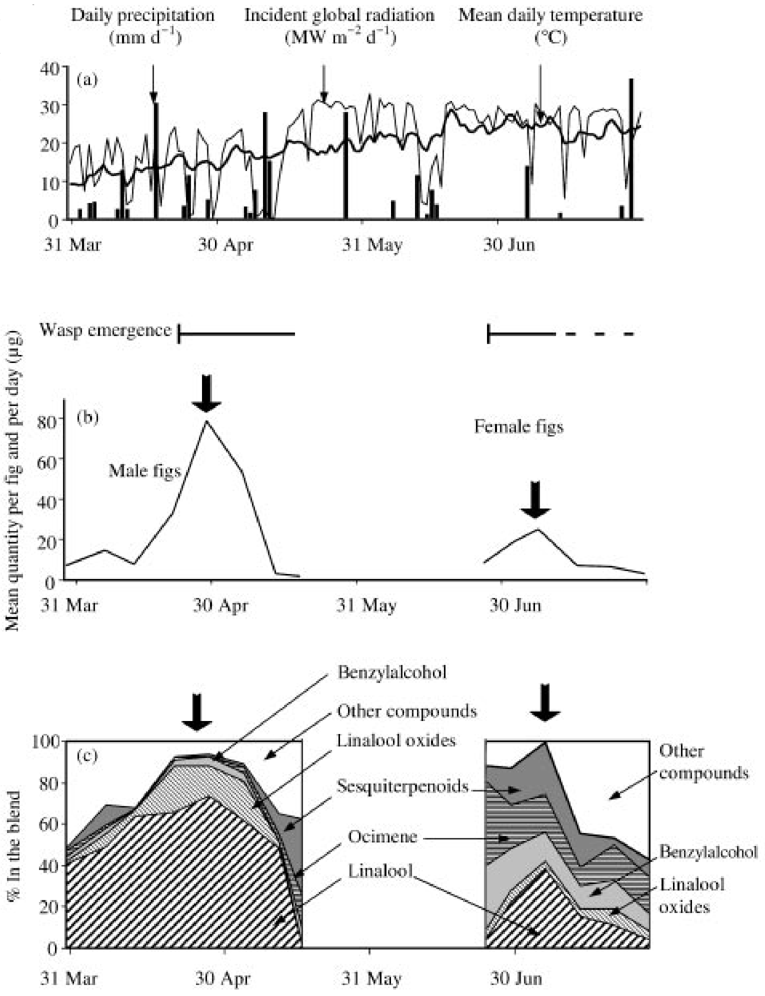

Fig. 2. Comparison between volatile compound emission from male and female figs. (a) Climatic parameters: mean temperature during daylight (°C, bold curve), sum of the irradiance per day (MW m^{-2} d^{-1}, fine curve) and rain episodes (mm d^{-1}, bars). (b) Period of wasp emergence and mean quantity of compounds released per tree for each sex (average value for the four branches per tree and the six trees). (c) Changes in the composition of the blend of volatiles emitted during the receptive period (percentage of the compounds in the blend, means of all trees of one sex).

DIFFERENCES BETWEEN SEXES

The mean total quantities of volatile compounds released over the season (± SD) were 1390 ± 840 µg and 460 ± 280 µg for a male and a female fig, respectively. This difference was highly significant, as was the difference in the quantity of linalool released (Table 1). Daily emissions at the period of maximum release averaged 76 ± 50 µg d^{-1} for male figs and 31 ± 19 µg d^{-1} for females (ANOVA: $F = 4{\cdot}29$, $P = 0{\cdot}07$; Fig. 2b). For both male and female figs, the period of maximum emission corresponded to the beginning of pollinator emergence (Fig. 2b).

The identity of the compounds was similar for both sexes, but the proportion of each compound in the blend differed (Fig. 2c). Linalool was the main compound in male blends, but was much less dominant in female blends (mean was 63% in male blends compared with 34% in female blends). A similar difference was found for the proportion of linalyl oxides (17% in male blends compared with 4% in female). Conversely, female scents contained proportionally more benzyl alcohol, β-ocimene and sesquiterpenoids. An analysis of variance with the effects of sex and tree nested in sex indicated that these differences in compound proportions were highly significant (Table 1).

