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Floral synomone diversification of *Bulbophyllum* sibling species (Orchidaceae) in attracting fruit fly pollinators

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ABSTRACT

Floral scent is one of the crucial cues to attract specific groups of insect pollinators in angiosperms. We examined the semiochemical diversity in the interactions between “fruit fly orchids” and their pollinator fruit fly species in two genera, *Bactrocera* and *Zeugodacus* (Tephritidae: Diptera). Two known attractants for the Dacini fruit flies, methyl eugenol (ME) and raspberry ketone (RK), have been identified from the *Bulbophyllum* orchids. Additionally, zingerone (ZN), with a hybrid chemical structure between ME and RK, and attracts both ME- and RK-sensitive fly species, was also identified. Male flies utilize the floral scent as sex pheromone precursor or components to attract conspecific females and gain mating advantage. We analyzed the floral components of two sibling orchids, *Bulbophyllum macranthum* collected from Southeast-Asian countries and *Bu. praetervisum* collected from Sabah, Malaysia. For *Bu. macranthum*, the major floral component from Malaysia and Thailand was identified as ZN; whereas that from the Philippines was ME. For *Bu. praetervisum*, RK was found as the major constituent, but chemical profiles of the attractants were different among individuals, i.e. in addition to RK, ZN was also found in some of the *Bu. praetervisum* flowers; and one of the specimens contained ME besides RK and ZN. These differences in fruit fly-attracting floral scents shown by the sympatric chemotypes of *Bu. praetervisum* are contrary to that shown by the allopatric chemotypes of *Bu. macranthum,* demonstrating the versatility in the floral synomone biosynthetic processes. Phylogenetic analysis using chloroplast DNA shows that the Malaysia- and Thailand-chemotypes of *Bu. macranthum* and *Bu. praetervisum* belong to the same lineage, although their chemical profiles are distinctly different. This demonstrates that diversification of floral synomone may happen even within a putative orchid species in order to attract a wider community of fruit fly pollinators from different genera to maximize pollination success.

1. Introduction

Floral scent is a key determinant of the diversity and abundance of insect visitors and/or pollinators of flowers (Dobson, 1994; Raguso, 2001). Evolutionary changes in floral traits, volatile chemical profiles in particular, will likely influence types of floral visitors, resulting in a shift in the associated pollinator assemblage (Okamoto et al., 2015; Peakall et al., 2010; cf. Van der Niet et al., 2014). However, pollinators may also be key factors driving floral divergence and eventually leading to plant speciation (Johnson and Steiner, 2000). Thus, changes in the biosynthesis of floral semiochemicals could have reciprocal impacts on plant-insect interactions. The process in which a change of floral chemical profiles within the same or very closely related species is associated with a consequent change of pollinators is well documented for the sexually deceptive orchids (Ayasse et al., 2011; Bohman et al., 2014).

The interaction of fruit fly species in two genera – *Bactrocera* and *Zeugodacus* (formerly a subgenus of *Bactrocera*) – in the tribe Dacini (Tephritidae: Diptera) with “fruit fly orchids” via floral scents is a suitable case to examine a variation of chemical profiles of flowers in association with a possible pollinator shift. The two fruit fly genera comprise more than 500 identified indigenous species centered in the Southeast Asian and Northern Oceanian regions and overlap with the habitat and distribution of fruit fly orchids. Some of these species were formerly categorized by males’ affinity to either methyl eugenol (ME; a phenylpropanoid) or raspberry ketone (RK; a phenylbutanoid) (or its

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acetyl derivative, cue-lure (CL)) (Metcalf, 1990; Tan and Nishida, 2012; Tan et al., 2014). The males are strongly attracted to various plant sources containing ME or RK to acquire sex pheromonal components or precursors to attract conspecific females and/or allomones (defense substances) for protection against predators (Nishida et al., 1990; Tan and Nishida, 1998; Wee and Tan, 2001). While males of *ca* 80 Dacini fruit fly species, including *Ba. carambolae* Drew & Hancock, *Ba. dorsalis* (Hendel) and *Ba. umbrosa* (Fabricius), are sensitive to ME, males of another *ca* 200 related species, such as *Ba. albistrigata* de Meijere, *Ba. melastomatos* Drew & Hancock, *Z. caudatus* (Fabricius), *Z. cucurbitae* (Coquillett) and *Z. tau* (Walker), are sensitive to RK (Tan et al., 2014). A number of orchid species in the Section Sestochilus Benth. & Hook. f. in the genus *Bulbophyllum* (Orchidaceae), which are endemic and distributed widely in Southeast Asia and Northern Oceania regions, selectively attract these fruit fly males as specific pollinators by emitting the male-attracting volatile – either ME or RK. Zingerone (ZN; a phenylbutanoid) (4-(4-hydroxy-3-methoxyphenyl)-2-butanone) has also been identified as a unique floral component that attracts both ME-sensitive and RK-sensitive species (Tan and Nishida, 2000). These "daciniphilous" (formerly bactrocerophilous; see Tan and Nishida, 2013) *Bulbophyllum* orchid species were broadly classified into three groups based on their major floral volatiles:

i) ME-producing species: *Bu. cheiri* (Nishida et al., 2004; Tan et al., 2002); *Bu. vinaceum* (Tan et al., 2006);

ii) RK-producing species: *Bu. apertum* (syn. *Bu. ecornutum*) (Tan and Nishida, 2005); and

iii) ZN-producing species: *Bu. patens* (Tan and Nishida, 2000); *Bu. baileyi* (Tan and Nishida, 2007).

