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Chemical diversity of floral scents in 9 species of *Philodendron* (Araceae) from French Guiana

Floral scent diversity in 9 species of *Philodendron* (Araceae) from French Guiana

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ABSTRACT

We provide a characterization of the floral scent chemistry of nine species of *Philodendron* present in French Guiana. The scent samples were obtained by dynamic headspace, *in situ* in French Guiana, or from plants in the living aroid collection at the Botanical Garden of the University of Brasilia. Overall, we identified 43 volatile organic compounds (VOCs) belonging

to the compound classes of monoterpenes, sesquiterpenes, irregular terpenes, benzenoids, aliphatics, jasmone derivatives, and nitrogen-containing compounds. Five of these floral VOCS are new reports for *Philodendron*. Interestingly, the floral blends in the investigated species were comprised of 3 - 22 VOCs; but when considering only major VOCs ($\geq 5\%$), each fragrant blend could be summarized into one up to four constituents. Except for *P. acutatum* and *P. billietiae*, whose floral scents were largely dominated ($\geq 93\%$) by 4-vinylanisole, fragrances of the investigated species were dominated ($\geq 62\%$) each by a different VOC (i.e., dehydrojasmone, dihydro- β -ionone, (*E*)-4,8-dimethylnona-1,3,7-trien-5-yl acetate, methyl benzoate, 1,3,5-trimethoxybenzene, dihydrobovolide, or (*Z*)-jasmone). Consequently, all floral scent compositions significantly differed from one other. We compare our results to published data to provide an insight into the floral scent chemistry within the genus *Philodendron*. We further discuss the diversity of VOCs in cyclocephaline scarab-pollinated aroids.

KEYWORDS: *Cyclocephala*, headspace sampling, pollination, volatile organic compounds.

Introduction

With ca. 490 species, *Philodendron* Schott is the second most speciose genus in the family Araceae, surpassed only by the megadiverse *Anthurium* (ca. 950 sp.) (Hartley and Gibernau 2019; Boyce and Croat 2020). It is currently subdivided into three subgenera, namely *Philodendron* Schott, *Pteromischum* (Schott) Mayo, and *Meconostigma* (Schott) Engler (Mayo 1990). These subgenera are phylogenetically supported (e.g. monophyletic) but details of their interrelationships are yet unresolved (Canal et al. 2018; Sakuragui et al. 2018). Consequently, the subgenus *Meconostigma* has been recognized as the new genus *Thaumatophyllum* Schott by some authors (Sakuragui et al. 2018) but not by others (Canal et al. 2018; Boyce and Croat 2020). Whatever the taxonomic status, all the studies on the reproductive ecology of *Philodendron* have demonstrated that pollination occurs at dusk or early evening and is exclusively attributed to cyclocephaline scarab beetles (Melolonthidae, Dynastinae, Cyclocephalini) (Moore et al. 2013; Gibernau et al. 2021). Aside from the crepuscular/nocturnal anthesis of *Philodendron*, two important physiological floral traits are related to the attraction of the flower-visiting cyclocephaline scarab beetles: floral thermogenesis and profuse scent emissions (Gottsberger and Amaral 1984; Gottsberger and Silberbauer-Gottsberger 1991; Gibernau et al. 1999, 2000; Gibernau and Barabé 2002; Maia et al. 2010; Gottsberger et al. 2013; Pereira et al. 2014; Maldonado et al. 2015; Gonçalves-Souza et al. 2017; Barbosa et al. 2019; Gibernau et al. 2021).

The *Philodendron* inflorescence is composed of a spathe, which is a modified bract enfolding an unbranched spike that bears minute unisexual flowers, called the spadix (Barabé and Gibernau 2015). The anthesis in all species is protogynous with female flowers being receptive first for a few hours the day but the receptive ends before the mature stamens release the pollen on the following day (Gottsberger and Amaral 1984; Gibernau et al. 1999, 2000; Gibernau and Barabé 2002; Maia et al. 2010; Pereira et al. 2014; Barabé and Gibernau 2015;

Barbosa et al. 2019; Gibernau et al. 2021). The *Philodendron* spadix is known to undergo floral thermogenesis through a non-oxidative respiration process in which the mitochondrial electrochemical potential is dissipated by heat through an alternative uncoupling protein (Ito and Seymour 2005). The thermogenic pattern during anthesis appears to be synchronized with consecutive pollination events, specifically the scent-mediated pollinator attraction phase (i.e., stigma receptivity, or the female phase) and pollinator departure time (i.e., stamen dehiscence, or the male phase). Additionally, it has been demonstrated that the heat generated by floral thermogenesis not only functions in aiding the volatilization of attractive floral scent compounds in the absence of heat generated by sunlight but also as an energy-saving boost for the endothermic cyclocephaline scarab beetles (Seymour et al. 2009). Many species of angiosperms pollinated by these insects (including *Philodendron*) remain thermogenically active throughout the night, thus increasing beetle activity and efficient pollen transfer (Gottsberger 2016).

In spite of the notable taxonomical diversity, floral scent composition of only seven species of *Philodendron* have been elucidated so far. Four of those species belong to the subgenus *Meconostigma*, namely *Philodendron adamantinum* Schott (Pereira et al. 2014), *Philodendron bipinnatifidum* Schott ex Endl. (Gottsberger et al. 2013), *P. form selloum* (considered to be a synonym of *P. bipinnatifidum* (<http://www.theplantlist.org/tpl1.1/record/kew-151939>) or the valid species *P. selloum* K. Koch (<https://www.tropicos.org/name/2103341>; Gottsberger et al. 2013), and *P. mello-barretoanum* G.M. Barroso (Maia et al. 2019); and three to the subgenus *Philodendron*, namely: *Philodendron acutatum* Schott (Maia et al. 2010), *Philodendron squamiferum* Poeppig (Maia et al. 2019), and *P. fragrantissimum* (Hooker) G. Don (Gibernau et al. 2021).