Table 1. Analysis of variance on the effect of sex on different parameters of the fig odour

	Sex effect (df = 1)		
	F	*P* < *F*	*P*
Total quantity (µg)	20·15	$< 10^{-4}$	< 0·01
Quantity of linalool (µg)	31·46	$< 10^{-4}$	< 0·01
% Linalool	126·28	$< 10^{-4}$	< 0·01
% Linalyl oxides	39·82	$< 10^{-4}$	< 0·01
% Benzyl alcohol	131·54	$< 10^{-4}$	< 0·01
% Ocimene	145·57	$< 10^{-4}$	< 0·01
% Sesquiterpenoids	15·17	$< 10^{-4}$	< 0·01

df, degrees of freedom; *F*, Fisher's statistic.

In both sexes, temporal variation of the mean composition of the blends was observed (Fig. 2c). The proportion of linalool was maximal at the time of maximum emission (Fig. 2c). In male figs, this was also the time at which proportions of benzylalcohol and linalool oxides were maximal. The proportion of 'other compounds' (mixture of monoterpenoids, aromatic and aliphatic and non-identified compounds), ocimene and sesquiterpenoids (for male figs) was very low at the emission peak, and higher at other times. No clear temporal pattern of variation was observed in the other cases (all compounds released by female figs except linalool and the group of 'other compounds'). In both sexes, linalool, linalool oxides and benzylalcohol were released at the moment of maximum emission. A mixture of these three compounds has been shown by Gibernau (1997) to be necessary and sufficient to attract pollinators at a distance, stimulate them once on the fig's surface and make them enter.

INTERTREE AND WITHIN-SEX VARIABILITY

The total quantity of volatile compounds released by a fig varied among trees of the same sex (Fig. 3), ranging from 470 to 2410 µg for male figs (trees M5 and M1, respectively) and from 300 to 1020 µg for female figs (trees F4 and F7, respectively). Temporal patterns of emission by male figs all showed one important peak and sometimes a smaller, earlier peak (effect of time on quantity released was significant, see Table 2). The main peaks of all trees were synchronized with each other and with wasp emergence, but the width of the peak emission varied (Fig. 3). The time × tree effect on the quantity of compounds released was significant, confirming the difference among the temporal patterns of emission (Table 2).

For female figs, the pattern was somewhat different, with one or two peak periods of volatile release, the second less pronounced than the first (Fig. 3). The first

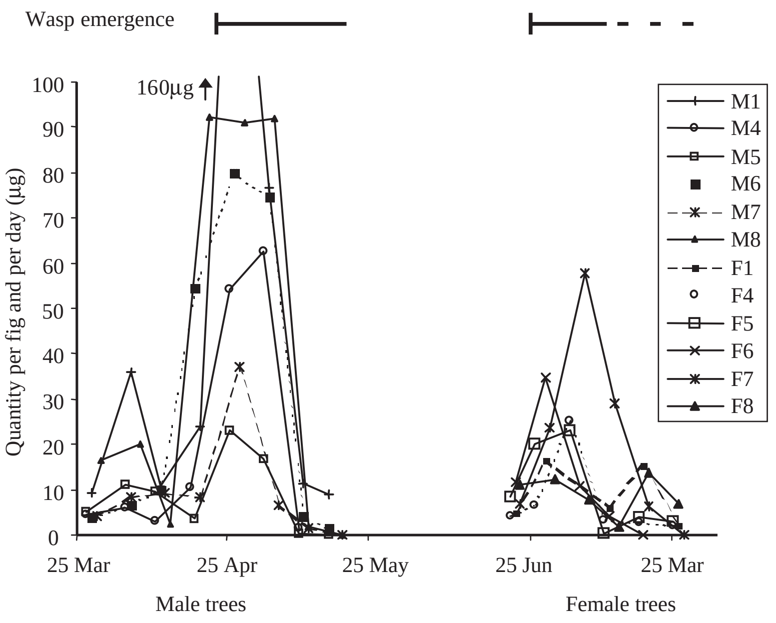

Fig. 3. Temporal patterns of emission and variability of the quantity released by individual tree of the same sex.

period involved all trees and was synchronized with wasp emergence. The effect of time on the quantity of volatile compounds released was significant, as was the time–tree interaction (Table 2).

