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## Geographic variation of fruit scents in a dispersion mutualism, the case of *Ficus lutea*

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### ABSTRACT

Chemical mediation is often involved in interactions between plants and animals, as in pollination and in seed dispersal mutualisms. Extensive investigation has been done in floral scents and on their interspecific and intraspecific variations, but similar research on fruit scent remains poorly explored and only focused on interspecific variations. We investigated in this study the intraspecific variations of volatile bouquet emitted by mature fruits of *Ficus lutea*, in two sites within its wide distribution range, *i.e.* in South Africa and in Madagascar. We demonstrated a clear geographic variation in the volatile bouquet emitted by ripe figs in these two study sites, especially due to the presence of sesquiterpenes in Madagascan bouquets, while scents present at both sites high amounts of fatty acid derivatives. We discuss here different possible explanations for such variations in fruit scents, potentially resulting from insular and/or geographic isolation. This novel result of an intraspecific variation linked to fig seed dispersal serves to increase our knowledge of the role of scents in seed dispersal mutualisms.

### 1. Introduction

Chemical mediation is often involved in interactions between plants and animals, as in many pollination mutualisms (Dudareva and Pichersky, 2006; Raguso, 2008) and in seed dispersal mutualisms (Borges et al., 2008; Hodgkison et al., 2007). The mutualistic interactions at seed dispersal stage have always fascinated naturalists, and are key processes in the functioning of tropical ecosystems where they ensure the reproduction of numerous seed-plant species (Van der Pijl, 1982; Vázquez et al. 2009). However, if extensive investigations have been conducted on Volatile Organic Compounds (VOCs) attracting pollinators (Knudsen et al., 2006), similar research on VOCs emitted by ripe fruits are much more scarce (Borges et al., 2008; Dudareva and Pichersky, 2006). Moreover, the studies on the chemical mediation of seed dispersal mutualisms are generally focused on interspecific variation in these signals, and very little is known about intraspecific variation in fruit scents (Hodgkison et al., 2013).

Intraspecific variation in chemical mediation (variation in the nature of VOCs and/or in their relative proportions) in plant-pollinator interactions has been tentatively explained by hypotheses such as relaxed selective pressure, genetic drift, introgression of scent traits through hybridization, pleiotropic effects of plant defence on scent biosynthesis, or phenotypic plasticity resulting from edaphic or climatic differences

(Raguso, 2008). One of the most frequently proposed explanations for such intraspecific variation are temporal (daily or seasonal) and/or spatial variation due to genetic divergence along the species distribution (Delle-Vedove et al., 2017; Schlumpberger and Raguso, 2008). We tested here the applicability of this explanation to a case of seed dispersal mutualism.

In the *Ficus* (Moraceae) system (roughly 800 species), flowers are enclosed within the fig, which will ripen to form a mature fruit. In fact, botanically, a fig is an infructescence, not a fruit. Throughout this paper, however, we refer to it as a 'fruit', in keeping with common usage in the fig literature and for easier understanding of the text by non-specialists. The fig is thus the unit of attraction for both pollinators and seed dispersers, which makes this system unique (Borges et al., 2008). The highly species-specific pollinating wasps use VOCs emitted by figs to localize the receptive figs where they can lay eggs (Grisson-Pigé et al., 2002; Hossaert-McKey et al., 1994, 2010; Ware et al., 1993). VOC signatures show temporal variation along the fig developmental cycle, so that pollinators and seed dispersers are attracted to the fig only during the appropriate time windows (Borges et al., 2011). Beside interspecific variation in the VOC signatures, several cases of intraspecific variations (e.g. intersexual variation) in chemically mediated interactions have been demonstrated in different fig species. However such variations have to stay relatively limited in order to avoid the disruption in partner recognition, which would directly impact their fitness

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(Hossaert-McKey et al., 2010; Soler et al., 2012). For example, some intraspecific variation of pollinator-attractive bouquets have been shown between biogeographic regions in two fig species (*F. racemosa* and *F. hispida*) with large distribution areas (Soler et al., 2011).