Volatile organic compounds (VOCs) identified in samples of the seven aforementioned species are mapped across five of the seven chemical compound classes inferred by Knudsen

et al. (2006) based on biosynthetic origin, namely: i) aliphatics (i.e., (*Z*)-2-pentenyl acetate, (*S*)-2-hydroxy-5-methyl-3-hexanone); ii) miscellaneous cyclic compounds (i.e., jasmone derivatives: (*Z*)-jasmone, (*Z*)-methyl jasmonate, dehydrojasmone, isojasmol), iii) terpenoids (i.e., irregular terpenes: dihydro- β -ionone, (*E*)-8,9-dehydro-4,5-dihydrotheaspiron, (*E*)-4,8-dimethylnona-1,3,7-trien-5-yl acetate, β -cyclocitral; monoterpenes: 1,8-cineole, linalool), iv) benzenoids and phenylpropanoids (4-vinylanisole, 3,4-dimethoxystyrene, methyl benzoate), and v) nitrogen-containing compounds (i.e., 2-isopropyl-3-methoxypyrazine). Moreover, the floral scents of the studied species are dominated (i.e., $\geq 85\%$ of the floral scent composition) either by a single major VOC (*P. adamantinum*, *P. squamiferum*) or combinations of two (*P. bipinnatifidum*, *P. acutatum*) to three VOCs (*P. form selloum*, *P. mello-barretoanum*, *P. fragrantissimum*). Consequently, the total number of the major floral VOCs (above 1% of the floral scent composition) is limited to 14 (listed above) for the seven investigated *Philodendron* species.

It is particularly remarkable that the attraction of different cyclocephaline scarab beetle taxa to *Philodendron* inflorescences, including species in the genera *Cyclocephala* and *Erioscelis*, is highly specific and linked to one or few behaviourally-active floral VOCs (Dötterl et al. 2012; Maia et al. 2012). Among such compounds are (*Z*)-jasmone and 4-vinylanisole (Dötterl et al. 2012), (*S*)-2-hydroxy-5-methyl-3-hexanone (Maia et al. 2013), dihydro- β -ionone (Pereira et al. 2014), and 2-alkyl-3-methoxypyrazines (Maia et al. 2019). These VOCs are selectively attractive to different species of cyclocephaline scarabs when presented in behavioural tests either alone or in simple combinations (2 – 3 VOCs), suggesting an olfactory-mediated mechanism of reproductive isolation (Gibernau 2016; Pereira et al. 2014).

In this paper, we provide a characterization of the floral scent chemistry of nine species of *Philodendron* (seven of which constitute new records) present in French Guiana (Barabé and Gibernau 2015), sampled by dynamic headspace methods. Our specific questions were: i) How

chemically diverse are the floral scents of the investigated *Philodendron* species?, ii) Are the floral scent bouquets from different species dominated by one to few compounds as previously documented?, and iii) Do the floral scents vary significantly among species?

Material and Methods

Study species

The study was conducted in French Guiana in January 2012 and in the living aroid collection at the Botanical Garden of the University of Brasilia (HBUCB; Gonçalves et al. 2013) in October 2012. In French Guiana, floral scent samples were collected *in situ* from wild-growing plants at two locations: the former Base-Vie camp near Petit Saut Dam, between the communes of Sinnamary and Saint-Elie (5°03'N, 53°03'W); and in the vicinities of the commune of Kourou, alongside “Route Nationale 1” (RN1; 5°13'N, 52°40'W). Six species were sampled in French Guiana (one inflorescence per plant): *Philodendron acutatum* Schott, *P. billietiae* Croat, *P. fragrantissimum* (Hooker) G. Don, *P. melinonii* Brongniart ex Regel, *P. pedatum* (Hooker) Kunth, and *P. solimoesense* A.C. Smith (Table 1). In Brazil, floral scent samples from three species - *P. asplundii* Croat & M.L. Soares, *P. callosum* K. Krause, and *P. squamiferum* Poeppig - were obtained from plants growing inside greenhouses from specimens originally collected in the northern Amazonian states of Amapá and Pará south to French Guiana (detailed in Table 1). These three species were included in this study because they are also reported in the flora of French Guiana (Barabé and Gibernau 2015).

Floral scent sampling

Floral scent samples were collected from inflorescences (N = 1 to 4 per species) excised at the basis of the peduncle during the peak of thermogenic activity (and floral scent emission) in the

female phase of anthesis. Each inflorescence was individually enclosed within a Nalophan[®] air sampling bag (NA colourless, calibre 90, ETS Charles-Frères, Saint-Etienne, France), cut open in its upper end to create a headspace. Sampling was conducted by dynamic headspace (Tholl et al. 2020), in which scented air was drawn for 30 - 60 min (depending on perceived concentration of scent emission) through adsorbent traps connected with silicone tubing to a rotary vane vacuum pump (ASF Thomas Inc, Memmingen, Germany) that worked at a constant flow of 250 mL min⁻¹. The adsorbent traps (10 cm long, 0.5 i.d.), made out of silanized glass cartridges, were filled with 50 mg of a 1:1 mixture of Tenax[™] TA (80/100 mesh, Macherey-Nagel 706318, Düren, Germany) and Carbopack[™] X (20/40 mesh, Supelco 1-0435), fixed inside the cartridges by silanized glass wool plugs (Supelco 20411). After collection, the traps were eluted with 300 µL of hexane (HPLC grade, bidistilled) and stored under -24°C refrigeration until analysis. To rule out environmental air contaminants, we collected control samples from empty bags simultaneously to each scent sample, following the same protocols described above.

The trapped volatiles were analysed by combined gas chromatography-mass spectrometry (GC-MS). For each sample, a 1 µL aliquot was injected in split mode (1:30) in a split/splitless injector. The oven temperature of the gas chromatography was set at 40°C for 2 min, then increased at a rate of 4°C min⁻¹ up to 230°C and held for 5 min. Helium was used as the carrier gas and maintained at a constant pressure of 7.0 psi. The MS interface was set at 230°C and the mass spectra recorded at 70 eV (in EI mode) with a scan rate of 0.5 scan.s⁻¹ of *m/z* 40-350.

Compounds were identified by comparing their mass spectra and retention times to those of authentic standards available from the reference libraries Adams, MassFinder 4, NIST14 and Wiley Registry[™] 9th Edition integrated into the Agilent MSD Productivity ChemStation software (Agilent Technologies, Palo Alto, USA). Peak areas in the

chromatograms were integrated to obtain the total ionic signal and their values used to determine the relative proportions of each compound, with the threshold of an abundance higher than 0.01%. The floral scent of two species were previously published by the authors (*P. squamiferum*, Maia et al. 2019; and *P. fragrantissimum*, Gibernau et al. 2021) but the corresponding chromatograms were reanalysed in order to include them in this comparative study. Floral scent composition variations among species were visualized with a redundancy analysis (RDA) using the function *rda* from the package *vegan* (RStudio 1.4.1717. 2021).

Results

Floral scent profiles

Out of the nine investigated species (Table 2), six emit floral scents that are predominantly comprised of a single VOC, encompassing 90 to 99% of the total composition (*P. asplundii*, *P. squamiferum*, *P. acutatum*, *P. billietiae*, *P. pedatum*). Floral scent samples of the remaining species (*P. callosum*, *P. fragrantissimum*, *P. melinonii*, *P. solimoesense*) are also dominated by one compound only, although in relatively smaller proportions (62-85%) and in conjunction with 1-2 additional prevalent VOCs (12-21%).

