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REVIEW

A review on natural phenylbutanoid attractants: Occurrence, distribution, and role in nature, especially in relation to Dacini fruit fly behavior and pollination

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Abstract

The natural occurrence, distribution (within a plant) and roles of four phenylbutanoid compounds (anisyl acetone, cue-lure, raspberry ketone and zingerone) are elucidated for the Asia-Pacific and Oceania regions. These phenylbutanoids may act individually or in combination to attract true fruit fly males belonging to a tribe Dacini of subfamily Dacinae (Diptera: Tephritidae). Of special interest are the mutualistic interactions between the Dacini fruit fly males and the tropical daciniphilous (attracting exclusively Dacini fruit flies) orchids – leading to cross pollination for the orchids and enchanced mating success for the flies. When offered to male flies, anisyl acetone and cue-lure are generally converted to raspberry ketone. Upon consumption, raspberry ketone and zingerone are individually sequestered in the male rectal (pheromonal) gland unchanged. Attracted male flies readily imbibe the phenylbutanoid(s) in the floral synomone to compliment the endogenously synthesized male sex pheromonal components – to enhance attraction of conspecific females during courtship as well as attract conspecific males to form 'leks'. The phenylbutanoid(s) may also act as an allomone to deter vertebrate predators, especially geckos, besides possessing antimicrobial and antioxidant activities. Cue-lure, raspberry ketone and zingerone are important attractants/lures used in pest surveillance and mass trapping under the integrated pest management (IPM) program against quarantine Dacini fruit fly pest species, particularly *Bactrocera tryoni* and *Zeugodacus cucurbitae*.

Keywords Anisyl acetone · Cue-lure · Raspberry ketone · Zingerone · Semiochemicals · Dacini fruit flies · Daciniphilous orchids · Sexual reproduction · Floral synomone

Introduction

Four known natural phenylbutanoids, anisyl acetone (AA), cue-lure (CL), raspberry ketone (RK) and zingerone (ZN) (Fig. 1), are specific and potent attractants for many fruit fly species belonging to the genera *Bactrocera, Dacus* and *Zeugodacus* within the tribe Dacini of the subfamily Dacinae (Diptera: Tephritidae). These molecules possess a common 4-phenyl-2-butanone structure typically with substituents (e.g. -OH and/or -OCH_3) on the benzene ring. AA and CL were first discovered as synthetic Dacini fruit fly attractants until recently when they were detected in plants, especially in *Bulbophyllum* (Asparagales: Orchidaceae: Epidendroideae) orchid flowers. It should be pointed out from the onset that the attractants may be released individually or in combination to influence the behavior of insects, especially Dacini fruit flies. Daciniphilous (attracting Dacini fruit flies) flowers, particularly certain *Bulbophyllum* orchids (the largest orchid genus with ca 2000 species; Frodin 2004), have an obligatory mutualistic interrelationship with the fruit fly males (Tan 2009; Ong et al. 2011; Tan and Nishida 2013; Nishida and Tan 2016), This group of flowers makes use of either phenylpropanoids or phenylbutanoids in their fragrances as floral synomones to exclusively attract male Dacini fruit flies for the sole purpose of pollination.

Traditionally, fruit fly species belonging to the *Bactrocera, Dacus* and *Zeugodacus* were categorized into three groups based on their specific response or non-response to two known male attractants CL and methyl eugenol: a) CL-responsive species (ca. 250 species (FAO/IAEA 2018) but now > 400

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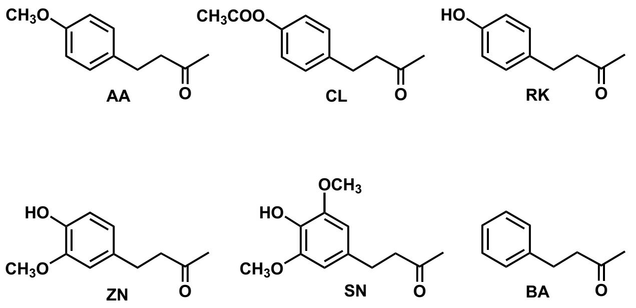

Fig. 1 Chemical Structures of phenylbutanoids found in plants. AA – Anisyl acetone; CL – Cue-lure; RK – Raspberry ketone; ZN – Zingerone; SN – Syringerone; BA – Benzyl acetone

species, see below), including mango fruit fly, *Bactrocera frauenfeldi* (Schiner), Queensland fruit fly, *B. tryoni* (Froggatt), *Zeugodacus caudatus* (Fabricius), melon fly, *Z. cucurbitae* (Coquillett), and pumpkin fruit fly, *Z. tau* (Walker); or b) methyl eugenol (ME, a phenylpropanoid); ca. 60 responsive species, FAO/IAEA 2018), including carambola fruit fly, *B. carambolae* Drew & Hancock, guava fruit fly, *B. correcta* (Bezzi), Oriental fruit fly, *B. dorsalis* (Hendel), and peach fruit fly *B. zonata* (Saunders); or c) non-responsive (> 500 mostly non-pest species) to these aromatic male attractants (neither phenylbutanoids nor phenylpropanoids), but including several serious pests, such as Chinese citrus fly, *B. minax* (Enderline), Japanese orange fly, *B. tsuneonis* (Miyake), and solanaceous fruit fly, *B. latifrons* (Hendel), as serious pests. More key pest species under each of these groups have been listed in various publications (CDFA [California Department of Food and Agriculture], 2013; Nishida and Tan 2016; FAO/IAEA 2018; Doorenweerd et al. 2018). It is important to note at this juncture, that none of the known male phenylbutanoid attractants is as potent as ME for *B. dorsalis* (see review by Shelly et al. 2010). ME is found in over 450 plant species (Tan and Nishida 2012), especially as a component of floral synomone involved in cross pollination for certain daciniphilous *Bulbophyllum* species [e.g. *B. cheiri* Lindl. subspecies *cheiri, Bu. macranthum* Lindl. s. l. (ecotype ex. Philippines), *Bu. sinapis* J. J. Verm. & P. O'Byrne and *Bu. vinaceum* Ames & C. Schweinf.] (Tan et al. 2002, 2006; Nishida et al. 2004, 2022; Tan and Nishida 2015; Nakahira et al. 2018). In several cases, daciniphilous orchids produce/emit phenylbutanoid synomone as a mixture of specific ratios of AA, RK, and ZN and in rare cases also as a mixture with ME (discussed below).

This review is a sequel to a preceding review for the natural occurrence of ME (Tan and Nishida 2012). It also describes the origin and ecological/physiological functions of the phenylbutanoid attractants in association with the largest group of CL-responsive Dacini fruit fly species (> 400 species), most of which are endemic in the Asia-Pacific region (particularly in Southeast Asia and Oceania).

Semiochemicals of Dacini fruit flies

Semiochemicals of Dacine fruit flies have recently been reviewed (Segura et al. 2018, Scolari et al. 2021), and a review related to chemosensory mechanisms involving semiochemicals in fruit flies, especially serious pest species, was published by Ono et al. (2021). Our intentions are to a) update and clarify current knowledge for a large group of true fruit fly species in the genera *Bactrocera, Dacus* and *Zeugodacus* in relation to both intra- and inter-specific interactions with other organisms in the natural ecosystems and b) review the actual role(s) of each attractant as to whether it is a precursor or a booster or a component of the male sex pheromone. Traditionally, semiochemicals have been categorized based on intra- and/or inter-specific behavioral and/or physiological effects induced in an organism during its interactions with other individuals/organisms (Nordlund and Lewis 1976).

Figure 2 shows the classification of semiochemicals specifically for Dacini fruit flies. Semiochemicals are subdivided into two groups - one with intra-specific activity (pheromone) and the other with inter-specific activity (allelochemicals). Pheromones and allelochemicals are further divided into the following (Nordlund and Lewis 1976):

1. Pheromones

    A) Sex pheromone

    Males of *Bactrocera* and *Zeugodacus* flies possess rectal pheromone glands and release characteristic "pheromone smoke" to attract conspecific females (See section IV-A).

    B) Aggregation pheromone

    Prior to courtship, Dacini males often form a lek. The pheromone emission signals conspecific males to aggregate to an arena where matings take place (See section IV-B).

    C) Host-marking pheromone

    Tephritidae females, particularly in the genus *Anastrepha*, *Ceratitis* and *Rhagoletis*, often secrete host marking substances in the sequential behavior of oviposition to deter intraspecific and interspecific oviposion on the same fruit (Scolari et al. 2021; Ono et al. 2021).