For male trees, these seasonal quantitative variations were mainly due to changes in the quantity of linalool released (time effect for male trees: $F = 51{\cdot}26$, $P < 0{\cdot}0001$; female trees: not significant), the period of maximum total emission corresponding to the period of maximum linalool emission. The emission of compounds also followed a diurnal pattern. For male figs, 31, 28 and 41% of the total quantity released per day were emitted in the morning, afternoon, and 'night' periods, respectively (SD = 9·6, 13·7 and 11·1, respectively). We should note that the 'night' period comprised several hours of daylight. For female figs, the proportions of the total quantity per day released during the morning, afternoon and 'night' periods were 41, 40 and 19%, respectively.

The composition of the scent showed similarities among trees of the same sex (Fig. 4), especially among male trees. For male fig blends, the main compound was always linalool, which represented 57–71% of the weight of all compounds released (mean of all samples analysed; mean proportion: 63%, SD = 5). Linalyl oxides (mean proportion: 17%, SD = 3), sesquiterpenoids (5%, SD = 3), benzylalcohol (3%, SD = 2) and β-ocimene (2%, SD = 1) were the other main compounds or groups of compounds in male fig blends. They represented, with linalool, 83–93% of the total amount of the compounds released. No differences were detected among male trees in the relative proportions of the different compounds (Table 2a). For female trees, linalool was generally the main compound, except in the cases of F1 and F6 (mean proportion: 34%, SD = 15). The average proportions of the other compounds were as follows: β-ocimene 19% (SD = 4), sesquiterpenoids 17% (SD = 6), benzylalcohol 16% (SD = 4), linalyl oxides 4% (SD = 4). Percentages of benzylalcohol, ocimene and linalool varied significantly among female trees (see Fig. 4 and Table 2b).

Table 2. Repeated-measures analysis of variance: time, tree and time × tree effects on several parameters of male (a) and female (b) fig odour. Greehouse-Geisser and Huynh-Feldt epsilons were averaged. If mean epsilon exceeded 0·7, the data were considered spheric and the results of the univariate test of hypothesis were taken (type III error). If mean epsilon was < 0·7, the Greehouse-Geisser probability was considered (Stevens 1992)

	Tree effect (df = 4)			Time effect (df = 6)			Tree–time interaction (df = 24)		
(a) Male figs	*F*	*P* < *F*	*P*	*F*	*P* < *F*	*P*	*F*	*P* < *F*	*P*
Total quantity	19·88	$< 10^{-4}$	< 0·01	57·66	$< 10^{-4}$	< 0·01	6·00	$< 10^{-4}$	< 0·01
Quantity of linalool	15·58	$< 10^{-4}$	< 0·01	39·84	$< 10^{-4}$	< 0·01	4·42	0·0006	< 0·01
% Linalool	1·65	0·21	ns	4·71	0·0003	< 0·01	1·46	0·10	ns
% Linalyl oxides	1·44	0·27	ns	19·97	$< 10^{-4}$	< 0·01	1·83	0·07	< 0·1
% Benzyl alcohol	0·81	0·54	ns	1·65	0·21	ns	1·43	0·22	ns
% Ocimene	1·84	0·17	ns	2·91	0·06	< 0·1	2·83	0·01	< 0·05
% Sesquiterpenoids	0·89	0·48	ns	1·67	0·21	ns	0·65	0·69	ns