Chemical diversity of floral scents

We identified 43 VOCs in the analysed floral scent samples, belonging to seven compound classes that are purportedly associated with distinct biosynthetic pathways (Knudsen et al. 2006; Table 2). The most frequent classes are the terpenes (including 9 monoterpenes, 4 sesquiterpenes, and 5 irregular terpenes) and the benzenoids (9 compounds), after the aliphatics

and the miscellaneous cyclic compounds represented by jasmone derivatives (6 compounds each), and finally two nitrogen-containing compounds. Based on a reduced sample size (e.g. 9 investigated species), it appears that the chemical diversity of *Philodendron* floral VOCs is high since only two chemical classes (C5-branched chain compounds and sulphur-containing compounds) are not represented (Knudsen and Gershenzon 2020).

The identified aliphatic VOCs are pent-3-yl acetate, penten-3-yl acetate, 2-hydroxy-5-methyl-3-hexanone, 3-hydroxy-5-methyl-2-hexanone, nonane, and 2-heptyl acetate. The miscellaneous cyclic compounds are the jasmone derivatives (*E*)- and (*Z*)-jasmone, dehydrojasmone, isojasmol, and methyl jasmonate; and the furanone dihydrobovolide. The benzenoids are benzyl alcohol, methyl benzoate, 4-ethylanisole, 1,2-dimethoxybenzene, 4-vinylanisole, 1,4-dimethoxybenzene, methyl salicylate, 3,4-dimethoxystyrene, and 1,3,5-trimethoxybenzene. The terpenes are represented by mono- and sesquiterpenes, as well as irregular terpenes. Identified monoterpenes are α -pinene, sabinene, β -pinene, D-limonene, 1,8-cineole, (*E*)- and (*Z*)- β -ocimene, γ -terpinene; and the sesquiterpenes are (*E*)- and (*Z*)- α -bergamotene, germacrene D, and (*E*)-nerolidol. The irregular terpenes are the homoterpenes (*E*)-4,8-dimethylnona-1,3,7-triene, and (*E*)- and (*Z*)-4,8-dimethylnona-1,3,7-trien-5-yl acetate; and the apocarotenoids dihydro- β -ionone and dihydro- β -iononol. Identified nitrogen containing compounds are the pyrazines 2-isopropyl-3-methoxypyrazine and 2-*sec*-butyl-3-methoxypyrazine (Table 2).

The floral scent compositions of *Philodendron acutatum* and *P. billietiae* are remarkably similar, both dominated (> 93% relative amount) by the same VOC, 4-vinylanisole, which is absent in samples of the other investigated species (Table 2). Similarly, the floral scent of *P. asplundii* is almost entirely constituted of dehydrojasmone (~ 99% relative amount), a VOC that was only present elsewhere in our investigation as a minor constituent in the floral scent of *P. solimoesense* (0.03%). Also, the floral scent of *P. squamiferum* is largely dominated

(> 98%) by (*E*)-4,8-dimethylnona-1,3,7-trien-5-yl acetate, a VOC unique to this species (Maia et al. 2019). Dihydrobovalide, the main constituent in the floral scent of *P. pedatum*, was also species-specific in our sampling effort (Table 2). The floral scent of *P. callosum* is dominated (~ 85%) by dihydro- β -ionone, which was not identified among the other investigated species, and 2-hydroxy-5-methyl-3-hexanone (~ 13%). The latter VOC is also a major constituent in the floral scent of *P. melinonii* (~ 17%), which in turn is dominated by 1,3,5-trimethoxybenzene (~ 62%) and 2-isopropyl-3-methoxypyrazine (~ 17%). 1,3,5-trimethoxybenzene is found in floral scent samples of five other of our investigated species of *Philodendron* but predominantly at lower proportions (< 0.7 to ~ 2.3%). On the other hand, 2-isopropyl-3-methoxypyrazine was only present in one other species, *P. acutatum*, as a minor constituent (~ 0.25%). The floral scent of *P. solimoesense* is dominated (~ 64%) by (*Z*)-jasmone, a VOC that is also prevalent in *P. fragrantissimum* (~ 6.3%). Other major constituents in the floral scent of *P. solimoesense* are pent-1-en-3-yl acetate (~ 21%) and pent-3-yl acetate (~ 6.8%), both of which found as minor constituents in few other investigated species, and D-limonene (~ 5.7%), a prevalent constituent in floral scent samples of *P. pedatum* (~ 1.13%). Finally, the floral scent of *P. fragrantissimum* is dominated by methyl benzoate (~ 72%), also identified as a minor constituent in four other investigated species, and isojasmol (~21%), a jasmone derivative exclusive to this species. Due to a typing error, this compound was misidentified as dehydrojasmone in a recent published characterization of the floral scent chemistry of *P. fragrantissimum* (Gibernau et al. 2021). We have addressed the issue in the present study (see Table 2).

Discussion

Philodendron floral scent diversity

Prior to the present study, the floral scent compositions of only seven species of *Philodendron* had been documented (Gottsberger et al. 2013; Pereira et al. 2014; Maia et al. 2010, 2019; Gibernau et al. 2021); we have reanalyzed the floral scent of two species (*P. fragrantissimum* and *P. squamiferum*) we already published (Maia et al. 2019; Gibernau et al. 2021) and added seven new species records (Table 1). Interestingly, the chemical diversity of the major compounds identified in this study, understood here as the number of chemical compound classes in which they are grouped (see Knudsen et al. 2006 for details), remains unchanged. The five compound classes identified to date in *Philodendron* are the aliphatics, the miscellaneous cyclic compounds (i.e. jasmone derivatives and pyranones), the benzenoids and phenylpropanoids, the nitrogen-containing compounds (i.e. pyrazines), and the terpenoids (i.e. monoterpenes and irregular terpenes). The main difference is that we identified sesquiterpenes among the terpenoids as major VOCs, adding this chemical class to the known VOC diversity in the genus.