2. Allelochemicals

    A) Allomone (emitter benefits and detrimental to receiver)

        a) In fruit fly-predator interactions, sex pheromonal components of *B. dorsalis*, e.g., 2-allyl-4,5-dimethoxyphenol, are moderate deterrents against Japa-

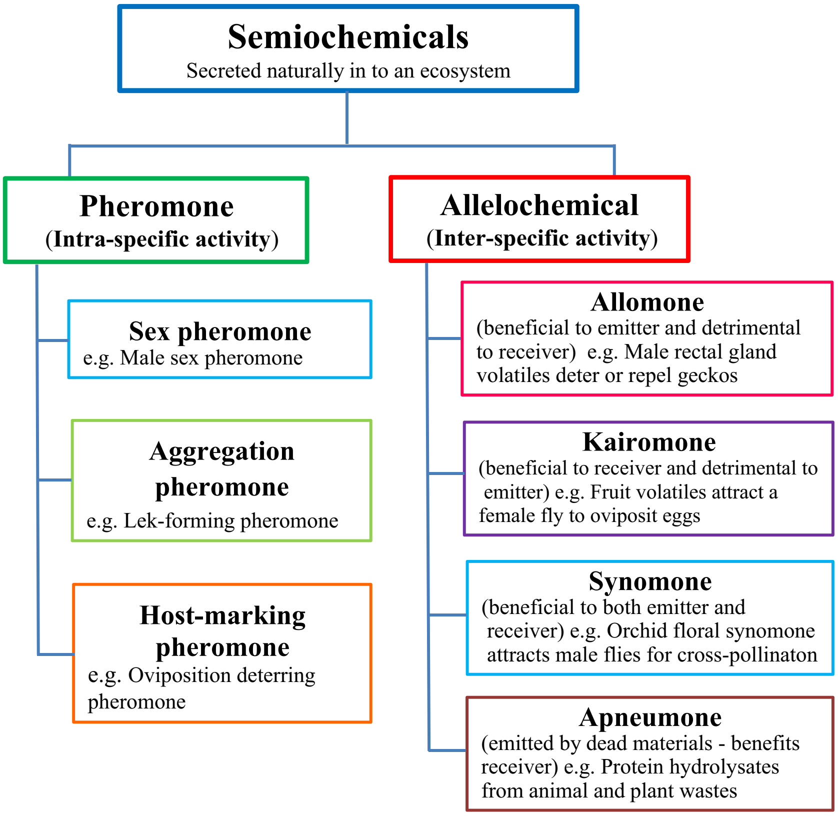

Fig. 2 Classification of semiochemicals in the life history of Dacini fruit flies

nese sparrows *Passer montanus* Linn. (Nishida and Fukami 1990) and coniferyl alcohol against European starlings, *Sturnus vulgaris* Linn. (Jakubas et al. 1992). The chemicals produced by *B. dorsalis* males also have allomonal and hepatotoxic effects against lizard predators, *Gekko monarchus* (Wee and Tan 2001).

b) In fruit fly-host fruit interactions, oviposition by female *B. carambolae* in mango fruits which subsequently produce deterrent chemicals that repel other gravid conspecific females (Muryati et al. 2017).

B) Kairomone (receiver benefits and detrimental to emitter)

Fruits generally release volatiles or fragrant chemicals during ripening. The fruit volatiles act as a ‘fruit kairomone’ that attracts gravid female fruit flies for oviposition, which subsequently causes fruit damage, dropping and/or infestation. γ-Octalactone has been characterized as an oviposition stimulant of *B. dorsalis* and *B. tryoni* (Damodaram et al. 2014; Kempraj et al. 2019), and a number of cucumber volatiles attract females of *B. cucumis* (French) (Royer et al. 2014) and *Z. cucurbitae* (Jang et al. 2017).

C) Synomone (benefits to both emitter and receiver)

A floral volatile compound, such as ME, attracts fruit fly males to execute cross-pollination. In this mutual interaction, both organisms gain reproductive benefits, i.e., the flower gets pollinated while the male fly gains either sex pheromone or sex pheromonal precursor via feeding on the flower. ME as a component of a floral synomone has been shown to attract ME-responsive *Bactrocera* species as exclusive myophilous pollinators of *Bulbophyllum cheiri* subspecies *cheiri* and *Bu. vinaceum* (Tan et al. 2002, 2006; Nishida et al. 2004; Tan and Nishida 2015). Below, we discuss floral synomones that consist of an individual or a blend of phenylbutanoids.

From the onset, it is paramount to bear in mind that semiochemicals may often simultaneously act as pheromones (during intraspecific interactions) as well as allelochemicals (during interspecific interactions) in a natural ecosystem e.g., male sex pheromone of *B. dorsalis* as in Item 2A above.

As for the chemicals not released/secreted naturally, it is important to note that in a review of insect para-pheromones, Renou and Guerrero (2000) restrict the term ‘para-pheromones’ to “chemical compounds of anthropogenic origin not known to exist in nature”. This had led to a very potent male attractant/lure, ME, found in over 450 plant species (Tan and Nishida 2012) but thus far not detected in the pheromonal/rectal gland of male fruit flies being erroneously referred to as a ‘para-pheromone’ in many publications – similarly, for CL (as used by Bakthavatsalam 2016). Hitherto CL, like ME, has not been detected in any Dacini male pheromonal/rectal gland and never been shown to induce sex pheromonal activity (Tan and Nishida 1995; Nishida et al. 2022); and strictly, should also not be referred to as a 'para-pheromone' but as a male attractant/lure instead, when used in fruit fly control or surveillance programs. Similarly, potent synthetic analogues of RK – raspberry ketone formate (melolure) (Oliver et al. 2002), and raspberry ketone trifluoroacetate (Siderhurst et al. 2016) were found to be superior to CL, and should also be categorized as male attractants/lures.

Natural Occurence, Distribution and Role of Individual Phenylbutanoids

Anisyl acetone [4-(4-methoxyphenyl)-2-butanone (CAS RN: 104-20-1)] (other names: *p*-methoxybenzylacetone; raspberry ketone methyl ether)

Anisyl acetone (AA) was the first synthetic fruit fly male attractant/lure discovered via mass screening of synthetic chemicals for the melon fly, *Z. cucurbitae* (Barthel et al. 1957). It was then used in Queensland, Australia from 1959 to 1962 (until the discovery of a new synthetic and more potent attractant, see cue-lure below) for trapping of eleven Dacini fruit fly species (unpublished data c/f Royer et al. 2020).

To date, AA has been detected in ten plant species belonging to eight families (Table 1). It is generally detected as a trace or minute/minor component in plants, except in flowers of *Bu. hahlianum* Ames & C. Schweinf. (Fig. 3) (Nishida et al. 2022). The natural role of AA as a constituent in plants, besides possessing some anti-oxidant properties (Yang et al. 2012), is not fully understood. Nonetheless, as a component in floral fragrance, AA in combination with RK and/or ZN is an important floral synomone component in enhancing cross-pollination of certain daciniphilous *Bulbophyllum* (Orchidaceae) species, such as, *Bu. hahlianum* (Nishida et al. 2022) and *Bu. macranthoides* Kraenzl. subspecies *tollenoniferum* (J.J. Sm.) J.J. Verm. (Katte et al. 2020).

Fruit fly field captures in Cairns, Australia, showed that *B. frauenfeldi* males were most responsive to CL, equally to RK and AA, and poorly to ZN (Royer et al. 2020). Furthermore, comparison of flies captured in PNG using three phenylbutanoid lures - AA, RK and ZN - showed that AA captured the highest number of individuals for *B. atramentata, B. bryoniae* and *B. fraeuenfeldi* (Nishida et al. 2022). AA, when offered to *B. frauenfeldi* males, was converted to RK and 4-(4-methoxyphenyl)-2-butanol (AL) for storage in the rectal (pheromonal) gland, while consumed RK is sequestered unchanged in the gland (Wee et al. 2020). Additionally, AA has also been detected in whole body extracts of *B. atramentata* and *B. fraeuenfeldi* males collected from flowers of *Bu. hahlianum* (Nishida et al. 2022).

Table 1 Anisyl acetone (AA) in plants

Species [Common name] and family	Remark	Reference
Aquilaria agallocha Roxb. (syn *A. malaccensis* Lam.) [agarwood] Thymelaeaceae	AA as a minor component in a commercial sample of agarwood oil.	Meier et al. 2003
Aquilaria crassna Pierre ex. Lecomte [Karas, agarwood, aloeswood, eaglewood] Thymelaeaceae	Three ecotypes in Vietnam contain 0.31 – 2.27% (peak area) AA.	Thuy et al. 2019
Agastache mexicana (Kunth) Lint & Epling [Mexican hyssop] Plantaginaceae	AA in trace quantities (< 0.01%) - Unpublished results of Schmaus et al.	c/f Meier et al. 2003
Bulbophyllum macranthoides Kraenzl. subspecies *tollenoniferum* (J.J. Sm.) J.J. Verm. Orchidaceae	AA (a minor component) with RK and ZN as major floral components.	Katte et al. 2020
Bulbophyllum hahlianum Schltr. Orchidaceae	AA largest, followed by RK ketone (major) and ZN (minor) floral components.	Nishida et al. 2022
Foeniculum vulgare Mill. [Fennel] Apiaceae	Aerial parts have 0.36% AA. Seed extract contains 0.40% AA.	Ebadollahi et al. 2014; Samadi Andzagi et al. 2017
Illicium verum Hook f. [Chinese star anise] Schisandraceae	AA in different organic solvent fractions (5.23 -19.51%); and in aqueous fraction 42.49%. 5.24-22.03 % of peak area in fruit extracts.	Yang et al. 2012; Ahmad and Youssef 2015
Limnophila rugosa (Roth.) Merr. [Swamp leaf/Finger grass] Scrophulariaceae	AA 0.03% of peak area in plant EO.	Yu & Cheng 1986
Pimpinella anisum L. [Anise] Apiaceae	AA detected in whole plant (0.3%) and seed (0.9%) EO - grown in Alberta, Canada.	Embong et al. 1977
Premna tomentosa Willd. [Woolly-leaved fire-brand teak] Lamiaceae	AA isolated from roots.	Ayinampudi et al. 2012

[*] *AA* anisyl acetone, *RK* raspberry ketone, *ZN* zingerone

Fig. 3 *Bulbophyllum hahlianum* flower possesses anisyl acetone (AA) as the largest floral synomone component and with a *Bactrocera bryoniae* (bearing a pollinarium on abdominal dorsum (white arrow) on petal (Courtesy of N. Howcroft). [Bar scale = 1 cm]

The presence of AA in anise, *Pimpinella anisum* L. (Apiaceae), depends on cultivated locations. It is detected in the Alberta anise oil but not in Michigan anise oil. It gives the Alberta oil "a sweet floral and slightly fruity, cherry preserve-like odor", and it consituted ca. 1% in seed oil and 0.3% in whole plant oil (Embong et al. 1977). Similarly, agarwood, *Aquilaria crassna* Pierre ex. Lecomte (Thymelaeaceae), showed significant variation in AA content cultivated in three provinces in Vietnam, with 2.27, 0.68 and 0.31 % peak area of plant essential oils, respectively (Thuy et al. 2019).