	Tree effect (df = 4)			Time effect (df = 5)			Tree–time interaction (df = 20)		
(b) Female figs	*F*	*P* < *F*	*P*	*F*	*P* < *F*	*P*	*F*	*P* < *F*	*P*
Total quantity	1·69	0·21	ns	19·01	$< 10^{-4}$	< 0·01	6·42	$< 10^{-4}$	< 0·01
Quantity of linalool	0·69	0·61	ns	4·13	0·06	< 0·1	0·95	0·46	ns
% Linalool	15·03	$< 10^{-4}$	< 0·01	17·38	$< 10^{-4}$	< 0·01	6·04	$< 10^{-4}$	< 0·01
% Linalyl oxides	0·64	0·64	ns	0·70	0·45	ns	0·90	0·51	ns
% Benzyl alcohol	2·41	0·09	< 0·1	8·52	$< 10^{-4}$	< 0·01	2·18	0·008	< 0·01
% Ocimene	3·28	0·053	< 0·1	11·21	$< 10^{-4}$	< 0·01	3·13	0·0004	< 0·01
% Sesquiterpenoids	0·42	0·79	ns	3·10	0·013	< 0·05	2·43	0·003	< 0·01

d.f., degrees of freedom; *F*, Fisher's statistic; ns, not significant ($P < 0{\cdot}1$)

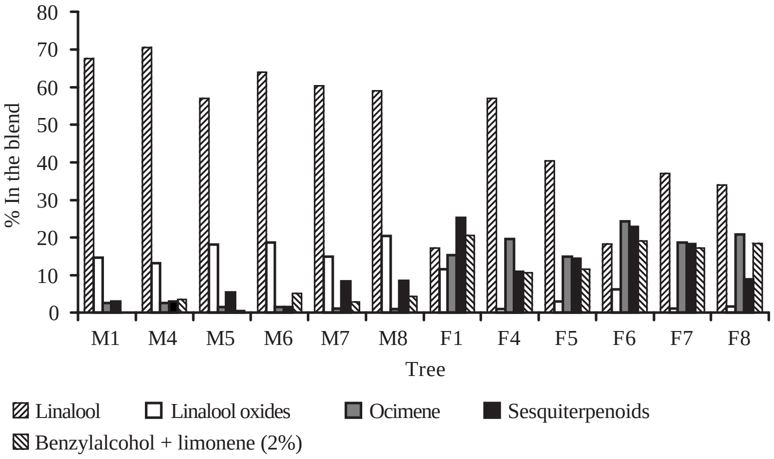

Fig. 4. Proportions of the main components in the fig blend (mean of all samples analysed for each tree).

Discussion

The composition of the blend of emitted volatiles varied over the receptivity period, but linalool, linalyl oxides and benzyl alcohol were generally present when the emission was maximal. This is in accordance with the results obtained by Gibernau (1997), who showed that a mixture of these three compounds was necessary and sufficient to attract pollinators as efficiently as the fig scent itself.

Seasonal and diurnal changes were observed in the quantities of volatile compounds released by figs during the receptivity period. For both sexes, the emission mainly occurred during the day. Wasps of *F. carica* figs emerge from mature figs in the morning (at around 0900–1000 h) and generally die that afternoon (especially in summer), but can survive up to 2 days in the wild (Kjellberg, Doumesche & Bronstein 1988). The volatile emission between 1700 and 0900 h was much less in summer (19% of the total quantity released in 24 h) than in spring (41%). There is, thus, synchronization between fig fragrance emission and pollinator presence at diurnal timescales.

The seasonal pattern of emission also suggests such a synchronization. For male trees, volatile emission was largely restricted to a 1–3 week period of massive release of compounds. Fig growth phenology can explain this massive release: buds are formed during the previous summer and are synchronized with each other after winter. Thus, figs on one branch are all of the same stage. Moreover, pollinator emergence often occurs when figs are already quite big, and large quantities of volatile compounds are released. Fig wasps were observed from 25 April, and were abundant until the beginning of May (Fig. 2a).