Now, considering specifically the VOC identities, our identifications greatly increase the chemical diversity of floral scent compositions in *Philodendron* (Table 2). Among the aliphatics, four new VOCs (i.e. pent-3-yl acetate, penten-3-yl acetate, nonane, and 2-heptyl acetate) were added to the three previously reported ((*Z*)-2-pentenyl acetate, 2-hydroxy-5-methyl-3-hexanone, and 3-hydroxy-5-methyl-2-hexanone) from the florals scents of *P. bipinnatifidum* and *P. acutatum* (Maia et al. 2010; Gottsberger et al. 2013). For the miscellaneous cyclic compounds, we retrieved the five known jasmone derivatives, ((*E*)- and (*Z*)-jasmone, (*Z*)-methyl jasmonate, dehydrojasmone, isojasmol) isolated from the floral scents of *P. adamantinum*, *P. bipinnatifidum*, *P. form selloum* and *P. fragrantissimum* (Gottsberger et al. 2013; Pereira et al. 2014, Gibernau et al. 2021). However, we also expand the list by adding a new compound and functional group, the furanone dihydrobovolide (i.e. 3,4-dimethyl-5-

pentyl-2(5H)-furanone). Only three benzenoid derivatives were reported as dominant compounds (methyl benzoate, 4-vinylanisole, 3,4-dimethoxystyrene) in *P. fragrantissimum* and *P. form selloum* (Gottsberger et al. 2013; Gibernau et al. 2021); in our samples, six benzenoid compounds, already reported as minor or traces in *Philodendron* floral scents, were identified as major constituents (benzyl alcohol, methyl salicylate, 4-ethylanisole, 1,2-dimethoxybenzene, 1,4-dimethoxybenzene, and 1,3,5-trimethoxybenzene). Concerning the nitrogen-containing compounds, we identified two 2-alkyl-3-methoxypyrazines, of which one had been previously reported in floral scent samples of *P. acutatum* from populations in northeastern Brazil (2-isopropyl-3-methoxypyrazine). The other, 2-*sec*-butyl-3-methoxypyrazine, is a new record for the genus. Finally, the highly diverse terpenoids are represented by mono- and sesquiterpenes, as well as irregular terpenes. The identified monoterpenes (α -pinene, sabinene, β -pinene, D-limonene, (*Z*)- β -ocimene, (*E*)- β -ocimene, γ -terpinene, 1,8-cineole, linalool) were already reported at different relative concentrations from the floral scents of *P. adamantinum*, *P. form selloum* and *P. bipinnatifidum* (Gottsberger et al. 2013; Pereira et al. 2014). Additionally, four of the five sesquiterpenes identified in the present study constitute new records for the genus ((*Z*)- α -bergamotene, (*E*)- α -bergamotene, germacrene D, and (*E*)-nerolidol). Last among terpenoids are the irregular terpenes represented by homoterpenes and apocarotenoids. Three homoterpenes were identified in the present study ((*E*)-4,8-dimethylnona-1,3,7-triene, (*Z*)-4,8-dimethylnona-1,3,7-trien-5-yl acetate, and (*E*)-4,8-dimethylnona-1,3,7-trien-5-yl acetate), the latter two already reported from the floral scent of *P. squamiferum* (Maia et al. 2019). Among the apocarotenoids, the four VOCs had been previously identified in the floral scents of *P. adamantinum*, *P. bipinnatifidum*, *P. form selloum* and *P. acutatum*, namely β -cyclocitral, (*E*)-8,9-dehydro-4,5-dihydrotheaspirone, dihydro- β -ionone, and dihydro- β -ionol (Maia et al. 2010; Gottsberger et al. 2013; Pereira et al. 2014). The latter two were also identified in the present study only in samples of *P. callosum*.

Floral scents of cyclocephaline scarab-pollinated aroids

The floral scent chemistries of non-*Philodendron* aroid taxa pollinated by cyclocephaline scarab beetles have also been studied. For instance, the floral scent of *Taccarum ulei* is dominated by two VOCs – 2-hydroxy-5-methyl-3-hexanone (76%) and dihydro- β -ionone (20%) (Maia et al. 2013) – which have been documented almost in reverse proportion in the floral scent of *Philodendron callosum* (13% and 85% respectively). Interestingly, the composition of *P. callosum* is strikingly similar to that recovered in samples of *P. acutatum* collected *in situ* in the Atlantic forest of northeastern Brazil (23% 2-hydroxy-5-methyl-3-hexanone and 74% dihydro- β -ionone (Maia et al. 2010). In turn, such composition is quite distinct from what we documented in wild-growing individuals of *P. acutatum* in French Guiana, among which the floral scent was largely dominated by 4-vinylanisole (94%). The first possibility to explain such discrepancy would be populational geographic variation, a trend previously documented among populations of *Xanthosoma striatipes* (Kunth & C.D. Bouché) Madison along a latitudinal gradient of about 2,000 km across the Brazilian states of Maranhão and São Paulo (Gottsberger et al. 2020). A second possibility is that the two populations of *P. acutatum* in question, although morphologically similar, are in fact taxonomically distinct units. A documented trend of rapid speciation among *Philodendron* subg. *Philodendron* offers support to this scenario (Canal et al. 2018), but further investigation is required to better interpret the degree of genetic similarity between the two populations of *P. acutatum* and even if their floral scent divergence could be used as a chemotaxonomic trait.

Recent assessments of the floral scent compositions of 14 species within the aroid genus *Xanthosoma*, also assumed as exclusively pollinated by cyclocephaline scarab beetles, have led to the characterization of 64 VOCs distributed across the same major compound classes highlighted for *Philodendron* in the present study (aliphatics, terpenoids, benzenoids and

phenylpropanoids, miscellaneous cyclic compounds, and nitrogen-containing compounds (Milet-Pinheiro et al. 2017; Maia et al. 2019). (*Z*)-Jasmone is the most common floral VOC in *Xanthosoma* (reported in 13 species), followed by methyl salicylate and methyl benzoate (found in samples from nine species each) and 1,2-dimethoxybenzene (isolated in samples from seven species). Other compounds, such as 4-vinylanisole, 2-isopropyl-3-methoxypyrazine, and (*E*)-4,8-dimethyl-1,3,7-nonatriene, although absent in many species, accounted for a significant proportion of total floral composition (Milet-Pinheiro et al. 2017). Note that *X. hylaeae* appears to be chemically original, as its floral scent contains two rare jasmone derivatives (*Z*)-3-methylene-2-(pent-2-enyl)cyclopentanol (isojasmol) and (*Z*)-3-methylene-2-(pent-2-enyl)cyclopentanyl acetate (isojasmyl acetate), associated to the more widespread benzenoids methyl salicylate and methyl benzoate (Maia et al. 2019). Almost all floral VOCs documented in *Xanthosoma* were also identified in *Philodendron* (Table 2) but their overall relative proportions as constituents in the scent blends differ between the two genera. Whereas among *Xanthosoma* the most frequent compounds are benzenoids, such as methyl benzoate, methyl salicylate, and 1,3,5-trimethoxybenzene, there appears to be a prominence and higher diversity of jasmone derivatives in floral scents of *Philodendron* (Gottsberger et al. 2013; Pereira et al. 2014, Gibernau et al. 2021, this study). There nonetheless appears to be a shared trend among species of these two genera, which is their unique floral scent blends resulting from original species-specific VOC combinations. One notable exception is *P. acutatum* and *P. billietiae*, whose individuals in syntopic populations in French Guiana emit floral scents largely dominated by 4-vinylanisole ($\geq 93\%$). Still, some discrimination exists between the two species (Figure 2), as the floral scent samples of *P. acutatum* contain two additional methoxylated benzenoids (3,4-dimethoxystyrene and 1,3,5-trimethoxybenzene) that are either absent or poorly represented in *P. billietiae*. Such original, species-specific combinations can be easily visualized on the graphical plot of the multivariate analysis (Figure 2). Similarly, the floral scent