From a pharmacological perspective, AA when inhaled induced good sedative effects against mice (Miyoshi et al. 2013). AA also possesses strong antimicrobial properties (Yang et al. 2010), especially against multidrug resistant bacteria - *Pseudomonas aeruginosa* (Schröter) Migula and *Acinetobacter baumannii* Bouvet and Grimont (Osoro et al. 2013). Extracts of *Illicium verum,* Chinese star anise (Schisandraceae), used as traditional Chinese medicinal herbs, revealed a strong synergistic antibacterial activity of AA, anisyl alcohol (4-methoxybenzyl alcohol), anisyl aldehyde (4-methoxybenzaldehyde) and (*E*)-anethole, against sixty-seven clinical antibiotic-resistant isolates; and thereby, demonstrating that the compounds might be the active ingredients against many species of bacteria (Yang et al. 2010).

Cue-lure [4-(4-acetoxyphenyl)-2-butanone) (CAS RN: 3572-06-3)] (other names: cuelure, cue lure)

Cue-lure (CL) was first discovered as a synthetic attractant and identified as a highly potent male attractant for *Z. cucurbitae* through mass screening of synthetic chemicals (Beroza et al. 1960). It was assumed for a long time to be solely a synthetic male attractant (Metcalf 1990). To date, a total of 410 CL-responsive Dacini species of which 206 are *Bactrocera,* 83 *Dacus* and 121 *Zeugodacus* species have been reported (Supplementary Table) (Doorenweerd et al. 2018).

After five decades of successful usage as a lure in surveillance, monitoring and control of certain pest fruit flies (see review by Vargas et al. 2010), CL was detected in two plant species. Trace quantities of CL were detected in flowers of an orchid species *Bulbophyllum hortorum* J.J. Verm. et al. (Orchidaceae) (Table 2, Fig. 4; Tan et al. 2014; Nishida and Tan 2016; Katte et al. 2020) and as a minor floral component in passion fruit, *Passiflora maliformis* L. (Passifloraceae) (Park et al. 2020) (Table 2).

In the orchid species, *Bu. hortorum*, traces of CL were detected in some whole flower samples (Katte et al. 2020). All floral parts possess three major floral phenylbutanoid components, AA, RK and ZN, plus their respective alcohol analogues: AL, 4-(4-hydroxyphenyl)-2-butanol (rhododendrol) (RL), and 4-(3-hydroxy-4-methoxyphenyl)-2-butanol (zingerol) (ZL) as minor components. However, at this juncture, the actual role of floral CL, besides aiding other phenylbutanoids in enhancing pollination by attracted CL-responsive Dacini fruit flies, is unknown. In passion fruit, *P. maliformis,* the combination of fruit fly attractants RK, CL, ZN and ZL was detected as trace components in petals and sepals but not in all floral parts (Park et al. 2020) (Table 2).

More males of *Z. cucurbitae* were attracted to CL in the morning [09:00-10:00 h] than mid-day [12:00-13:00 h] or late afternoon [15:00-16:00 h] (Manoukis and Jang 2013). This diurnal rhythm is corroborated by an earlier field trapping conducted by Nakamori and Soemori (1985), who showed the male melon flies were trapped at highest numbers between 07:00 to 09:00 h, with a steep decline of fly numbers at other day-time periods.

To date, CL has never been detected in fruit flies, especially in the male rectal/pheromonal gland. But when synthetic CL (with high purity - >95%) was offered to males of *Z. cucurbitae* and *B. tryoni,* it was rapidly hydrolysed to RK, probably in the crop, that was eventually sequestered for storage in the rectal gland (Nishida et al. 1990; Tan and Nishida 1995). Likewise, consumed CL was converted to RK for storage in the rectal gland of *B. melanotus* (formerly *B. melanota*) (Coquillett) (Fletcher and Kitching 1995). Additionally, in the case of *B. tryoni*, a trace quantity of CL was biotransformed to and stored as RL (Kumaran et al.

Table 2 Cue-lure (CL) in plants

Species [Common name] and family	Remark	Reference
Bulbophyllum hortorum J.J. Verm., P. O'Byrne & A.L. Lamb Orchidaceae	Traces of CL detected in whole flowers.	Tan et al. 2014, Nishida and Tan 2016, Katte et al. 2020
Passiflora maliformis L. [Passion fruit] Passifloraceae	CL detected in flowers - 1.10 and 0.12 % of peak area inner and outer coronal filaments, respectively.	Park et al. 2020

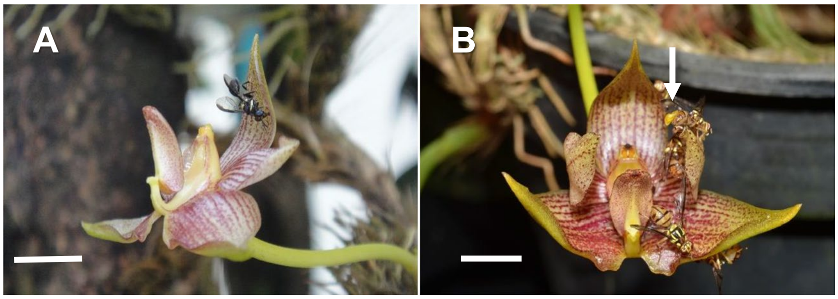

Fig. 4 Flowers of *Bulbophyllum hortorum* possessing cue-lure (CL) as a trace component together with AA, RK and ZN. [Bar scale = 1 cm]. **A** - A freshly bloomed flower with *Dacus maculipterus* male probing on the medial sepal;. **B** - A characteristic second day flower (reopened after partial closing on first night – petals unspread) with a melon fly, *Zeugodacus cucurbitae*, male bearing a pollinarium (white arrow - from a different *Bulbophyllum* species, probably from *Bu. macranthum* or its sibling species) on its abdominal dorsum. N.B. *Bu. hortorum* pollinarium when removed by a fly adheres to the thoracic dorsum – see (Tan et al. 2023)

2014a). Therefore, CL would potentially act as an exogenous male sex pheromonal precursor for CL-responsive species.

Males of *Z. cucurbitae* exposed to CL on the day of or a day prior to testing mated more frequently than unexposed males; but for a relatively short period of two days; additionally, CL might further enhance mating performance via increased male wing-fanning activity (Shelly and Villalobos 1995).

Previously, CL was reported to capture two times more number of *Z. cucurbitae* males than RK (Beroza et al. 1960) and ca. 1.5 times more *B. tryoni* males than RK (Monro and Richardson 1969). A recent quantitative study conducted in Queensland, Australia, confirmed that CL is a more potent attractant than RK in the attraction of Dacini fruit fly species that are specifically responsive to phenylbutanoid attractants (Royer et al. 2020). This might reflect a higher release rate and vapour pressure of CL, ca. five fold that of RK (Metcalf 1990), and also possible chemo-structural differences that affect ligand-receptor binding (Royer et al. 2020). Furthermore, CL has been assumed for many years to be hydrolysed to RK – the true attractant for CL-responsive species (Drew 1974; Metcalf 1990) - until it was shown by Park et al. (2016) that CL remains intact in the atmosphere as a male attractant/lure.

Regarding capture probability of released males, it is very low for *Z. cucurbitae* in CL-baited traps when compared with *B. dorsalis* in ME-baited traps (Shelly et al. 2010). The capture percentage at a central trap from release points of males at 25, 50 and 100 m distance from the CL-baited trap was 5.29, 4.66 and 0.40 %, respectively. This study conducted in California by Shelly and co-workers (2010) showed that the capture probability of released sterile males, particularly for CL-responsive species, drops drastically when the distance between release-point and trap is beyond 50 m.

From a pest management perspective, traps baited with 'dorsalure' (a commercial mixture of CL and ME) attracted significantly fewer *B. dorsalis* males than traps baited with ME alone (Tan and Lee 1982). Combining CL and ME (either as liquid mixture or physically apart each in separate cotton rolls within each trap) as baits in traps captured significantly fewer *B. dorsalis* and *B. umbrosa* males than ME-baited traps (Tan 1983). This was further corroborated by Vargas et al. (2000) who showed that CL-ME baited traps captured similar numbers of the CL-responsive pest species *Z. cucurbitae* as traps baited with CL alone but significantly fewer ME-responsive species *B. dorsalis* than traps baited with ME alone. Additionally, field studies in Australia and PNG showed that combining CL and ME in equal parts placed in each Steiner trap significantly reduced captures of most species of Dacini fruit flies (Royer and Mayer 2018). These studies have shown that the presence of CL in the lure-mixture interfered in the capture of fruit flies, especially those of ME-responsive species when used as simultaneous control programs for both CL- and ME-responsive fruit fly pest species, particularly against the notorious invasive and quarantine species *Z. cucurbitae* and *B. dorsalis*, respectively. This phenomenon is contrasted by a study in Hawaii, in which the CL-ME mixture was replaced by the RK-ME mixture, and no significant differences in captures of either *Z. cucurbitae* or *B. dorsalis* males between traps baited with a single lure and the mixture (Shelly and Kurashima 2016). The cause of reduction in trap captures of both the CL- and ME-responsive pest species due to the presence of CL in bait mixtures warrants in-depth investigations.

Raspberry ketone [4-(hydroxyphenyl)-2-butanone (CAS RN: 5471-51-2)] (other names: *p*-hydroxybenzylacetone; frambinone; oxyphenylon; rasketone; rheosmin)

Raspberry ketone (RK), known as the most characteristic aromatic flavor of raspberry fruit, *Rubus idaeus* (Rosaceae), has been detected in 18 plant species from 9 families, including Actinidiaceae (1 species), Asteraceae (1), Ericaceae (2), Lamiaceae (1), Orchidaceae (7), Pinaceae [Gymnosperm] (2), Polygonaceae (1), Rosaceae (2), and a Gymnosperm family Taxaceae (1) (Table 3). All the seven orchid species listed have floral RK that attracts males of CL-responsive species belonging to the three Dacini genera - *Bactrocera, Dacus* and *Zeugodacus*.