The synchronization between fig fragrance emission and pollinator presence is probably necessary because of the strong seasonality of the climate in the south of France. At both timescales, the effects of this synchronization may reflect an optimization of the efficiency of the chemical signal and of the cost–benefit balance associated with this process. Emission of volatile compounds is presumed to be metabolically costly, as the energy and resources invested in their biosynthesis cannot be allocated to other functions such as vegetative growth (see Pichersky *et al.* 1994; Euler & Baldwin 1996; but Grison-Pigé *et al.*, in prep. showed that for *F. carica*, this cost is actually very small).

This seasonal pattern of synchronization was less obvious in summer, when pollinator emergence began on 21 June and lasted several weeks. The long period of pollinator presence and the climatic stability at this time of the year can explain the greater heterogeneity of emission patterns among trees compared with male trees in spring. Variations in the quantity and composition of floral emissions have been observed in other species, but they are mainly daily rhythms. On that timescale, Altenburger & Matile (1988) (for *Hoya carnosa* flowers), Helsper *et al.* (1998) (for *Rosa hybrida* flowers) and Shaver *et al.* (1997) (for *Gaura drummondii* flowers) showed rhythmicity in the emission of volatile compounds. Pecetti & Tava (2000) found seasonal and diurnal patterns in the release of scent from alfalfa flowers (*Medicago sativa*). For *R. hybrida*, alfalfa and *G. drummondii* flowers, the rhythm of release varied among the compounds, thus affecting the composition of the fragrance. But each of these flowers is pollinated by many insect species, unlike *F. carica*. Volatile compound emission by *Ophrys sphegodes* flowers also follows a diurnal pattern, with the composition differing between night and day (Schiestl *et al.* 1997). In that case pollination is specific (as in *F. carica*) and also occurs during daylight. Daily rhythms have sometimes been shown to be endogenous (Altenburger & Matile 1988; Helsper *et al.* 1998), while in other cases they are more or less correlated with irradiance (Pecetti & Tava 2000). The effect of this rhythm is often a correlation of the volatile emission with the time of day (or the period in the season) when pollinators are active (Shaver *et al.* 1997; Pecetti & Tava 2000; Altenburger & Matile 1988). Hence, volatile release and pollinator activity may be synchronized diurnally or seasonally.

Interindividual differences in mean scent composition were mainly observed between male and female figs. This confirms the hypothesis that in a seasonal environment, where pollinators almost never have to choose between the two kinds of figs, selection for a strict chemical mimicry between sexes does not occur (Patel *et al.* 1995). This also confirms the analyses of pentane extracts of male and female receptive figs (Gibernau 1997). Basically, both sexes produced compounds that have been shown to be active, but they also produced other compounds that could have enabled the wasps to discriminate between sexes and avoid female figs if that trait had been selected for. Indeed, *Blastophaga psenes* wasps mainly choose male figs when tests of choice with pentane extracts are performed (Anstett *et al.* 1998). In contrast, Tollsten & Knudsen (1992) studied three dioecious *Salix* species and found that the two species that are mainly pollinated by insects have similar male and female odours, as well as similar floral shapes and colours. In these species, male flowers offer nectar and pollen to insects, whereas female flowers offer only nectar. This precise chemical and visual mimicry between sexes is expected to ensure insect visits to male and female flowers. This seems to apply also to several species of phytelephantoid palms (Araceae), in which chemical mimicry between sexes ensures visits of pollinators to both inflorescences, whereas short-term benefits should incite them to avoid female trees (Ervik *et al.* 1999). These examples suggest that the degree of similarity between male and female fragrances depends on whether the male and female flowers are simultaneously present or not.

In our study, interindividual variability in the composition of emitted volatiles was small within a sex. This chemical homogeneity indicates a strong control of the composition of the fragrance, either by genetic or environmental factors (both differing among sexes, but being the same within sex). In contrast, the floral fragrances of *Epidendrum ciliare* are highly variable among individual plants and populations (Moya & Ackerman 1993). Those authors suggested that since the flowers do not offer any reward to the pollinator, this variability provides insects with no cues by which to learn to avoid the flowers.

We showed that for *F. carica*, the chemical signal that mediates the interaction varied temporally and among individuals. The three-compound mixture, known to be the basis of the attraction, was generally released when emission was at a maximum.

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