blends of *Xanthosoma* species appeared as scattered units in an NMDS plot representing the scent-space (which also included other Neotropical aroid species pollinated by cyclocephaline scarab beetles), reinforcing their species-specific character (Milet-Pinheiro et al. 2017).

The floral scent chemistries of two other cyclocephaline scarab beetle-pollinated aroid genera have been studied: *Montrichardia* and *Caladium* (Gibernau et al. 2003; Maia & Schlindwein 2006; Maia et al 2012). Floral VOCs identified in samples of *Montrichardia arborescens* (Gibernau et al. 2003) are common among other species associated with cyclocephaline scarab beetles, namely (*Z*)-jasmane (37%), 1,3,5-trimethoxybenzene (26%), methyl salicylate (7%), and methyl benzoate (8%). But, once again, their combination in the blend appears to be unique when compared to other aroid taxa (Maia et al. 2010, 2013; Gottsberger et al. 2013; Pereira et al. 2014; Milet-Pinheiro et al. 2017; Maia et al. 2019; Gibernau et al. 2021). The floral scent of *Caladium bicolor* is similarly rich in methoxylated benzenoids (1,3,5-trimethoxybenzene and methyl salicylate) and (*Z*)-jasmane. However, it also contains relatively high concentrations of the less frequent monoterpene linalool (7-9%) and 4-methyl-5-vinylthiazole (20-36%), an original sulfur-containing compound also identified as the main constituent (i.e. $\geq 97\%$) in floral scents of night-blooming *Annona* spp. and provenly attractive to different species of *Cyclocephala* (Maia et al. 2012). Finally, the furanone dihydrobovolide, the almost exclusive ($> 96\%$) VOC in scent samples of *P. pedatum* was previously unreported as a floral scent constituent (Knudsen et al. 2006) and is an otherwise rare natural compound [best known only as a flavour component in a variety of teas \(Kawakami 2002\)](#). Our identification of the molecule was tentative and its absolute configuration is yet unassigned.

Volatile communication

Adult cyclocephaline scarab beetles are crepuscular/nocturnal with a keen sense of olfaction (Gottsberger & Silberbauer-Gottsberger 1991; Ratcliffe 2003; Maia et al. 2012, 2019; Dupuis and Perrin 2020). For male and female individuals alike, floral VOCs indicate specific micro-niches where they reliably find shelter, plentiful food sources and, most importantly, optimal mating opportunities (Gibernau et al. 1999; Maia et al. 2012; Maldonado et al. 2015; Gottsberger 2016; Gibernau 2016). As previously detailed the floral VOCs derived from several different biosynthetic pathways. Interestingly, whatever the number of emitted floral VOCs, the blend is generally dominated (i.e., $\geq 85\%$ of the floral scent composition) by a reduced number of compounds. In the genus *Philodendron*, the number of floral VOCs varies from 3 to 40 among currently studied species (Maia et al. 2010, 2013, 2019; Gottsberger et al. 2013; Pereira et al. 2014; Gibernau et al. 2021, this study). Out of the 13 documented species, six species emit floral scents that are predominantly comprised of a single VOC (*P. acutatum*, *P. adamantinum*, *P. asplundii*, *P. billietiae*, *P. pedatum*, *P. squamiferum*); three species (*P. callosum*, *P. bipinnatifidum*, *P. solimoesense*) exhibit combinations of two VOCs; and four species (*P. fragrantissimum*, *P. form selloum*, *P. melinonii*, *P. mello-barretoanum*) combinations of three VOCs. Concerning the floral scent chemistry of *P. solimoesense*, it is dominated at 85% by two compounds ((*Z*)-jasmone (64%) and penten-3-yl acetate (21%)) but two others are prevalent (pent-3-yl acetate (7%), and D-limonene (6%)). Consequently, depending on the point of view, the floral scent of *P. solimoesense* could be considered to a blend of four main compounds.

Similarly, the number of floral VOCs present in samples belonging to different species of *Xanthosoma* varied considerably, ranging from eight in *X. pottii* up to 40 in *X. rubrispathum* (Milet-Pinheiro et al. 2017). Within the genus, few dominant compounds dominate the floral scent bouquets. In fact, three main constituents alone accounted for more than 80% of total relative scent emissions in all studied species (Milet-Pinheiro et al. 2017). Altogether, these results strongly suggest that *Xanthosoma* species release floral scents of limited complexity in

terms of the number of VOCs, a trait also reported here in *Philodendron* and among other cyclocephaline scarab-pollinated angiosperms (Dötterl et al., 2012; Maia et al., 2010; Pereira et al., 2014; Carreño-Barrera et al. 2019; Maia et al. 2020).

Remarkably, the attraction of different cyclocephaline scarab beetle taxa to the flowers/inflorescences of their plant hosts is linked to one or few behaviourally-active floral VOCs dominating the floral scent blends as demonstrated with scent-baited traps (Dötterl et al. 2012; Maia et al. 2012; Carreño-Barrera et al. 2019). Among such compounds are (*Z*)-jasmone and 4-vinylanisole (Dötterl et al. 2012), 4-methyl-5-vinylthiazole (Maia et al. 2012), (*S*)-2-hydroxy-5-methylhexan-3-one (Maia et al. 2013), dihydro- β -ionone (Pereira et al. 2014), methyl 2-methylbutyrate (Gottsberger et al. 2012), 2-alkyl-3-methoxypyrazines (Maia et al. 2019), 4-methylanisole (Maia et al. 2020), (*3S,6E*)-nerolidol (Favaris et al. 2020) or dehydrojasmone and isojasmol (Stamm et al. 2021). A recent study (Maia et al. 2020) showed that the floral scent of the palm *Acrocomia aculeata* is a simple blend dominated by 4-methylanisole (97 – 99.9%), plus two minor compounds: 2-isopropyl-3-methoxypyrazine (0.3 – 1.6%) and 2-*sec*-butyl-3-methoxypyrazine (0.04 – 1.4%). Electroantennographic assays with male and female *Cyclocephala forsteri*, specialized florivores associated with *A. aculeata*, evidenced responses to these three VOCs (Maia et al. 2019b). Field tests also showed that 4-methylanisole alone functioned as an efficient attractant, as > 83% of scent-baited traps caught an average of three individuals of *C. forsteri*. A mixture of the three VOCs was also highly-attractive to the beetles, leading to 100% trapping success and an average of 45 individuals of *C. forsteri* per trap. These results should nevertheless be compared with caution because a piezoelectric diffuser was used in the second experiment (Maia et al. 2020).