Among orchid species, floral RK was first detected in all three color (purple, white and mixed of the two colors) varieties of *Dendrobium superbum* (Nishida et al. 1993). Nevertheless, the actual role of RK in the three floral-color varieties of this *Dendrobium* species is still uncertain as attracted fruit fly males apparently lick the petal area but approach neither the floral column nor the inner surface of the large immovable lip where the pollination would occur. Furthermore, the stiff and relatively large lip does not have a mechanism to tip a fly in to the column cavity to remove or deposit pollinia (Nishida et al. 1993). Therefore, in this particular case, attracted fruit fly males do not act as pollinators, and RK in the floral fragrance of *D. superbum* may attract other pollinator species, such as bees, and/or deter florivores (see below).

RK is a major component of floral synomones released to attract many CL-responsive species of the Dacini fruit flies to assist in the pollination of several daciniphilous *Bulbophyllum* species, such as *Bu. ecornutum* J. J. Sm (syn. *Bu. apertum*) (Fig. 5A), *Bu. gerlandianum*, Kraenzl. (syn. *Bu. emiliorum* Ames & Quisumb.) (Fig. 5B), *Bu. hahlianum* Schltr. (Fig. 3), *Bu. hortorum* J.J Verm., P. Oyrne & A.L. Lamb (Fig. 4), *Bu. macranthoides* Kraenzl. subspecies *tollenoniferum* (J.J. Sm.) J.J. Verm. and *Bu. praetervisum* J. J. Verm. (Fig. 5C), (Table 3). The whole process of cross-pollination of *Bu. praetervisum* flowers – pollinarium removal and pollinia deposition by two of the CL-responsive Dacini fruit fly species, namely *B. fraeunfeldi* and *Z. caudatus* - has been reported by Tan and Tan (2018). It is interesting to note that there is intraspecific variation in morphological characters and even in the floral chemical composition of phenylbutanoid components acting as synomone in the interactions between the daciniphilous orchids and the Dacini fruit flies. Although RK is the major floral component of *Bu. praetervisum* (Fig. 5C) in Malaysia, there are three different ecotypes based on major synomone components – a) RK + RL, b) RK + RL + ZN, and c) RK + ME + RL + ZN (Nakahira et al. 2018). Also, in *Bu. ecornutum* subspecies *verrucatum,* solitary flowers of Nabawan-ecotype emit a characteristic fragrance of RK along with smaller amounts of RL (Tan and Nishida 2005), while those of Apin-Apin-ecotype emit ZN and ZL as major components (Tan et al. 2021).

RK when consumed remained unchanged and ultimately sequestered in the rectal gland of *Z. tau* (Nakahira et al. 2018). RK was detected from male body extracts of five Dacini species (*B. atramentata, B. bryoniae, B. frauenfeldi, B. pseudodistincta* and *Z. cucurbitae*) captured while feeding on flowers of *Bu. hahlianum*, which contain RK as the major floral volatile. This observation strongly suggests that RK may have a role as an allomone and/or sex pheromone (Nishida et al. 2022) as discussed below.

RK generally attracts the same species that are responsive to CL belonging to the genera *Bactrocera, Dacus* and *Zeugodacus* (FAO/IAEA 2018; Doorenweerd et al. 2018). Attracted *Bactrocera* and *Zeugodacus* males readily consume and sequester RK to be incorporated as one of the male sex pheromonal components (Nishida et al. 1993; Tan and Nishida 2005; Wee et al. 2020; Tan et al. 2021). *Z. cucurbitae* males release sex and aggregation pheromone at dusk during courtship (Kuba and Sokei 1988). The aggregation pheromone attracts other conspecific males to form ‘leks’ (Kuba et al. 1984), while the sex pheromone attracts conspecific females during courtship (Nishida et al. 1990; Tan 1983, Tan 2000a).

Another important role of RK in *Z. cucurbitae* males is acting as an allomone for defence against vertebrate predators (Tan 2000b). The Asian house gecko, *Hemidactylus frenatus* Duméril & Bibron, consumed significantly fewer houseflies (*Musca domestica* L.) topically treated with RK (5 µg /fly) than controls (untreated houseflies) (Tan 2000b).

Affinity of fruit fly males to RK seems to be selected by the conspecific female's preference towards RK-scented males via sexual selection, as in the case of *B. dorsalis* in that males acquired ME as sex pheromone and females prefer to mate with males signaling with ME-metabolites (Tan and Nishida 1996; Shelly 2007; Kumaran et al. 2014b; Nishida 2014).The bird's nest fungus, *Nidula niveo-tomentosa* (Hennings) Loyd (Agaricaceae) has RL and RK as major and minor components, respectively, in submerged cells of the basidiomycete (Zorn et al. 2003). The ratio of RK: RL in this fungus is completely different from that found in floral synomone, in which RL is always present in minute

Table 3 Raspberry ketone (RK) in plants

Species [Common name] and family	Remark*	Reference
Abies koreana [Korean fir] Pinaceae	RK and RL detected in needle leaves; and RK inhibited lipopolysaccharide-induced nitric oxide production in BV-2 microglia cells.	Baek et al. 2011
Actinidia argute (Siebold & Zuss.) Planch ex Miq. [baby kiwi] Actinidiaceae	RK 0.00081 mg/kg in fruits.	Garcia et al. 2011
Artemisia hispanica Jacq. [*mugwort*] Asteraceae	RK detected as minor component in EO of aerial parts.	Marco et al. 1988
Bulbophyllum ecornutum (J. J. Sm.) J. J. Sm (Syn. *B. apertum* Schltr.) –[Nabawan ecotype] Orchidaceae	RK, mean quantity of 5.9 - 9.2 *μg* per flower, highest concentration in floral lip with much lower quantities in petals.	Tan & Nishida 2005
Bulbophyllum emiliorum Ames & Quisumb. (syn *B. gerlandianum* Kraenzl.)	RK in floral fragrance that attracted *B. frauenfeldi* (a CL-responsive species).	Tan 2009
Bulbophyllum hahlianum Schltr. [The marked *Bulbophyllum*]	RK (ca 180 μg /flower) second major component after AA as the largest floral component.	Nishida et al. 2022
Bulbophyllum hortorum J.J. Verm., P. O'Byrne & A.L. Lamb	RK (ca 13 μg /flower), AA and ZN (highly variable quantities) as major floral components.	Katte et al. 2020
Bulbophyllum macranthoides Kraenzl. subspecies *tollenoniferum* (J.J. Sm.) J.J. Verm. [The Macrantha-like *Bulbophyllum*]	RK (ca 16 μg /flower) and ZN as major floral components.	Katte et al. 2020
Bulbophyllum praetervisum J. J. Verm. [The overlooked *Bulbophyllum*]	RK major floral component in three chemotypes – RK (ca 100 *μg*/flower); RK (ca 20 *μg*/flower + ZN; and RK (ca 50 μg /flower) + ME + ZN.	Nakahira et al. 2018; Tan & Tan 2018
Dendobium superbum Rchb. f. (syn. *D. anosmum* Lindl. – a misnomer) [Raspberry jam orchid] Orchidaceae	RK (mean ± s.d. per flower) in petal: 60.4 ± 9.1 *μg*, lip: 15.4 ± 0.6 *μg*, calyx: 20.0 ± 4.0 *μg*. RK present in all 3 Malaysian color varieties.	Nishida et al. 1993
Pinus contorta Douglas [Lodgepole pine or shore pine] Pinaceae	RK and its glucoside (unknown quantity detected in needles of the pine.	(Bauer et al. 1955 & Higuchi et al. 1977) - c/f Borejsza-Wysocki & Hrazdina 1994
Juniperus chinensis L., var. Kaizuka Hort. Cupressaceae	Minor component in leaf ethanolic extract. Male melon flies observed to probe on leaves during SIT program.	Nishida and Iwahashi (unpublished data)
Rheum palmatum L. [Chinese/ ornamental rhubarb] Polygonaceae	RK detected (quantity unknown).	c/f Hokkanen et al. 1980
Rubus chingii Hu [Fu-Pen-zi, Chinese raspberry] Rosaceae	RK present in fruits.	Zhang 2014
Rubus idaeus L. [Raspberry/ Red raspberry]	RK content 3.1; 1.09–4.20 mg/kg in fruits. RK content 3X more in wild than cultivated varieties.	Hokkanen et al. 1980; Larsen et al. 1991; Winter 1961
Scutellaria rivularis Wall. ex Benth. [Skullcaps] Labiatae	RK (quantity unknown) and its glucoside present in fruits.	(Lin & Chou 1984,1985) - c/f Borejsza-Wysocki & Hrazdina 1994
Taxus baccata L. [Common yew, European yew] Taxaceae	RK 135 ± 2.1 ppm.	Fronza et al. 1998, 1999
Vaccinium oxycoccus L. [European cranberry] Ericaceae	RK and its glucoside detected in fruits; berries have RK in trace quantities.	c/f Hokkanen et al. 1980; Hirvi et al. 1981
Vaccinum vitis-idaea L. [Lingonberry or cowberry]	RK detected (quantity unknown).	Hokkanen et al. 2009

* *AA* anisyl acetone, *CL* cue-lure, *RK* raspberry ketone, *ZN* zingerone, *ME* methyl eugenol

quantity relative to that of RK. RK is also detected in minute quantities (<1 μg/kg) from brewed coffee (*Coffea arabica* L.) (Akiyama et al. 2007, 2008); and in petals and sepals of passion fruit as trace quantities (Park et al. 2020). The quantity of RK in raspberries is extremely low (1-4 mg/kg); and natural RK is very expensive for flavouring industries (Milke et al. 2020). To improve production and reduce cost of natural RK, bioengineered candidate genes from raspberry and other plants into bacterial and yeast expression systems yielded significant production of natural RK, up to 5 mg/L (Beekwilder et al. 2007). The biosynthesis of RK in raspberry fruits and its tissue cultures has been investigated, and characterized a RK/ZN synthase which catalyzes the NADHP-reduction of 4-hydroxybenzalacetone to RK and ZN, respectively (Koeduka et al. 2011). Synthesis of natural RK was further improved using a bioengineered strain of a Gram-positive bacterium, *Corynebacterium glutamicum* (Kinoshita et al.) Abe et al., which was able to accumulate up to 99.8 mg/L from *p*-coumaric acid as supplement (Milke et al. 2020). More recently Koeduka et al. (2021) demonstrated the production of RK by redirecting the metabolic flux using tobacco plants, *Nicotiana tabacum*.