Most of *Ficus* species fruit year-round, and are thus often considered as keystone resources for frugivores in tropical ecosystems; long lists of associated frugivore species have been recorded (Shanahan et al., 2001). Recent studies showed interspecific variation in fruit scents (Borges et al., 2008; Hodgkison et al., 2013, 2007) and a few studies have demonstrated that scents are used as important cues for plant-frugivore interactions and that they are shaped by selection (Borges et al., 2008; Hodgkison et al., 2013; Lomascolo et al., 2010; Lomascolo and Schaefer, 2010). Intraspecific variation of scent emitted by fig fruit remains unstudied so far. However, similarly to floral scent, geographical variations of fig fruit scent could be also expected, especially in species with wide distributions, where geographical barriers may occur.

We investigated the intraspecific variations in the volatile bouquet emitted by mature fruit of *Ficus lutea*. This species is widely distributed, from West Africa to South Africa and Madagascar. It displays a high morphological homogeneity with mature fruits having similar physical characteristics (red fruits, 20–30 mm diameter) along all its range (F. Kjellberg, pers. obs.). To investigate contrasting situations, we study the scent of fig fruits at two separated sites in its range, i.e. in South Africa and in Madagascar Island (more than 2500 kms distant).

## 2. Material and methods

*Ficus lutea* Vahl (Moraceae; Ficus; Urostigma; Galoglychia) is a monoecious terrestrial tree up to 20 m tall found in Africa and Madagascar. This species have a generalist guild of dispersers including bats, birds, monkeys and lemurs (the latter only in Madagascar) (Dalecky et al., 2003; Goodman and Benstead, 2003; Shanahan et al., 2001; C. Soler pers. obs.). The South African odour samples were obtained from six individuals in KwaZulu-Natal province, in the region of Pietermaritzburg (S 29°22'; E 30°14') in March 2008; the samples from Madagascar were obtained from four individuals in January 2009, in the region of Antananarivo (S 18°53'; E 47° 31'). The Chromatoprobe head-space method was used for scent extraction (as described in Soler et al., 2012). Several ( $7 < N < 17$ ) mature figs were used to obtain each sample. The samples were then stored at  $-20^{\circ}\text{C}$  until chemical analysis by GC-MS and compound identification (as described in Soler et al., 2012). We thus obtained a global dataset, where the scent of each individual tree is expressed by the relative proportions of each volatile organic compound in the emitted bouquet. To test if the scents emitted by Madagascar *F. lutea* figs were globally different from those of South African, we ran Non-Parametric Manova (R, Vegan package), as well as Wilcoxon tests with corrections for multiple testing to test each VOC independently.

## 3. Results

Fifty-two different VOCs were found in the scents emitted by mature figs, most of them identified as fatty acid derivatives (58% and 43% of the South African and Madagascan bouquets respectively, see Fig. 1). Although figs from both regions emitted high amounts of fatty acid derivatives, the main VOCs of the bouquets were different, both in their identity and in their proportion (see Table 1). Fruits of *F. lutea* emitted significantly different scents in Madagascar and in South Africa (NP-Manova,  $1.10^6$  permutations,  $F = 2.4579$ ;  $p = 0.0095$ ). The VOCs responsible for this difference (Wilcoxon pair-wised tests) were  $\alpha$ -bergamotene, ( $p = 0.009$ ),  $\beta$ -caryophyllene ( $p = 0.013$ ),  $\alpha$ -copaene ( $p = 0.040$ ), dodecene ( $p = 0.013$ ) and undecane ( $p = 0.031$ ). These differences are quantitative with relative proportions of each of these VOCs high in one site but low in the other. The first three significant VOCs are sesquiterpenes, present in higher proportions in the Madagascan bouquets than in those from South African mature figs. The last two are fatty acid derivatives, which are important in bouquets from South African mature figs while almost absent from the bouquets of Madagascan figs (see Table 1).

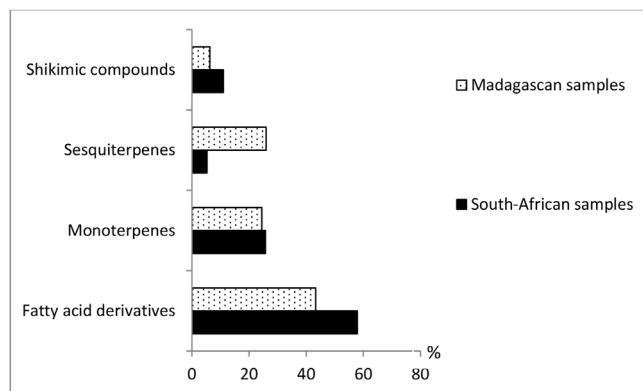


Fig. 1. Intraspecific variation of chemical categories of scents (relative amounts) emitted by ripe *Ficus lutea* figs between the two study sites.

