



Floral scent emitted by white and coloured morphs in orchids



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ABSTRACT

Polymorphism of floral signals, such as colour and odour, is widespread in flowering plants and often considered to be adaptive, reflecting various pollinator preferences for particular floral traits. Several authors have recently hypothesized that particular associations exist between floral colour and scent, which would result from shared biochemistry between these two floral traits. In this study, we compared the chemical composition of floral volatiles emitted by white- and purple-flowered morphs of three different orchid species, including two food-deceptive species (*Orchis mascula* and *Orchis simia*) and a food-rewarding species (*Anacamptis coriophora fragrans*). We found clear interspecific differences in floral odours. As expected from their pollination strategy, the two deceptive orchids showed high inter-individual variation of floral volatiles, whereas the food-rewarding *A. c. fragrans* showed low variation of floral scent. Floral volatiles did not differ overall between white- and coloured-flowered morphs in *O. mascula* and *A. c. fragrans*, while *O. simia* exhibited different volatile profiles between the two colour morphs. However, a detailed analysis restricted to benzenoid compounds (which are associated with the production of floral anthocyanin pigments) showed that white inflorescences emitted more volatiles of the shikimic pathway than coloured ones, both for *O. mascula* and *O. simia*. These results are consistent with the current hypothesis that shared biochemistry creates pleiotropic links between floral colour and scent. Whether intraspecific variation of floral signals actually affects pollinator attraction and influences the reproductive success of these orchids remains to be determined.

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Introduction

Many flowering plants show substantial variation in floral traits at individual or population levels (Galen, 1999; Warren and MacKenzie, 2001; Weiss, 1995). Ecologists have focused primarily on interpreting colour variation in flowers, asking why different colour morphs have evolved and how they are maintained in populations. In many flowering plant species, pollinator insects have been shown to play a key role. Pollinator-mediated selection is frequently proposed to explain floral colour polymorphism, with different colour morphs likely reflecting selection driven by different pollinators with different colour preferences (Brown and Clegg 1984; Eckhart et al., 2006; Jones and Reithel, 2001; Juillet et al., 2010; Malerba and Nattero, 2012; Suchet et al., 2011). For example, the two main pollinators of *Mimulus aurantiacus* have been shown to exhibit strong preferences for either the red-flowered morph (hummingbirds) or for the yellow-flowered morph (hawk-moths) (Streisfeld and Kohn, 2007), and floral divergence has been

experimentally demonstrated to be governed by insect preference. In the deceptive orchid *Disa ferruginea*, the flower colour shift has been shown to be driven by geographical variation of colour preference of the same pollinator: allopatric red and orange floral morphs of this orchid mimic the flowers of sympatric nectar-producing species, and the butterfly *Aeropetes tulbaghia* prefers red or orange floral signals in different parts of its range (Newman et al., 2012). More recently, pleiotropic effects of selection exerted by agents other than pollinators have been reported to explain flower colour variation in some cases (Coberly and Rausher, 2008). Colour polymorphism might reflect multiple selection pressures, involving not only pollinators but also herbivore-protection strategies, local abiotic conditions or indirect selection (Majetic et al., 2009; Schemske and Bierzychudek, 2007; Strauss and Whittall, 2006).

Together with floral colour, odour emitted by flowers represents a key floral signal used by insects to detect and select rewarding flower species (Chittka and Raine, 2006; Delle-Vedove et al., 2011; Suchet et al., 2011; Tremblay et al., 2005; Raguso, 2008a; Wang et al., 2013). The importance of floral scent has long been neglected in studies of pollination biology (Adler and Irwin, 2012; Raguso, 2008b). Most flower-visitor species orient their

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flight behaviour by exploiting simultaneously volatile and visual cues provided by flowers (Burger et al., 2010; Dötterl et al., 2011; Milet-Pinheiro et al., 2012). Recent studies have shown experimentally that colour and scent can be equally important for pollinator choices (Glover, 2011; Klahre et al., 2011; Kunze and Gumbert, 2001). The chemical composition of floral volatiles has been investigated and detailed in many plant species (reviewed by Knudsen et al., 2006; Schiestl, 2010), but contrary to colour variation, the variability of floral scent within a plant species and its effect on pollination rate have received limited attention (Delle-Vedove et al., 2011; Dormont et al., 2010a; Soler et al., 2012).

Some authors have compared the composition of floral volatiles in plants showing intraspecific variation of floral colour, and found that colour morphs of the same species consistently differ in scent chemistry (Flamini et al., 2002; Olesen and Knudsen, 1994; Salzmann and Schiestl, 2007; Zuker et al., 2002). It has been suggested that specific floral scent-colour combinations may result from related biochemical processes, because volatile compounds and colour pigments often share common biosynthetic pathways (Knudsen et al., 2006; Majetic et al., 2007; Zuker et al., 2002). If precursor molecules are channelled to production of one product, less of the other product may be formed. For example, volatile benzenoid compounds and anthocyanin-derived pigments responsible for blue, red or purple flower colouration are both produced by the phenylpropanoid biosynthetic pathway. This biosynthetic connection might explain specific floral colour-scent associations, such as white flower morphs that emit more benzenoid volatiles than coloured morphs in some plant species (Majetic et al., 2007; Zuker et al., 2002).