Natural anti-oxidant properties of RK have been demonstrated through a) increased total anti-oxidant capacity; b) upregulated anti-oxidant enzymes, e.g. superoxide dismutase and catalase; and c) improved lipid peroxidation. These activities are directly or indirectly linked to RK's other various physiological activities (see review by Lim and Choi 2021). RK prevents obesity and fatty liver in mice (Morimoto et al. 2005); and it enhanced metabolic activity in adipose tissue plus impeded small-intestinal absorption of lipids (Beekwilder et al. 2007). Additionally, RK and hydroxycitric acid from *Garcinia gummi-guta* (L.) N. Robson (syn. *G. camboagia* (Gaertn.) Desr.) have anti-obesity properties in rats; and "nutraceutical agents are extensively promoted and used over the counter to manage obesity" (Attia et al. 2019). Nevertheless, there is inadequate scientific evidence in support of RK being actually an anti-obesity chemical for human to counter obesity; and supplementary-diet containing high RK content "should be consumed with restraint" (Lee 2016).

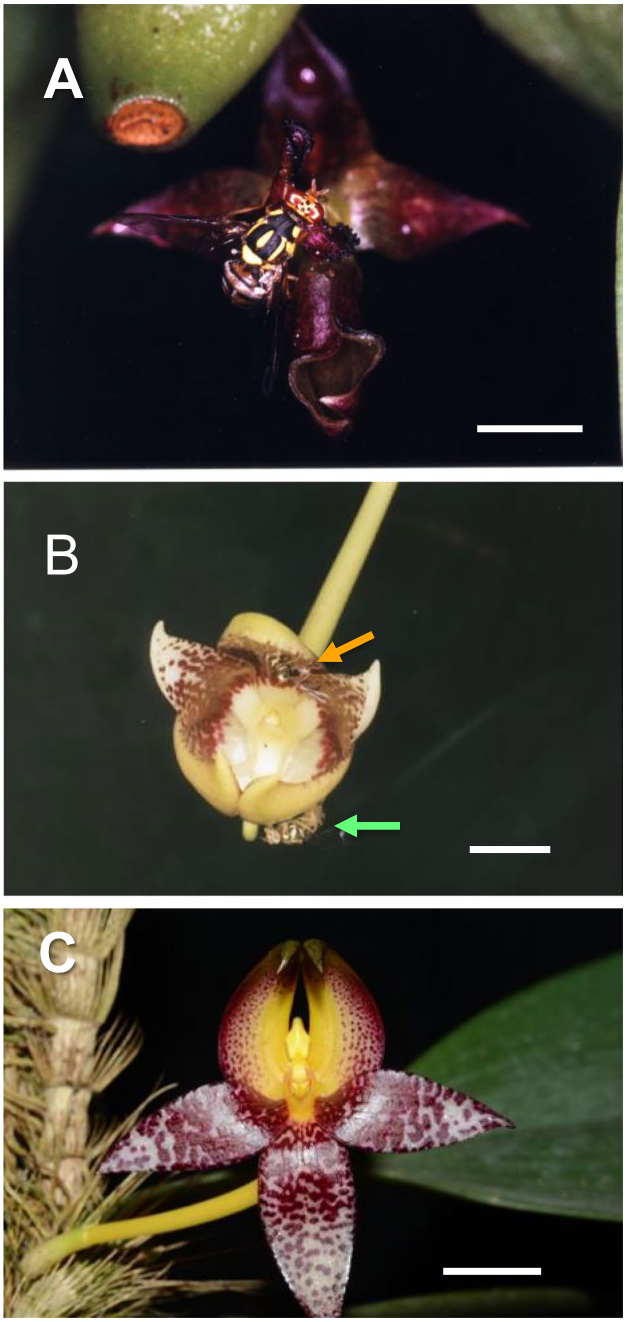

Fig. 5 *Bulbophyllum* flowers emitting raspberry ketone (RK) as a major floral synomone component. [Bar scale = 1 cm]. **A.** *Bulbophyllum ecornutum* (syn. *B. apertum*) subsp. *verrucatum* (Nabawan-ecotype) with a male Zeugodacus caudatus feeding on the small lip. **B.** *Bulbophyllum gerlandianum* (syn. *B. emiliorum*) with two male fruit flies, *Bactrocera frauenfelidi,* on medial sepal (orange arrow), and a *Zeugodacus caudatus* on lateral sepals (green arrow). **C.** *Bulbophyllum praetervisum*

Zingerone [4-(4-hydroxy-3-methoxyphenyl)-2-butanone (CAS RN: 122-48-5)] (other names: 4-hydroxy-3-methoxybenzylacetone; vanillylacetone)

At the turn of the new millennium, ZN was first identified as the attractive component in the flowers of the *Bulbophyllum* orchids e.g. *Bu. patens* King (Fig. 6A), *Bu. macranthoides* Kraenzl subsp. *tollenoniferum*, *Bu. macranthum sensu stricto* (ecotypes ex. Malaysia) (Fig. 6B), *Bu. baileyi* F. Muell. (Suppl. Fig. A), *Bu. cheiri* subsp. *subuliferum* (Schltr.) J.J. Verm., P. O'Byrne & A.L. Lamb (Suppl. Fig. B) and *Bulbophyllum macranthoides* subsp. *tollenoniferum* (J.J. Sm.) J.J. Verm. (Suppl. Fig. C) (Tan & Nishida 2000, 2007; Nakahira et al. 2018; Katte et al. 2020). To date, natural ZN is known to exist mainly in certain orchid flowers and is an important floral synomone component in seven daciniphilous *Bulbophyllum* species (Table 4). It specifically enhances cross-pollination of these orchids by Dacini fruit fly pollinators. Additionally, ZN has also been detected in non-orchid flowers, e.g., *Passiflora maliformis* L. (Passifloracea) and *Semecarpus australiensi* (Anacardiaceae) Engl. (Park et al. 2020, 2022) (Table 4).

The discovery of ZN as a major floral synomone component of *Bu. patens* by Tan and Nishida (2000) was an important landmark in research related to male fruit fly attractants, because ZN's chemical structure has both the functional moieties of RK (with a phenylbutanone) and ME (with a methoxybenzene) and attracts certain species unresponsive to either of the two established attractants. Hence, a new group of ZN-responsive species was identified and to date includes 24 species of Dacini fruit flies attracted exclusively to ZN (Table 5). Furthermore, a group of CL- and ME-responsive species was found to respond, though weakly or moderately, to ZN (Table 6).

Field tests conducted in Penang, Malaysia, showed that ZN was found to weakly attract several CL-responsive species [*B. frauenfeldi* Meijere, *Z. caudatus* Fabricius, *Z. cucurbitae*, *Z. tau* (Walker)] and ME-responsive species [*B. carambolae* Drew & Hancock, *B. dorsalis*, *B. indonesiae* Drew & Hancock, and *B. umbrosa* (Fabricius)] (Tan and Nishida 2000, 2007; Tan et al. 2006). We were initially puzzled as to why we never detected any Dacini fruit fly species, strictly ZN-responsive species, attracted specifically to flowers of local endemic orchids that release floral synomone containing ZN as a major component, until recently. The attraction of *B. pendleburyi* (Perkins), a species known to respond exclusively to ZN, to a daciniphilous *Bulbophyllum* flower, *Bu. cheiri* subspecies *subuliferum* (Schltr.) J. J. Verm. et al. was observed in 2022 in an orchard in Kajang, Selangor, Malaysia, (Fig. 6D – Ong, personal communication; also Table 5). Further field tests in Queensland, Australia, showed ZN to be very attractive to a minor pest species, *B. jarvisi* (Tryon) which is previously known to be a CL-responsive species (Fay 2012). As a result of several recent field studies and area-wide surveys using ZN along with CL and ME as male attractants, there is now a new group of species that are attracted exclusively to ZN (Table 5). It should be noted that all the ZN-responsive species listed in Table 6 belong to the two genera, *Bactrocera* and *Dacus*, without any species from the genus *Zeugodacus*. We are of the opinion that more ZN-responsive Dacini fruit fly species will be found when further in-depth and large scale area-wide surveys are conducted in other tropical and subtropical countries, especially within the Asia-Pacific region, where some endemic plant species whose flowers are known to specifically release ZN as a major floral synomone component.

The fact that both CL-and ME-responders are attracted to ZN may provide circumstantial evidence that ZN might represent the divergent point in i) the evolution of the Dacini fruit fly's responsiveness to the phenylpropanoids and phenylbutanoids, especially ME and RK, respectively; and ii) the co-evolution between daciniphilous *Bulbophyllum* species and the Dacini fruit fly species. The hypothetical perspectives are possibly i) ZN may have evolved to attract both types of flies, convergently; or ii) ZN could be a template or an ancestral compound from which ME and RK would have evolved divergently - through a runaway process, by manipulating the phenylpropanoid/phenylbutanoid synthetic pathway (Tan and Nishida 2000), thereby, need more in depth investigations.