The efficient attraction of cyclocephaline scarab beetles is probably based on a strategy of ‘specific communication channel’, since all available chemoecological studies evidence

peculiar behaviourally-active compounds dominating the floral scents of angiosperms associated with them and particularly the genus *Philodendron*. It is also hypothesized that these attractive floral allelochemicals explore innate pre-existing olfactory preferences of different species of cyclocephaline scarab beetles (Schiestl & Dötterl 2012).

Further studies are still required to better understand the pollination chemoecology of *Philodendron* and other angiosperm taxa associated with cyclocephaline scarab beetles (i.e., Nymphaeaceae, Magnoliaceae, Annonaceae, and Araceae). In particular, it would be of great interest, on the one hand, to link pollinator attraction specificity to floral semiochemicals; and, on the other, to study the geographical and/or temporal (i.e., seasonal) variations in floral scent chemistry and sensory preferences of selected species of cyclocephaline scarab beetles.

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Disclosure statement

No potential conflict of interest was reported by the authors

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Table 1. Sampled *Philodendron* species (by alphabetical order), number of inflorescences sampled per species, locality of the sampled specimens: in the wild in French Guiana or in the living aroid collection of the Botanical Garden of the University of Brasilia (HBUCB), and sampling date (month year).

<i>Philodendron</i> species	nb of samples	locality	sampling date
<i>P. acutatum</i>	4	French Guiana	Jan. 2012
<i>P. asplundii</i>	1	HBUCB (Specimen(s) collected in the state of Amapá, Brazil)	Oct. 2012
<i>P. billietiae</i>	3	French Guiana	Jan. 2012
<i>P. callosum</i>	2	HBUCB (Specimen(s) collected in the state of Amapá, Brazil)	Oct. 2012
<i>P. fragrantissimum</i>	4	French Guiana	Jan. 2012
<i>P. melinonii</i>	4	French Guiana	Jan. 2012
<i>P. pedatum</i>	3	French Guiana	Jan. 2012
<i>P. solimoesense</i>	4	French Guiana	Jan. 2012
<i>P. squamiferum</i>	4	HBUCB (Specimen(s) collected in the state of Pará, Brazil)	Oct. 2012

Table 2. Floral scent composition for the 9 studied species of *Philodendron*: compound name, compound class, mean \pm standard deviation (%). In bold volatile compounds representing more than 1% of the total blend composition.

KI	Compound identification	compound class	<i>P.</i>	<i>P.</i>	<i>P.</i>	<i>P.</i>	<i>P.</i>	<i>P.</i>	<i>P.</i>	<i>P.</i>	
			<i>asplundii</i>	<i>callosum</i>	<i>squamiferum</i>	<i>acutatum</i>	<i>billietiae</i>	<i>fragrantissimum</i>	<i>melinonii</i>	<i>pedatum</i>	<i>P. solimoense</i>
			N=1	N=2	N=3	N=4	N=3	N=4	N=4	N=3	N=4
833	Pent-3-yl acetate	al	-	-	-	-	-	-	-	-	6,77 \pm 3,74
833	m/z: 43, 111, 69, 41, 67	-	-	-	-	-	-	-	-	0,16 \pm 0,28	-
839	m/z: 43, 58, 59, 101, 44	-	-	-	-	-	-	-	-	0,38 \pm 0,66	-
849	Pent-1-en-3-yl acetate	al	-	-	-	tr	-	-	tr	0,28 \pm 0,39	21,3 \pm 6,12
900	Nonane	al	-	-	tr	-	-	-	-	0,05 \pm 0,10	-
932	α -Pinene	mo	-	-	-	-	-	-	1,05 \pm 2,04	0,16 \pm 0,27	0,96 \pm 0,88
942	2-Hydroxy-5-methyl-3-hexanone	al	-	12,8 \pm 13,7	-	0,07 \pm 0,15	-	-	16,7 \pm 14,4	0,08 \pm 0,14	-
947	3-Hydroxy-5-methyl-2-hexanone	al	-	0,13 \pm 0,15	-	tr	-	-	0,58 \pm 0,98	-	-
972	Sabinene	mo	-	-	-	-	-	-	0,02 \pm 0,04	-	tr
975	β -Pinene	mo	-	-	-	-	-	-	0,34 \pm 0,65	-	0,02 \pm 0,01
991	Myrcene	mo	-	-	-	-	-	-	0,03 \pm 0,06	-	0,12 \pm 0,13
1028	D-limonene	mo	-	-	-	tr	tr	-	0,11 \pm 0,18	1,13 \pm 0,19	5,69 \pm 9,80
1030	1,8-cineole	mo	-	-	-	-	-	-	-	-	0,05 \pm 0,03
1033	Benzyl alcohol	be	-	-	-	-	-	0,06 \pm 0,02	-	-	-
1038	(<i>Z</i>)- β -Ocimene	mo	-	-	-	-	-	-	-	-	0,07 \pm 0,07
1044	2-Heptyl acetate	al	-	-	-	-	tr	-	-	-	0,04 \pm 0,07
1048	(<i>E</i>)- β -Ocimene	mo	-	-	-	-	-	-	-	0,01 \pm 0,02	0,23 \pm 0,22
1058	γ -Terpinene	mo	-	-	-	-	-	-	-	-	0,05 \pm 0,03
1094	Methyl benzoate	be	-	0,09 \pm 0,12	-	-	0,02 \pm 0,02	71,7 \pm 8,70	-	0,07 \pm 0,12	0,01 \pm 0,01
1094	2-Isopropyl-3-methoxypyrazine	Ni	-	-	-	0,25 \pm 0,42	-	-	17,4 \pm 19,0	-	-
1113	4-Ethylanisole	be	-	-	-	0,05 \pm 0,04	0,08 \pm 0,03	-	-	-	-

