



Short communication

Floral volatile profile in Pleurothallidinae, an orchid subtribe pollinated by flies: ecological and phylogenetic considerations



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ABSTRACT

The Pleurothallidinae are recognized as the largest orchid group pollinated by Diptera. This subtribe has been focus of ongoing phylogenetic studies, in which the floral biology and mating systems of their representatives have been recently assessed and some synapomorphies pointed out, all of them regarding features or processes occurring in flowers. Data about the flower volatiles are still scarce, although it may offer valuable information about the floral biology of this subtribe. Here, we collected and analyzed the volatiles emitted from flowers at anthesis. We selected seven Brazilian species representing both late and early-divergent clades of Pleurothallidinae aiming to describe the chemical profile of flower volatiles and relate the identified compounds to the reproductive biology of the selected species. The outstanding feature regarding the floral scent profile is the ubiquitous occurrence in remarkable concentrations of alkanes, a situation not found in Laellinae, a closed subtribe of Pleurothallidinae. We also present a discussion concerning the ecological aspects of the flower volatiles and their pollinators.

1. Introduction

The subtribe Pleurothallidinae is the largest orchid group pollinated by Diptera (Pridgeon et al., 2001; 2010; Borba et al., 2011). Due to the poly and paraphyletic nature of some genera (Pridgeon et al., 2001, 2010), this subtribe has been a focus of phylogenetic studies and taxonomic revision. Recently, Borba et al. (2011) proposed the split of Pleurothallidinae as recognized by Pridgeon et al. (2001, 2005) into two subtribes: one comprising the former representatives (Luer, 1986; Dressler, 1993) with self-incompatibility and myophily as biological synapomorphies, and another one comprising the small clade consisting of ornithophilous, self-compatible genera (*Dilomilis*, *Neocogniauxia*, and *Tomzania*). This new proposal based on floral features highlights the need for studies to evaluate morphological, chemical and biological characters that may aid in a cohesive circumscription of Pleurothallidinae.

Orchid flowers display visual, chemical and morphological advertisements to guide their pollinators, and may offer rewards as nectar, pollen, fragrance or oil, or rewardless (Dressler, 1993; Pemberton, 2010). In fact, a high occurrence of non-rewarding flowers is noticed in orchids compared to other plant families (Jersáková et al., 2006;

Humeau et al., 2011). Pleurothallidinae present both rewarding species that offer nectar (Barbosa et al., 2009; Borba et al., 2011), and non-rewarding ones that mimic food, a brood-place or a female of the pollinator are food, brood place or sexual-deceived (Borba and Semir, 2001; Blanco and Barboza, 2005; Pemberton, 2010; CaraDonna and Ackerman, 2012; Duque-Buitrago et al., 2014).

Myophily is a syndrome corresponding to elements of morphological, behavioral and physiological adaptations of flower-visiting Diptera (Borba and Semir, 1998; Woodcock et al., 2014). Nectar is the main attractant and reward to some pollinators, in which visual and chemical cues provide information to potential pollinators about the location and access to this reward (Jersáková et al., 2006; Woodcock et al., 2014). Sapromyophily is a case of deception in which plants deceive their pollinators by producing odors mimicking the decaying flesh where these flies normally lay their eggs (Melo et al., 2010; Humeau et al., 2011; Woodcock et al., 2014). In Pleurothallidinae, the combination of pheromone attraction and nectar feeding is probably a generalized pollination syndrome (Karremans et al., 2015). Although nectar is not commonly found among sapromyophilic flowers, it seems to be an important element in the mechanism of deceit-pollination in some partially deceitful species of a Brazilian group of *Acianthera*

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(Pleurothallidinae). Pollination biology of these *Acianthera* species were studied by Borba and Semir (2001), who found that species pollinated by Phoridae flies have nectar on the labellum, while those pollinated by Chloropidae flies are nectarless and use deceit-pollination.

The remarkable glands in Pleurothallidinae are the osmophores (scent glands), apparently ubiquitous within this subtribe (Pridgeon et al., 2010), which mediate the different strategies of pollination exhibited by the representatives of this subtribe by means of production of varied volatiles. Floral scent stands out for its chemical complexity and variation, both among and within taxa (Raguso, 2004). Their constituents often correlate strongly with specific phylogenetic related groups of pollinators that are not necessarily tied to only one or a few specific compounds in a scent bouquet (Steiner et al., 2011; Schiestl, 2015). Information concerning chemical profiles of the volatiles emitted by Pleurothallidinae flowers is still incipient, restricted to a screening in *Masdevallia*, *Dracula* and *Dryadella* species (Kaiser, 1993). Besides the further use of chemical markers in a phylogenetic frame, studies that characterize the volatile floral compounds are essential for a better understanding of the relationship between Pleurothallidinae species and their (mostly still unknown) pollinators.

Among myophilous flowers we investigated *Octomeria crassifolia*, representing the sister group of the remaining Pleurothallidinae (Pridgeon et al., 2001; Chiron et al., 2012, 2016), a species that offer nectar and is pollinated by Sciaridae flies (Barbosa et al., 2009; Borba et al., 2011), and *Anathallis obovata* that exhibits the same pattern of coloration, morphology and pleasant perceptible odor, but belongs to an early-divergent clade. We also studied five other Brazilian sapromyophilous species representing both late and early-divergent clades of this subtribe whose floral biology is still unknown. Here we describe the volatile profile of Pleurothallidinae flowers, and compare to the ones provided by literature to some Laeliinae species seeking for ecological and phylogenetic insights.