In terms of biological functions related to consumption of ZN by fruit flies, males of *B. dorsalis* biotransform

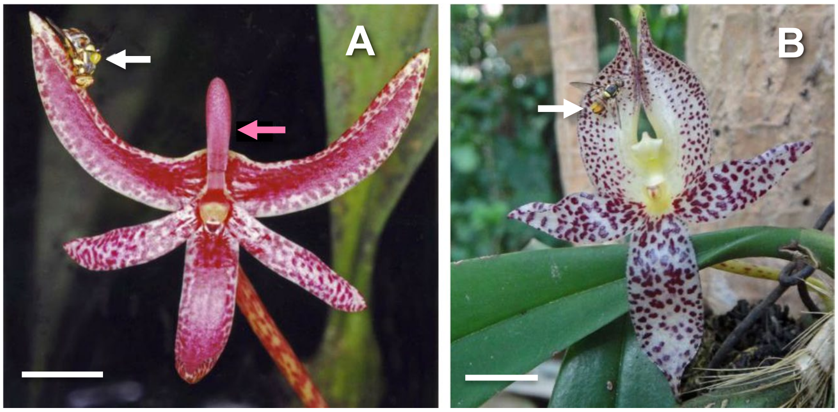

Fig. 6 Zingerone (ZN) as a major floral synomone component in daciniphilous *Bulbophyllum* flowers. [Bar scale = 1 cm]. **A.** *Bulbophyllum patens* with a *Bactrocera dorsalis* (bearing a pollinarium on a lateral sepal - white arrow) which would eventually moved to the see-saw lip (pink arrow) prior to depositing the pollinia when tipped in to the column cavity. **B.** *Bulbophyllum macranthum* (ex Indonesia) with a *Bactrocera dorsalis* (bearing the former's pollinarium on the abdominal dorsum (white arrow) on tips of lateral sepals

ZN to ZL for temporary storage in the rectal gland, while males of *Z. cucurbitae* sequester ZN unchanged into the rectal gland (Tan and Nishida 2000). The respective compounds stored in the male rectal gland are released during courtship to attract conspecific females (Khoo and Tan 2000). Response of *B. jarvisi* males to ZN is at nanogram levels (an ED_{50} of 179 ng), with an olfactory threshold >1600x than to RK (Wee et al. 2018). ZN-feeding, but not RK-feeding, by *Z. tau* males was shown to improve mating performance through enhancement of male courtship activity and sexual signalling (Shamshir and Wee 2019). Likewise, *B. jarvisi* females, when given a choice, preferred to mate with ZN-fed than RK-fed males (Wee and Clarke 2020). However, ZN-fed males of *B. tryoni* in comparison to CL-fed males did not show enhanced mating success (Kumaran et al. 2014a).

From a pharmaceutical perspective, ZN is only found in dried or cooked ginger and *Zingiber* rhizomes oils (Ahmad et al. 2015). The oils with anti-oxidant and anti-microbial properties have been commonly used for preserving foods against microbial spoilage and autoxidation (Singh et al. 2008; El-Baroty et al. 2010; Bellik 2014). The anti-microbial potential of *Zingiber* plant extracts has been demonstrated against both Gram-negative (*Escherichia coli* (Migula) Castellani & Chalmers, *Salmonella typhi* Lignières, *Pseudomonas aeruginosa* (Schröter) Migula, *Klebsiella pneumonia* (Schroeter) Trevisan); and Gram-positive (*Bacillus cereus* Frankland & Frankland, *Staphylococcus aureus* Rosenbach) bacteria (Kumar et al. 2011). The essential oils also possess anti-fungal properties against *Candida glabrata* (H.W. Anderson) S.A. Mey. & Yarrow, and *C. albicans* (C.-P. Robin) Berkhout. ZN also has potent anti-inflammatory, anti-diarrhoeic, anti-diabetic, anti-lipolytic, anti-spasmodic properties (see review by Ahmad et al. 2015).

Combination of Phenylbutanoids in Natural Sources

There are a number of other 4-phenyl-2-butanone type compounds, known as natural products, besides AA, CL, RK, and ZN. Initially, among more than 1000 synthetic compounds under screening, *Z. cucurbitae* males were found to be attracted to benzylacetone (BA, 4-phenyl-2-butanone) (Fig. 1), although BA was proven to be less attractive than AA in field tests (Barthel et al. 1957). Flath and Ohinata (1982) identified BA by a headspace collection of a melon fly-attracting *D. superbum* blossoms before Nishida et al. (1993) characterized RK as the main component to attract *Z. cucurbitae* males. BA has been shown to attract certain potential nocturnal pollinators in coyote tobacco (*Nicotiana atenuata*) flowers (Baldwin et al. 1997).

As noted above, AA, RK and ZN in dacinphilous orchid flowers are often accompanied by their corresponding 2-hydroxy derivatives, namely 4-(4-methoxyphenyl)-2-butanol (AL), 4-(4-hydroxyphenyl)-2-butanol (rhododendrol) (RL), and 4-(4-hydroxy-3-methoxyphenyl)-2-butanol (zingerol) (ZL), respectively, as minor components. AL, RL and ZL were shown to be attractive to *Z. cucurbitae* males to a much lesser degree when compared with the corresponding ketones (i.e. AA, RK and ZN, respectively) (Katte et al. 2020). Furthermore, 4-(4-hydroxy-3,5-dimethoxyphenyl)-2-butanone (proposed common name, syringerone (SN) (Fig. 1) was characterized from a daciniphilous orchid, *Bu. macranthoides* subsp. *tollenoniferum* as a minor component (together with AA, RK and ZN), and this compound did not induce any attractive responses from *Z. cucurbitae* males (Katte et al. 2020). Nonetheless, the individual role of the accompanying minor components in floral fragrances needs further investigation.

Pheromonal Function of Phenylbutanoids in the Sexual Interactions of Fruit Flies

Sex Pheromonal Function

Major components of *Z. cucurbitae* male rectal gland secretions were derivatives of pyrazines and aliphatic amides (Baker et al. 1982), while several aliphatic compounds were detected in the smoke-like fume emitted by males as sex pheromone during courting (Ohinata et al. 1982). The endogenously produced rectal volatiles in a Malaysian strain have six volatiles with ethyl 4-hydroxybenzoate as the major endogenous component; RK was accumulated from feeding on synthetic CL (Nishida et al. 1990). In addition, it was shown that *Z. cucurbitae* males accumulate RK from *D. superbum* flowers for more than six days in the pheromonal gland (Nishida et al. 1993). RK and ZN enhance sexual performance as *Z. cucurbitae* males fed CL-/RK- or ZN-fed attracted significantly more conspecific females than lure-deprived males in the laboratory (Khoo and Tan 2000). Thus, the exogenous source of phenylbutanoids, RK or ZN, plays a vital role in affecting the mating success of *Z. cucurbitae*. Similarly, consumption of ZN also significantly increased male mating success in another CL-responsive species, *Z. tau* (Wee et al. 2020).

In *B. tryoni*, the pheromonal constituents recovered from the rectal gland of lure-deprived flies are six aliphatic amides (Bellas and Fletcher 1979). More females responded to squashed rectal glands extracted from CL-fed males than to glands from control (CL-deprived) males. Furthermore, more females responded to the pheromone of calling CL-fed males than to control males (Kumaran et al. 2014a). However, ZN-fed *B. tryoni* males did not attract more females when compared with ZN-deprived males (Kumaran et al. 2014a). This phenomenon of a male attractant incorporated in to the endogenously produced sex pheromonal components

Table 4 Zingerone (ZN) in plants

Species [Common name] and family	Remark*	Reference
Bulbophyllum baileyi F. Muell. [*Bailey's Bulbophyllum*] Orchidaceae	Quantities of ZN and ZL vary - range 19 - 25 and 1.3 - 4.6 µg per whole flower, respectively. The ratio of floral ZN:ZL is approximately 85:15.	Tan & Nishida 2007
Bulbophyllum ecornutum J. J. Smith (*Syn. B. apertum* Schlechter) subspecies *verrucatum* J.J. Verm., P. O'Byrne and A.L. Lamb – Apin-Apin ecotype	ZN as major floral component in Apin-Apin chemotype while in Nabawan chemotype has RK as major component without any ZN.	Tan et al. 2021
Bulbophyllum hortorum J.J. Verm., P. O'Byrne and A.L. Lamb	ZN (ca 20 µg/flower) with RK as major and AA as minor floral components.	Katte et al. 2020
Bulbophyllum macranthoides Kraenzl. subspecies tollenoniferum (J.J. Sm.) J.J. Verm. [The Macrantha-like *Bulbophyllum*]	ZN (ca 28 µg/flower) as major (with AA and RK as minor) floral components.	Katte et al. 2020
Bulbophyllum macranthum Lindl. [The Large Flowered *Bulbophyllum*]	ZN (ca 25 µg) is the major floral component; and ZL only detected in lateral sepals as a minute component.	Nakahira et al. 2018.
Bulbophyllum patens King [Ginger orchid]	ZN as major with ZL (minor) and ME (traces) floral components. Quantity of ZN 10 - 90 µg per whole flower; and highest concentration of ZN in lip (9.3 µg/10 mg lip (930 ppm).	Tan & Nishida 2000.
Bulbophyllum praetervisum J. J. Verm. [The Overlooked *Bulbophyllum*]	ZN a minor component in 2 of 3 chemotypes (all 3 have RK as the major floral component).	Nakahira et al. 2018
Passiflora maliformis L. [sweet calabash, conch apple, wild purple passionfruit] Passifloracea	ZN and CL in floral parts - ZN 1.10 and 0.12% (CL 0.16 and 1.11%) in inner and outer coronal filaments, resp.	Park et al. 2020
Semecarpus australiensis Engl. [native cashew, tar tree, marking nut, or cedar plum] Anacardiaceae	ZN (< 0.05 µg /flower) was detected in flowers of this species – a native plant of Australia.	Park et al. 2022
Zingiber officinale Roscoe [Ginger] Zingiberaceae	ZN (14.2%) 2nd major component in original aroma of fresh ginger. ZN (5.68%) in fresh ginger rhizome extract; and 7.7% by solvent extract. ZN (ca 9.25%) in 'zingiberis' rhizoma (dried ginger root). Cooking and drying also converts gingerol to ZN.	Menon et al. 2007; Purnomo et al. 2010; Sota et al. 2006;Ahmad et al. 2015; Zhang et al. 2012

[*] *AA* anisyl acetone, *CL* cue-lure, *ZN* zingerone, *ZL* zingerol, *ME* methyl eugenol