1117	(E)-4,8-Dimethyl-1,3,7-nonatriene	it	-	0,12 ± 0,17	0,01 ± 0,008	0,04 ± 0,05	-	-	-	-	0,15 ± 0,12
1147	1,2-Dimethoxybenzene	be	-	0,17 ± 0,24	-	-	-	-	tr	0,02 ± 0,04	-
1164	4-Vinylanisole	be	-	-	-	93,8 ± 3,27	98,7 ± 0,64	-	-	-	tr
1165	1,4-Dimethoxybenzene	be	-	-	-	0,01 ± 0,003	0,08 ± 0,03	-	-	-	-
1173	2-sec-Butyl-3-Methoxypyrazine	Ni	-	-	-	-	-	-	0,07 ± 0,15	-	-
1194	Methyl salicylate	be	0,42	0,04 ± 0,05	0,05 ± 0,08	-	-	0,12 ± 0,05	1,0-,20	-	0,03 ± 0,02
1295	(Z)-4,8-Dimethylnona-1,3,7-trien-5-yl acetate	it	-	-	0,97 ± 0,54	-	-	-	-	-	-
1302	isojasmol	mcc	-	-	-	-	-	21,2 ± 5,17*	-	-	-
1306	dehydrojasmone	mcc	99,3	-	-	-	-	-	-	-	0,03 ± 0,05
1368	3,4-Dimethoxystyrene	be	-	-	-	2,76 ± 1,75	0,04 ± 0,05	-	-	-	-
1381	(E)-4,8-dimethylnona-1,3,7-trien-5-yl acetate	it	-	-	97,9 ± 0,65	-	tr	-	-	-	-
1396	(E)-Jasmone	mcc	-	-	-	-	-	-	-	-	0,01 ± 0,01
1400	(Z)-Jasmone	mcc	0,10	-	-	-	tr	6,30 ± 4,42	-	-	64,0 ± 1,71
1410	1,3,5-Trimethoxybenzene	be	-	-	-	2,28 ± 3,60	-	0,01 ± 0,02	61,9 ± 19,4	0,61 ± 0,12	0,01 ± 0,03
1417	cis- α -Bergamotene	se	-	-	-	0,01 ± 0,00	0,54 ± 0,24	-	0,24 ± 0,24	0,06 ± 0,11	tr
1438	trans- α -Bergamotene	se	-	-	-	0,03 ± 0,05	0,11 ± 0,05	-	0,04 ± 0,07	0,01 ± 0,01	0,01 ± 0,01
1442	Dihydro- β -ionone	it	-	85,5 ± 14,0	-	-	-	-	-	-	-
1447	Dihydro- β -ionol	it	-	0,31 ± 0,05	-	-	-	-	-	-	-
1484	Germacrene D	se	-	-	-	-	-	-	0,02 ± 0,05	-	-
1526	Dihydrobovolide	mcc	-	-	-	-	-	-	-	96,4 ± 1,22	-
1565	(E)-Nerolidol	se	-	-	-	0,37 ± 0,34	-	-	-	-	-
1680	methyl jasmonate isomer I	mcc	-	-	-	-	-	0,28 ± 0,12	-	-	-

Compound classes (according to Knudsen et al. 2006): al: aliphatic, mo: monoterpene, se: sesquiterpene, be: benzenoid, Ni: Nitrogen containing compound, it: irregular terpene, mcc: miscellaneous cyclic compound.

tr: trace compound (<0.01%). *isojasmol was mistakenly named dehydrojasmone in Gibernau et al. (2021).