2. Material and methods

2.1. Plant material, collection and characterization of flower volatiles

Flowers (Fig. 1, Table 1) at anthesis were analyzed from plants cultivated in the living orchid collection of the Núcleo de Pesquisa Orquidário do Estado (Instituto de Botânica, São Paulo, Brazil; Table 1).

The volatile analysis from all species were performed at the second day of anthesis, from 9 am to 6 pm, in sampling periods of 1 h 30 min. Flowers were kept apart from their vegetative constituents with aluminum foil and introduced in small Teflon bags with side vents for air input and output, ensuring the maintenance of gas exchange. The volatiles were collected through cartridges containing 100 mg of Tenax TA absorbents (Supelco, mesh 60/80), with one end fixed in a bag opening and the other connected to a suction pump, ensuring the passage of the air inside the cartridge. The flow of the sampled air was 180 ml min⁻¹ and the air inserted into the bags was 240 ml min⁻¹.

Volatile compounds were analyzed by gas chromatography-mass spectrometry (GC-MS) (MSD 5973; Agilent GC 6890). Trapped compounds were desorbed with a thermal desorption unit (Perkin-Elmer ATD400 Automatic Thermal Desorption system; Perkin Elmer, Waltham, MA, USA) at 250 °C for 10 min, cryofocused at -30 °C and injected onto an HP-5 capillary column (50 m × 0.2 mm i.d. × 0.5 µm film thickness; Hewlett-Packard) with helium as a carrier gas. The oven temperature program was held at 40 °C for 1 min and then raised to 210 °C at a rate of 5 °C min⁻¹, and finally further to 250 °C at a rate of 20 °C min⁻¹. Volatile identification was undertaken by comparing the recorded mass spectra using Wiley library. The peak identification was performed when the similarity of mass spectra was higher than 80%. The linear retention index was used to secure the identification of each molecule. Retention index was calculated by injecting saturated *n*-alkanes standards solution C7-C30 (Supelco, Belgium) using the definition of Kovats retention. The identification was not confirmed using

standards due to limited availability of chemicals. Absolute peak areas were used to calculate the percentage of each compound in the sample. The percentage was performed comparing the sum of peaks areas (hundred percent of compounds, including unidentified compounds) and the individual area of each compound.

3. Results and discussion

3.1. Chemical composition of floral volatiles

Table 2 summarizes the compounds detected from the flowers' headspace of all analyzed species. A number of unidentified compounds was also detected; those in which the identification by the mass spectral and retention index libraries was below 80% of confidence were not considered for description. A total of 28 volatile compounds was identified from *Octomeria crassifolia* inflorescences, largely dominated by aromatic compounds and terpenoids, such as cinnamyl alcohol, α -farnesene, *trans*-linalool oxide, and nerolidol. In *Echinosepala aspicensis*, 16 volatile compounds were identified from isolated flowers, predominantly the emissions of alkenes and alcohols, such as tridecane, tetradecane, 2-methyl-1-hexadecanol. Mono and sesquiterpenes were not detected in the floral scent of this species. A total of 30 volatile compounds were detected from inflorescences of *Acianthera aphthosa*, composed by alkenes, aromatic compounds, mono and sesquiterpenes, in which tridecane, methyl salicylate and α -farnesene represented more than 50% of total volatiles emitted. Mono and sesquiterpenes were not identified neither in inflorescences of *Acianthera fenestrata* and *Anathallis obovata* nor in isolated flowers of *Zootrophion atropurpureum* and *Phloeophila nummularia*. The chemical composition of flower volatiles from these species was dominated by alkenes and aromatic compounds, highlighting tridecane and benzaldehyde.

3.2. Ecological considerations

Concerning the attraction of pollinators, Reis et al. (2004) described the floral fragrances of six orchid species from different Epidendroideae subtribes and compared them to the offered rewards (pollen, nectar, pseudopollen and fragrant oil), so that the authors concluded that in most pollination systems, the attraction could not be assigned to one compound or class of compounds but to the "bouquet" that is an ensemble of compounds belonging to different compound classes. Thus, the floral bouquet composition of the species analyzed here have been compared to data available in the literature regarding their odor, presence in other sapromyophilous taxa, possible role as semiochemicals, and presence in decaying organic matter. However, the prediction of pollinators as well as their behavior in the flower based solely on the volatiles emitted is completely speculative, besides the absence of species-specific relationship between the orchids and flies (Karremans et al., 2015). Moreover, the floral biology of the species analyzed here is beyond the scope of the present study.

Volatiles are used as semiochemicals by Diptera species (Bohman et al., 2016); at close range, odor can act similarly to visual nectar guides, by directing the visitor to the resources, and position them appropriately to contact sexual structures and perform pollination (Woodcock et al., 2014; Bohman et al., 2016). Scent differences are combined with different color and morphology (Policha et al., 2016). *Echinosepala aspicensis*, *Acianthera fenestrata*, *A. aphthosa*, *Zootrophion atropurpureum* and *Phloeophila nummularia* exhibit features typical of sapromyophilous flowers, as a strong purple and yellow color, with purple lines and dots, unpleasant odors, and absence of nectar (Humeau et al., 2011; Woodcock et al., 2014). The "lateral windows", regions of detachment of the coherent sepals, observed in *A. fenestrata* and *Z. atropurpureum* (see the floral morphology at Fig. 1) are also linked to this pollination syndrome, since they act as attractants and direct the movements at close range of positively phototactic visitors. The absence of nectar in sapromyophilous systems is effective in trap-like

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