## 4. Discussion

Our results clearly show an intraspecific variation of the scent of ripe fig fruits of *F. lutea* at the time of dispersion. This geographic difference in fruit chemistry in the same fig species is based on both identity and relative proportions of the emitted VOCs. Indeed, while both South African and Madagascan scents present high amounts of fatty acid derivatives, the difference among them lies in the presence of some sesquiterpenes (representing 25.9% of Madagascan bouquets but only 5.3% of the South African ones, see Fig. 1), which are well known for their major roles in the interactions of plants with other plants, pathogens, herbivores and pollinators (Cheng et al., 2007).

Such intraspecific variation of fruit scent may be explained by isolation by distance and/or by spatial barriers such as mountains between the two study sites, as well as by the insular situation of Madagascar (separated from the mainland of Africa for 160 million years, Goodman and Benstead, 2003). Indeed, such a pattern of variation between populations of tropical African trees has been shown in some genetic studies (Dawson and Powell, 1999; Dick et al., 2003). Large islands such as Madagascar are well known to favour the evolution of particular traits in species in relation to local adaptation constraints (Goodman and Benstead, 2003). Since *F. lutea* originated in Africa and then colonized Madagascar (Berg and Wiebes, 1992), dispersal scents of its fruits may have evolved under the pressure of the local environment. Moreover, different species usually vary in multiple traits, and the influence of confounding factors (herbivore/frugivore pressure, dryness, pathogen load or microbial communities for instance) should not be excluded.

Thus, our main goal is to incite further studies addressing the same question in this fig species but in other sites within the distribution of *F. lutea*. It would notably be interesting to sample in the African mainland country near to Madagascar (e.g. Mozambique) to test for the impact of insular isolation, as well as in extreme West Africa (e.g. Senegal) to estimate the impact of larger distance between populations on scent variation. We encourage more generally the investigation of variations in the fruit chemistry and in other traits linked to the dispersal of fig seeds, especially because of the keystone role of fig for frugivores in tropical ecosystems (Shanahan et al., 2001). Fig ecology provides a unique system in which advanced results in chemical mediation in their pollination mutualism which may inspire studies in their seed dispersal.

## Author contributions

CS wrote the main manuscript text and analyzed the data. CS, MH and BS conceived and designed the project. CS and MH collected the data. JMB identified the chemical compounds. All authors reviewed the manuscript.

Table 1

Volatile compounds emitted by ripe figs (mean percentages) for the two study sites (mean  $\pm$  SD). VOCs responsible for the difference are highlighted in grey RI: Retention Index.