Table 5 List of Dacini fruit fly species attracted exclusively to zingerone (ZN): ZN-responsive species – a new group

Name of species	Region & pest status	Reference
Bactrocera abbreviata (Hardy)	Asia. Non-pest.	Leblanc et al. 2018a; Doorenweerd et al. 2020
Bactrocera adamantea Leblanc & Doorenweerd	Vietnam. Non-pest.	Leblanc et al. 2018a
Bactrocera bipustulata (Bezzi)	Asia-Pacific. Non-pest.	Doorenweerd et al. 2018
Bactrocera clarifemur Leblanc & Doorenweerd	Vietnam. Non-pest.	Leblanc et al. 2018a
Bactrocera connecta Leblanc & Doorenweerd	Vietnam. Non-pest.	Leblanc et al. 2018a
Bactrocera ernesti Leblanc & Doorenweerd	Vietnam. Non-pest.	Leblanc et al. 2018a
Bactrocera kolombangarae Leblanc & Doorenweerd	Solomon Islands – Kolombangara, forest.	Leblanc et al. 2021
Bactrocera neoaglaiae Drew & Romig	Papua New Guinea. Non-pest.	Drew & Romig 2022
Bactrocera noboynyi Drew & Romig	Papua New Guinea. Non-pest.	Drew & Romig 2022
Bactrocera pagdeni (Malloch)	Leblanc et al. 2021	Leblanc et al. 2021
Bactrocera pendleburyi (Perkins)	Asia. Non-pest.	Leblanc et al. 2018a; Doorenweerd et al. 2020; Ong (unpublished)
Bactrocera perigrapha White & Tsuruta	Asia-Pacific. Non-pest.	Doorenweerd et al. 2018
Bactrocera rubigina Wang & Zhao	Asia-Pacific. Non-pest.	Leblanc et al. 2018a; Doorenweerd et al. 2018
Bactrocera satanas (Hering)	Vietnam. Non-pest.	Leblanc et al. 2018a
Bactrocera syzygii White & Tsuruta	Asia. Non-pest.	Leblanc et al. 2018a, b; Doorenweerd et al. 2020
Bactrocera tsatsiai Leblanc & Doorenweerd	Solomon Islands – Guadalcanal, forest.	Leblanc et al. 2021
Bactrocera vargasi Leblanc & Doorenweerd	Solomon Islands - Kolombangara, forest.	Leblanc et al. 2021
Bactrocera wilhelmiae Drew & Romig	Papua New Guinea. Non-pest.	Drew & Romig 2022
Dacus ancoralis Leblanc & Doorenweerd	Sri Lanka. Non-pest.	Leblanc et al. 2018b
Dacus aneuvittatus (Drew)	New Caledonia. Non-pest	Royer et al. 2019
Dacus bimaculosus Drew & Romig	Papua New Guinea. Non-pest.	Drew & Romig 2022
Dacus satanas Hering	Asia-Pacific. Non-pest.	Leblanc et al. 2018a; Doorenweerd et al. 2018
Dacus trimacula Wang	Asia-Pacific. Non-pest.	Doorenweerd et al. 2018
Dacus vijaysegarani Drew & Hancock	Asia-Pacific. Non-pest.	Doorenweerd et al. 2018

probably indicates that *B. tryoni* is strictly a CL-/RK- responsive species, and the weak response to ZN may be an ancestral trait in the effectiveness of male sex pheromone.

Aggregation Pheromone and Lek Formation

Leks in Dacini fruit fly species generally consist of 2-10 males (Shelly 2018) as reported for *B. dorsalis* (Shelly and Kaneshiro 1991) and *Z. cucurbitae* (Iwahashi and Majima 1986; Mir and Mir 2016). For *B. carambolae* males, ME is converted to *E*-coniferyl alcohol; while for *B. dorsalis,* ME is converted mainly to 2-allyl-4,5-dimethoxyphenol and *E*-coniferyl alcohol, for storage in the pheromonal gland. *E*-coniferyl alcohol attracts conspecific males of the two species, while the dimethoxyphenol is a strong male attractant for *B. dorsalis* males, as potent as ME (Nishida et al. 1988; Tan and Nishida 1996). Thus, when released as pheromonal components, they act as an aggregation pheromone to attract other males, especially males deprived of ME to form a lek in a field cage (Wee et al. 2007). Furthermore, a previously deprived and marked *B. carambolae* male was shown to approach the anal section of a ME-fed male that had just begun copulating, after releasing sex pheromone with an attracted conspecific female (Wee et al. 2007). Likewise, although not much research has been conducted on CL-responsive species, males generally sequester phenylbutanoid attractants in the pheromonal gland in the form of either RK or ZN (as mentioned above for the potent natural phenylbutanoid attractants). For *Z. cucurbitae,* when released as a component in the aggregation pheromone, either RK or ZN would attract other conspecific males to form a lek. As mentioned previously, rectal volatiles are released by males during courtship at dusk that act as a sex and aggregation pheromone (Kuba and Sokei 1988), and the aggregation pheromone attracts other conspecific males to form a 'lek' (Kuba et al. 1984). A nonresourced-based lek mating system was presumed to occur in the Queensland fruit fly, *B. tryoni* (Ekanayake et al. 2017). To clarify and confirm that lek formation in Dacini fruit fly species, for CL-responsive species particularly *B. tryoni* and *Z. cucurbitae*, is probably the result of a resource-based lek mating system, i.e. to obtain phenylbutanoid(s) to compliment male sex pheromonal component(s) synthesized endogenously. Further investigations need to be conducted to determine i) males display lek

Table 6 List of cue-lure (CL)- and methyl eugenol (ME)-responsive Dacini fruit fly species also attracted to zingerone (ZN)

Name of species	Region & pest status	Lures	Reference
Bactrocera abdomininigra	Asia-Pacific. Non-pest.	CL & ZN	Leblanc et al. 2021
Bactrocera aeroginosa (Drew & Hancock)	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera albistrigata (Meijere) (syn to *B. freunfeldi*)	South East Asia. Fruit pest.	CL & ZN	Tan and Nishida 2007; Nakahira et al. 2018
Bactrocera aglaiae (Hardy)	Australia. Non-pest.	CL & ZN	Fay 2012; Royer et al. 2020
Bactrocera alyxiae (May)	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera atramentata (Hering)	Asia-Pacific. Fruit pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera aurea (May)	Australia. Non-pest.	CL & ZN	Fay 2012; Royer et al. 2020
Bactrocera bipustulata (Bezzi)	Southern India. Non-pest.	CL & ZN	LeBlanc et al. 2019
Bactrocera breviaculeus (Hardy)	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera bryoniae (Tryon)	Asia-Pacific. Fruit pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera caccabata Drew & Romig	Papua NewGuinea. Non-pest.	CL & ZN	Drew & Romig 2022
Bactrocera carambolae Drew & Hancock	Asia-Pacific. Fruit pest.	ME & ZN	Tan & Nishida 2000, 2007; Doorenweerd et al. 2018
Bactrocera digressa Radhakrishnan	Asia. Non-pest.	CL & ZN	Leblanc et al. 2019
Bactrocera dorsalis (Hendel)	Asia-Pacific. Fruit pest.	ME & ZN	Tan & Nishida 2000, 2007; Nakahira et al. 2018
Bactrocera frauenfeldi (Schiner)	Asia-Pacific. Fruit pest.	CL & ZN	Royer et al. 2017, 2020; Wee et al. 2020
Bactrocera fulvifacies (Perkins)	New Caledonia. Non-pest.	CL & ZN	Royer et al. 2019
Bactrocera fuscitibia Drew & Hancock	Asia-Pacific. Fruit pest	CL & ZN	Doorenweerd et al. 2020
Bactrocera illusioscutellaris Drew & Romig	Vietnam. Non-pest.	CL & ZN	Leblanc et al. 2018a
Bactrocera indonesiae Drew & Hancock	Asia-Pacific. Non-pest.	ME & ZN	Tan & Nishida 2007; Doorenweerd et al. 2018
Bactrocera jarvisi (Tryon)	Asia-Pacific. Fruit pest.	CL & ZN	Fay 2012; Doorenweerd et al. 2018; Royer et al. 2020
Bactrocera murrayi (Perkins)	Asia-Pacific. Fruit pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera mesonotochra Drew	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera moluccensis (Perkins)	Asia-Pacific. Fruit pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera neohumeralis (Hardy)	Asia-Pacific. Fruit pest.	CL & ZN	Royer et al. 2017; Doorenweerd et al. 2018
Bactrocera niogreta Doorenweerd	Asia. Non-pest.	CL & ZN	Doorenweerd et al. 2020
Bactrocera rufofuscula (Drew & Hancock).	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera silvicola (May)	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera splendida (Perkins)	Indonesia. Non-pest.	CL & ZN	Doorenweerd et al. 2020
Bactrocera tigrina (May)	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Bactrocera trivialis (Drew)	Asia-Pacific. Fruit pest.	CL & ZN	Royer et al. 2017; Doorenweerd et al. 2018
Bactrocera tryoni (Froggatt)	Asia-Pacific. Fruit pest.	CL & ZN	Doorenweerd et al. 2018; Royer et al. 2020
Bactrocera umbrosa (Fabricius)	Asia-Pacific.-Artocarpus fruit pest.	ME & ZN	Tan & Nishida 2007; Nakahira et al. 2018
Dacus absonifacies (May)	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Dacus aequalis Coquillett	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Dacus aneuvittatus (Drew)	New Caledonia. Non-pest.	CL & ZN	Royer et al. 2019
Dacus axanus (Hering)	Asia-Pacific. Cucurbit fruit pest.	CL & ZN	Royer et al. 2017; Doorenweerd et al. 2018
Dacus bellulus Drew & Hancock	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Dacus durbanensis Munro	Africa. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Dacus frontalis Becker	Africa. Cucurbit fruit pest.	CL & ZN	Doorenweerd et al. 2018
Dacus jacobi David & Sachin	Asia. Non-pest.	CL & ZN	Leblanc et al. 2021
Dacus pedunculatus (Bezzi)	Indonesia. Non-pest.	CL & ZN	Doorenweerd et al. 2020
Dacus pullus (Hardy)	Indonesia. Non-pest.	CL & ZN	Doorenweerd et al. 2020
Dacus secamoneae Drew	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Dacus tenebrosus Drew & Hancock	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018.
Dacus trimacula Wang	Asia-Pacific. Non-pest.	CL & ZN	Doorenweerd et al. 2018
Zeugodacus caudatus (Fabricius)	Asia-Pacific. Non-pest.	CL & ZN	Tan & Nishida 2000; Nakahira et al. 2018