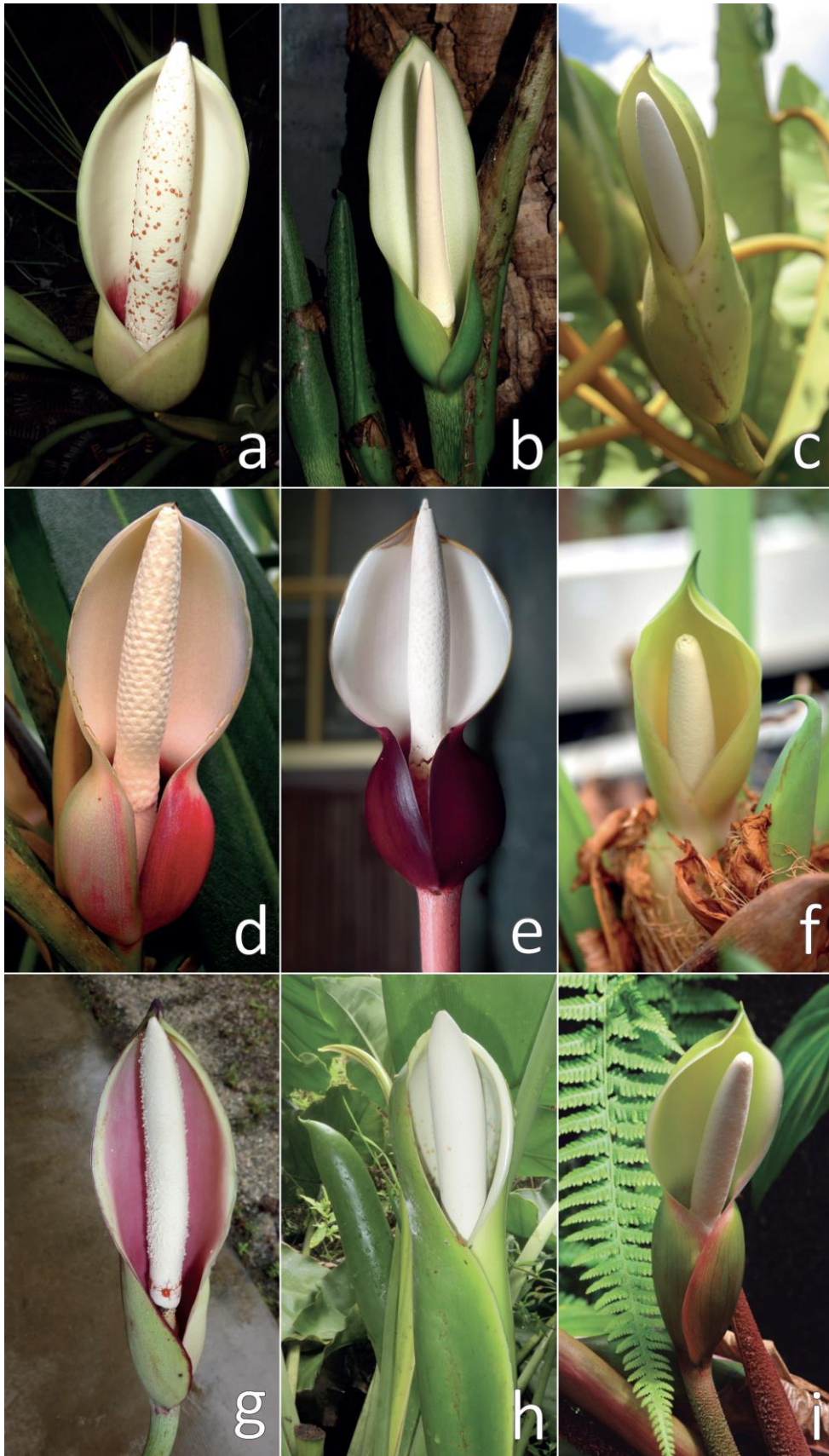


Figure 1. Inflorescences of the 9 studied *Philodendron* species: **a.** *P. acutatum*, **b.** *P. asplundii*, **c.** *P. billietiae*, **d.** *P. callosum*, **e.** *P. fragrantissimum*, **f.** *P. melinonii*, **g.** *P. pedatum*, **h.** *P. solimoense*, and **i.** *P. squamiferum*.

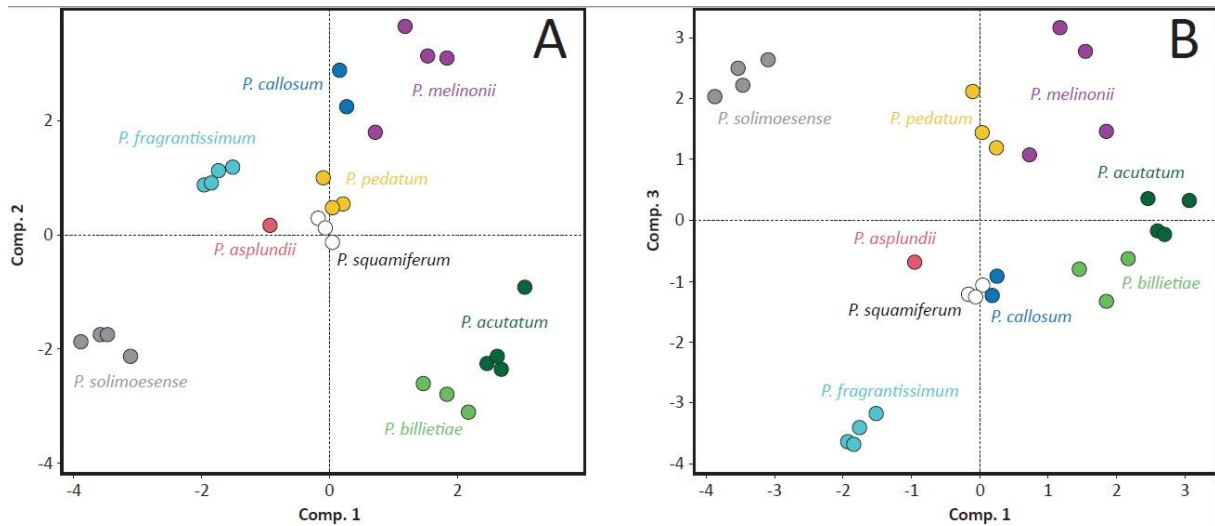


Figure 2. Graphical score plots of the Redundancy Analysis (RDA) representing the individual floral scents. **A.** for the first two-dimensional space (constrained axis 1: 30% of the variance - constrained axis 2: 18.7%). **B.** for the second two-dimensional space (constrained axis 1: 30% - constrained axis 3: 17.7%). The different sampled species are coloured differently.

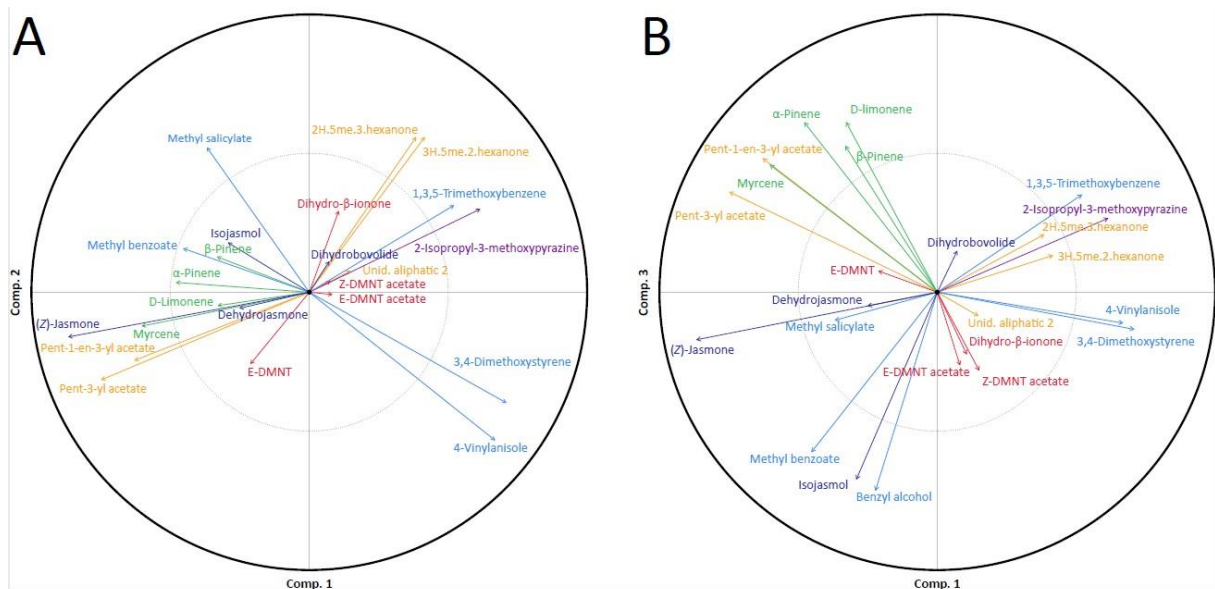


Figure 3. RDA correlation circles representing the main compounds (> 0.5%). **A.** for the first two-dimensional space (constrained axis 1: 30% of the variance - constrained axis 2: 18.7%). **B.** for the second two-dimensional space (constrained axis 1: 30% - constrained axis 3: 17.7%). Colours correspond to compound classes: aliphatics (yellow), benzenoids (blue), jasmone derivatives (dark blue), Nitrogen-containing compounds (purple), monoterpenes (green), irregular terpenes (red). DMNT: Dimethyl nonatriene, me: methyl.