	RI	South-African samples		Madagascan samples	
		N = 6		N = 4	
<b>Fatty acid derivatives</b>					
(E)-2-hexenol	854	5.90	$\pm$ 6.78	8.31	$\pm$ 7.36
(Z)-3-hexenol	857	7.74	$\pm$ 10.53	6.71	$\pm$ 7.95
2-pentylfuran	993	0.68	$\pm$ 1.14	2.54	$\pm$ 2.38
decane	1000	0.37	$\pm$ 0.91	1.54	$\pm$ 2.52
(Z)-3-hexenyl acetate	1007	3.21	$\pm$ 6.47	0.41	$\pm$ 0.79
(E)-2-hexenyl acetate	1018	0.02	$\pm$ 0.05	0.00	$\pm$ 0.00
nonanal	1098	0.16	$\pm$ 0.27	3.92	$\pm$ 5.17
undecane	1100	9.66	$\pm$ 12.38	0.00	$\pm$ 0.00
undecanal	1156	0.02	$\pm$ 0.06	0.30	$\pm$ 0.61
dodecene	1194	4.72	$\pm$ 3.53	0.11	$\pm$ 0.23
decanal	1204	0.91	$\pm$ 1.00	12.50	$\pm$ 17.36
tridecene	1292	0.63	$\pm$ 1.02	0.00	$\pm$ 0.00
tridecane	1300	3.15	$\pm$ 5.71	2.55	$\pm$ 3.94
tetradecane	1400	0.38	$\pm$ 0.37	0.57	$\pm$ 0.90
dodecanal	1407	0.04	$\pm$ 0.06	0.00	$\pm$ 0.00
pentadecane	1500	0.86	$\pm$ 0.82	1.33	$\pm$ 1.36
unknown a		0.81	$\pm$ 1.74	0.69	$\pm$ 0.82
unknown b		3.37	$\pm$ 4.08	0.42	$\pm$ 0.57
unknown c		13.74	$\pm$ 16.26	0.61	$\pm$ 1.19
unknown d		1.55	$\pm$ 2.21	0.76	$\pm$ 1.06
<b>sum</b>		<b>57.93</b>		<b>43.31</b>	
<b>Monoterpenes</b>					
alpha-pinene	932	3.03	$\pm$ 3.47	2.40	$\pm$ 4.57
sabinene	965	0.18	$\pm$ 0.38	1.87	$\pm$ 3.62
6-methyl-5-hepten-2-one	983	0.71	$\pm$ 1.75	0.75	$\pm$ 0.82
p-cymene	1026	0.84	$\pm$ 1.44	9.24	$\pm$ 8.65
1,8-cineole	1030	0.83	$\pm$ 2.04	0.10	$\pm$ 0.21
limonene	1031	0.87	$\pm$ 2.13	0.10	$\pm$ 0.21
(E)-beta-ocimene	1047	3.77	$\pm$ 5.22	3.42	$\pm$ 5.59
gamma-terpinene	1062	2.46	$\pm$ 2.29	0.89	$\pm$ 0.71
terpinolene	1088	0.79	$\pm$ 0.74	0.46	$\pm$ 0.36
linalool	1099	0.98	$\pm$ 2.18	3.00	$\pm$ 5.02
perillene	1103	1.17	$\pm$ 1.42	0.16	$\pm$ 0.33
beta-terpineol cis	1140	1.39	$\pm$ 0.81	0.84	$\pm$ 1.00
a-terpineol	1189	8.71	$\pm$ 12.26	1.30	$\pm$ 1.15
<b>sum</b>		<b>25.75</b>		<b>24.47</b>	
<b>Sesquiterpenes</b>					
cyclosativene	1368	2.23	$\pm$ 3.32	1.01	$\pm$ 0.85
alpha-copaene	1377	0.18	$\pm$ 0.28	3.08	$\pm$ 3.25
beta-elemene	1392	0.55	$\pm$ 0.43	1.52	$\pm$ 2.10
alpha-gurjunene	1409	0.19	$\pm$ 0.32	1.57	$\pm$ 1.18
beta-caryophyllene	1421	0.33	$\pm$ 0.54	5.56	$\pm$ 2.10
alpha-bergamotene	1436	0.01	$\pm$ 0.02	2.71	$\pm$ 2.68
alpha-humulene	1462	0.39	$\pm$ 0.64	0.94	$\pm$ 0.73
alpha-curcumene	1481	0.00	$\pm$ 0.00	0.23	$\pm$ 0.45
germacrene-D	1484	0.01	$\pm$ 0.02	4.38	$\pm$ 5.41
beta-selinene	1492	0.23	$\pm$ 0.36	0.45	$\pm$ 0.90
alpha-selinene	1494	0.01	$\pm$ 0.03	1.10	$\pm$ 0.80
delta-cadinene	1521	0.08	$\pm$ 0.17	1.84	$\pm$ 1.29
alpha-cadinene	1538	0.54	$\pm$ 1.21	1.13	$\pm$ 1.36
unknown e		0.55	$\pm$ 0.69	0.43	$\pm$ 0.44
<b>sum</b>		<b>5.30</b>		<b>25.94</b>	
<b>Shikimic compounds</b>					
anisole	917	4.11	$\pm$ 5.31	0.00	$\pm$ 0.00
benzaldehyde	996	2.06	$\pm$ 1.67	2.57	$\pm$ 3.20
acetophenone	1065	2.54	$\pm$ 3.79	0.47	$\pm$ 0.80
2-phenylethanol	1110	0.59	$\pm$ 0.90	2.23	$\pm$ 1.55
veratrol	1147	1.71	$\pm$ 2.08	1.00	$\pm$ 1.41
<b>sum</b>		<b>11.02</b>		<b>6.28</b>	

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