In the Southeast Asia and Northern Oceania regions, the distribution of daciniphilous orchids overlaps with the habitats of indigenous Dacini fruit fly species that are strongly attracted to ME, RK or ZN. These floral volatiles were found to play an important role in the mutualistic interaction between the orchids and fruit flies (Tan et al., 2014).

Over a hundred years ago, Henry Ridley (1890) first described the process of pollination in a daciniphilous orchid, *Bu. macranthum* Lindl. (Fig. 1A), in which the non-resupinate flower mechanically trapped a pollinator fly with slippery lateral sepals and a mobile lip. He reported that the flowers possessed a strong scent, similar to that of cloves or Turkey rhubarb, that likely navigated the fly. Although the fly species was not identified, he observed that the same fly species visited flowers of *Dendrobium anosmum* Lindl. (syn. *D. superbum*). Since the flowers of this species attract males of the melon fly, *Z. cucurbitae*, with a sweet scent of RK (Nishida et al., 1993), it has been assumed that *Bu. macranthum* also emits RK and thereby the fly species he observed on *Bu. macranthum* was probably either *Z. cucurbitae* or another species sensitive to RK. However, our field observations of visiting flies and chemical analyses of the floral volatiles revealed a more complex system than initially predicted. Variation of floral volatile components within the same orchid species and the pollinating fruit fly species appear to reflect the possible pollinator shift within the tribe, Dacini. Thus, we investigated the chemical constituents responsible for fruit fly attraction in several chemotypes of *Bu. macranthum* and its very close sibling species, *Bu. praetervisum* J. J. Verm. (Fig. 1B).

In orchids, instead of producing enormous amounts of powdery pollen grains, a relatively large pollinarium, bearing pollinia containing very fine pollens, is carried by a highly reliable and specific pollinator (Nilsson, 1992) (Fig. 1C). Thus, the pollinarium is known as a key innovation in the evolutionary radiation of orchids (Johnson and Edward, 2000). Many orchids deceive pollinators by producing odors that mimic food or sex pheromone to bring them to the floral reproductive organs without providing rewards (Dobson, 1994; Jasáková et al., 2006; Ong and Tan, 2011). In euglossine bee-orchid interactions, the males positively accumulate terpenoid and aromatic volatiles from the flowers, but it has not been fully understood how these floral fragrances are used by the male bees (Dressler, 1982; Pokorny et al., 2017; Zimmermann et al., 2006). However, in the case of daciniphilous orchid–fruit fly interactions, the flowers supply the sex pheromone/allomone materials to the male flies as a reward for aiding pollination. Since these Dacini males positively accumulate floral phenylpropanoids/phenylbutanoids in the rectal pheromone gland as sex pheromone to attract conspecific females (reviews, Shelly, 2010; Tan et al., 2002, 2006, 2014), the floral attractant is defined as synomone – a released semiochemical benefitting both interacting organisms (Nordlung and Lewis, 1976). This further reinforces the true mutualistic relationship between flowers and fruit fly pollinators.

The males of several ME-sensitive pollinator fruit fly species have been known to positively acquire sex pheromone precursor substances by feeding on daciniphilous orchid flowers that release ME (Nishida and Tan, 2016; Tan et al., 2002, 2006, 2014). Variations in floral synomone components among these orchids would directly influence the sex pheromone composition, and thereby, the females' response to males scented with the 'orchid fragrance'. Thus, another objective of this article is to investigate the fate and accumulation of male rectal gland components in two RK-sensitive fruit fly species after feeding on the synomonal components.

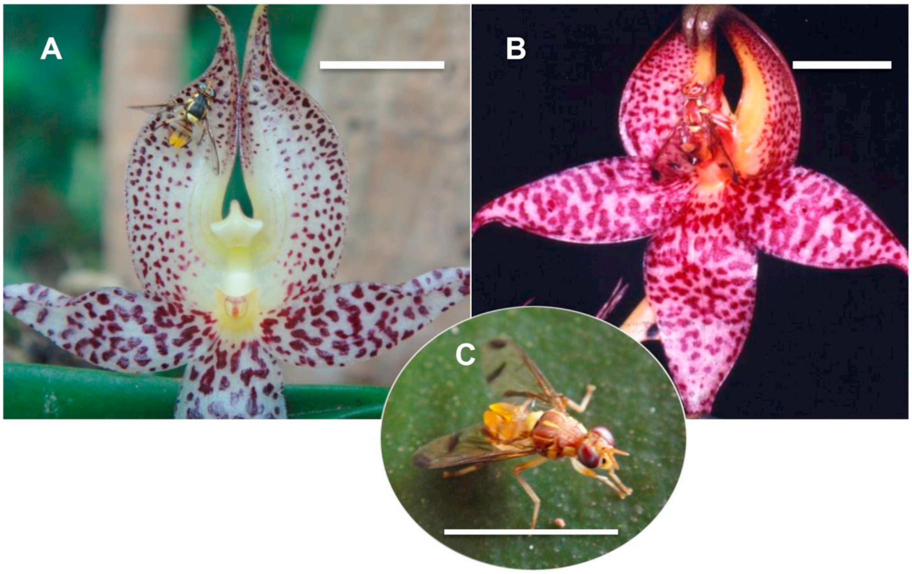

Fig. 1. A) A flower of *Bulbophyllum macranthum* (Malaysia-chemotype) visited by a *Bactrocera dorsalis* male bearing the pollinia on its abdominal dorsum; B) *Bu. praetervisum* (Malaysia-chemotype) flower visited by a *Z. cucurbitae* male being stuck to the floral column via viscidium before pollinia removal from the anther (right); C) A *Z. cucurbitae* male bearing pollinia of *Bu. praetervisum*. Bar = 10 mm.

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