In this study, we investigated the composition of floral scent emitted by different colour morphs in orchids, which represent numerous very interesting cases of floral polymorphism. The great diversity of floral colour characters in this family is generally associated with animal (mainly insect) pollination (Claessens and Kleyen, 2011; Van der Cingel, 1995). Approximately one-third of all orchid species achieve pollination through food deception, i.e., flowers contain no nectar or other rewards but resemble or mimic floral signals of rewarding plants to attract pollinators (Jersakova et al., 2006). Consequently, intraspecific variation in floral traits is expected to be high in food-deceptive orchids, because flowers must delay the avoidance learning of pollinators (Jersakova et al., 2006; Schiestl, 2005). After visiting flowers that did not offer a nectar reward, insects have been observed to fly greater distances, or to switch to flowers with different form or colour characters (Smithson and MacNair, 1997). Because frequent floral morphs are more quickly recognized and avoided by pollinators, rare morphs could gain a selective advantage by being more frequently visited and pollinated. This rare-morph advantage through negative frequency-dependent selection has been hypothesized to explain the maintenance of floral polymorphism in rewardless orchids, at least for colour traits (Gigord et al., 2001; Smithson and MacNair, 1997). For example, in *Dactylorhiza sambucina*, frequencies of the yellow- and red-coloured morphs have been shown to reflect pollinator preference for the rare colour morph (Gigord et al., 2001). Among the wide range of colour variants in orchid flowers, the occurrence of rare hypochromatic inflorescences (very pale morphs and even entirely white flowers) remains intriguing. Many orchid species occasionally show a few white-flowered individuals within natural populations of the common coloured morph (Bournérias and Prat, 2005; Weiss, 1995). Until recently, it was unknown whether such white orchid flowers differ from coloured morphs in their production of olfactory signals. If they do, this may affect pollinator behaviour and thereby also reproductive success of the white morphs (Ackerman and Carronero, 2005; Koivisto et al., 2002; Schatz et al., 2013). In other plant families in which similar floral colour polymorphisms have been described, the

white-coloured flower morphs have been shown to clearly differ in scent chemistry from pigmented morphs (Li et al., 2006; Majetic et al., 2007; Zuker et al., 2002). In deceptive orchids, it could be expected that different colour morphs also exhibit different scent profiles, so that pollinators just deceived by one colour morph can be attracted by a flower showing simultaneously distinct colour and odour (Kunze and Gumbert, 2001). In a preliminary study, we showed for the food-deceptive orchid *Orchis mascula* that purple-flowered morphs did not clearly differ in their floral scent from the white-flowered morphs. Overall, floral volatiles were highly variable in both morphs (Dormont et al., 2010a, 2010b).

Here, we ask whether this situation also characterizes two other orchid species with different reproductive strategies. Like *Orchis mascula*, *O. simia* and *Anacamptis coriophora fragrans* typically exhibit common coloured flowers (purple, pink, and red/brown, respectively), but in each of these, rare white-flowered individuals can also be observed, always at low frequency, within populations dominated by coloured-flowered individuals (Fig. 1). We analyzed and compared the floral scent emitted by white and coloured inflorescences in these three orchid species. They display three different strategies of pollinator attraction: both *Orchis* species are food-deceptive species, in which pollinator attraction is based on pollinator naiveté in *O. mascula* and on visual mimicry in *O. simia*, while *A. c. fragrans* is nectar-rewarding. More specifically, we aimed at answering two questions: (1) Does floral scent differ between white- and coloured-flowered morphs in these three orchid species? We focused particularly on benzenoid compounds in floral volatiles of the two morphs, as these compounds are hypothesized to be linked to the production of anthocyanin pigments. (2) Does scent difference between colour morphs depend on reproductive strategy, i.e. between non-rewarding (food-deceptive) species and food-rewarding species? As explained above, it can be expected that intraspecific variation of floral volatiles will be higher in food-deceptive orchids than in food-rewarding species, in order to minimize the avoidance learning ability of pollinators.

Results and discussion

Chemical composition of floral volatiles from both colour morphs

A total of 47 volatile compounds were identified from emissions of *O. mascula* inflorescences (Table 1). The volatile profile was largely dominated by terpene products: 38 of the 47 compounds (81%) originated from the terpenoid biosynthetic pathway. The major components (each with >10% of the profile) were (E)-ocimene, limonene, (Z)-3-hexenyl acetate, and linalool. No difference was observed between the two populations studied.

In *O. simia*, 41 volatile compounds were isolated and identified from emissions of flowers. As in *O. mascula*, terpene products were predominant in the floral scent of *O. simia*: α -pinene, myrcene, β -phellandrene. However, several lipids were found to dominate the volatile profile in a few individuals: (Z)-3-hexenyl acetate (mean 17% of the profile in the white morph, but up to 35% in some individuals of the white morph), nonanal and decanal.

A total of 27 volatile compounds were found in emissions of inflorescences of *A. c. fragrans*, including 17 compounds from the shikimic pathway. The chemical composition of the floral scent was largely dominated by two benzenoid compounds: p-anisaldehyde and p-dimethoxybenzene, which accounted for 38% and 31% of all floral volatiles, respectively. These two major compounds were followed by two other benzenoid components: methyl anisate (9%) and 1,2,4-trimethoxybenzene (7%). These four major compounds accounted for 85% of the total volatile profile in the coloured morph (82% in the white morph), whilst the overall terpene products represented less than 1% of the profile.

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