Table 6 (continued)

Name of species	Region & pest status	Lures	Reference
Zeugodacus cucurbitae (Coquillett)	Asia-Pacific. Cucurbit fruit pest.	CL & ZN	Tan & Nishida 2000; Nakahira et al. 2018; Doorenweerd et al. 2018
Zeugodacus heinrichi (Hering)	Asia-Pacific. Non-pest.	CL & ZN	Leblanc et al. 2018a; Doorenweerd et al. 2018
Zeugodacus hochii (Zia)	Asia-Pacific. Cucurbit fruit pest.	CL & ZN	Leblanc et al. 2018a; Doorenweerd et al. 2018
Zeugodacus strigifinis (Walker)	Australia & PNG. Pest of pumpkin and zucchini flowers.	CL & ZN	Royer et al. 2020
Zeugodacus tau (Walker)	Asia-pacific. Pumpkin flower pest.	CL & ZN	Tan & Nishida 2000; Nakahira et al. 2018
Zeugodacus triangularis (Drew)	Asia-Pacific. Cucurbit flower pest.	CL & ZN	Royer et al. 2017; Doorenweerd et al. 2018

behavior dependent or independent of obtaining the relevant phenylbutanoid attractant (RK/ZN); and ii) the actual pheromonal components released by males (to compare RK-/ZN-fed and deprived) during courtship and/or male fanning activity e.g. via headspace-gas chromatography-mass spectrometry (GC/MS) analyses.

Allomonal Function of Phenylbutanoids in Prey-Predator Interactions

Asian house gecko, *H. frenatus* consumed significantly fewer houseflies topically treated with RK (at 5 µg/fly) than controls (untreated houseflies) (Tan 2000b). In contrast, ME imbibed by *B. dorsalis* males is converted to two ME-analogues which strongly deter vertebrate predation (mentioned under allomone in item I above). Although, a major rectal pheromone gland component of *Z. cucurbitae*, 1,3-nonanediol, produced endogenously, is a potent allomone against vertebrate predator (Tan 2000b). The quantity of the sex pheromonal component stored in the pheromonal (rectal) gland increased significantly with age, beginning with sexual maturity about two weeks after adult eclosion (Nishida et al. 1990, 1993). Synthetic 1,3-nonanediol when applied topically to the thorax of the common housefly, *Musca domestica* L, at a dosage of 80-320 ng/fly, significantly reduced consumption by the Asian house gecko (Tan 2000b). Therefore, *Z. cucurbitae* males, after consumption of RK, probably induced a synergistic effect for the endogenously synthesized pheromonal components to deter predation by lizards. Whether this allomonal phenomenon also occurs in other phenylbutanoid-responsive species after consuming either RK and/or ZN (a known natural pungent tasting irritant – Ahmad et al. 2015) may be more significant in the natural ecosystem needs further investigations.

Synomonal Function of Phenylbutanoids in Fruit Fly-Orchid Interactions

Flowers of a number of orchid species in the genus *Bulbophyllum* selectively attract certain Dacini fruit fly species for pollination with specific fragrances in the tropical rain forests of Asia-Pacific and Oceanian regions. These synomonal components are either phenylpropanoids (mainly ME, see I-2C) or phenylbutanoids (AA, RK and ZN, often acompanied by their corresponding analogs, AL, RL and ZL respectively) as listed in Tables 1, 3 and 4, respectively. The relative concentrations of the synomonal component(s) are usually highest in the lip to lure a pollinator fly into a right alignment prior to conducting pollination.

Three important points related to the role of phenylbutanoid attractants in the mutualistic interactions between Dacini fruit flies and daciniphilous *Bulbophyllum* flowers are:

A) As each flower produces only one pollinarium (bearing four pollinia for most daciniphilous *Bulbophyllum* species), regardless of the number of attracted flies to a flower, only one of the few flies initially attracted, if not the first fly, would eventually remove the only pollinarium. The fly would probe on the dynamic floral lip or slip on to the lip (for species belonging to the *Bu. macranthum* species complex while probing on the lateral sepals) and eventually be catapulted into the floral column, and ultimately, would remove the floral pollinarium to initiate pollination.
B) The placement of pollinarium on either abdominal or thoracic dorsum of a potential fruit fly pollinator does not depend entirely on the type of floral attractant/synomone but the placement is entirely dependent on the floral structure and posture.
C) Generally, for daciniphilous *Bulbophyllum* flowers the floral emission of synomone occurs, over a relatively short period (1-3 days), during the day-time when the male flies are most active in foraging for specific attractant(s).

Pertaining to the above item (B), the placement of pollinarium on an attracted fly is entirely dependent on the floral structure and dynamic lip mechanism to temporarily trap a fly - i.e. depending on floral natural posture either as a non-resupinate or a resupinate flower (Tan and Nishida 2015). The entrapment lip mechanism plays an essential and vital role in pollinarium removal. When an attracted male fly is forcibly tipped in to the column cavity a) head first, then pollinarium would invariably be stuck to the thoracic dorsum e.g. *Z. cucurbitae* male removed from *Bu. patens* (Figs. 6A and 7A); and *Z. cucurbitae* and *Z. hochii* males removed pollinarium from *Bu. hortorum* (Tan et al. 2023); and b) backward abdomen first, then pollinarium would certainly be attached to the abdominal dorsum when removed e.g. a male *B. dorsalis* attracted to floral ZN of, and removing pollinarium from *Bu. macranthum* sensu stricto (Fig. 7B) (Nakahira et al. 2018); and males of two other CL-responsive Dacini species (mentioned above) removing pollinarium from *Bu. praetervisum* that releases RK as floral synomone (Tan and Tan 2018)

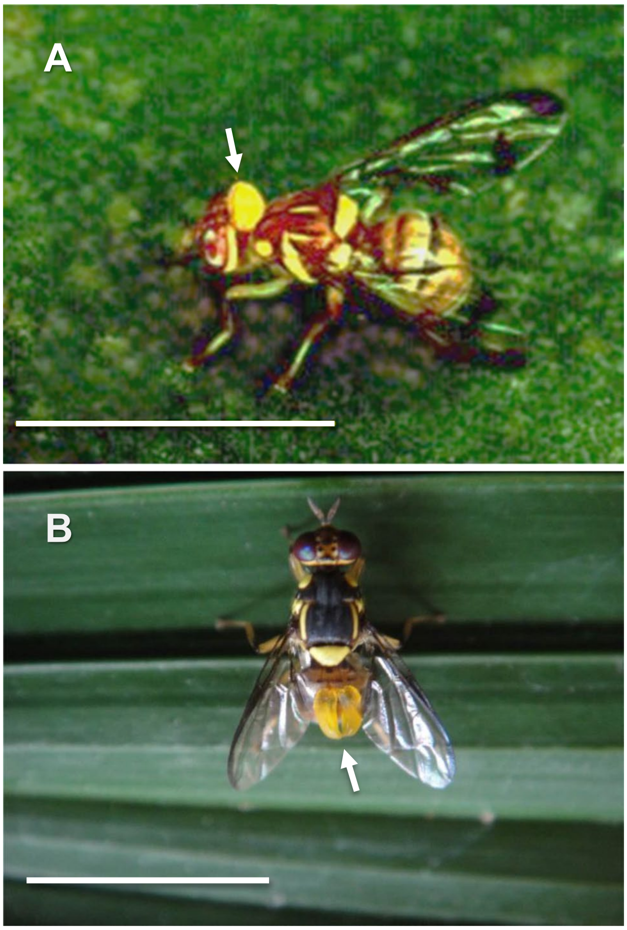

Fig. 7 Pollinarium (arrow) attachment on potential pollinators - either on thoracic or abdominal dorsum of Dacini fruit flies. [Bar scale = 1 cm]. **A.** Pollinarium of *Bulbophyllum patens* (with zingerone as floral synomone) on thoracic dorsum of a melon fly, *Zeugodacus cucurbitae*. **B.** Pollinarium of *Bulbophyllum macranthum* (with zingerone as floral synomone) on the abdominal dorsum of an oriental fruit fly, *Bactrocera dorsalis* (a methyl eugenol responsive species but weakly attracted to zingerone)

Natural Phenylbutanoids in Pest Management of Dacini Fruit Fly Pest

Detection, monitoring, surveillance. trapping plus control/management techniques, especially male annihilation technique (MAT), for Dacini fruit fly pests, particularly *Z. cucurbitae* and *B. tryoni*, have been reviewed via using mainly CL/RK baited traps (Vargas et al. 2010, Shelly et al. 2014, Tan et al. 2014). Recently, sterile *B. tryoni* males when fed with RK prior to release showed a) significantly reduced captures in CL-baited traps and b) higher post-release survival in the field when compared with unfed (control) males (Khan et al. 2017). Furthermore, sterile males, previously fed with RK at the sexually-immature adult stage, showed reduced attraction to CL probably due to a consequence of modified expression of genes responsible for chemoreception (Khan et al. 2021). These findings may allow simultaneous application of the sterile insect technique (SIT) and the MAT, which may be more effective than sequential use of the two techniques (Barclay and Hendrichs 2014) – both the techniques are inherently incompatible management tools, thereby, considered as an effective integrated management program against *B. tryoni* (Khan et al. 2017).

Conclusion

The natural occurrence of each of the phenylbutanoid attractants - AA, CL, RK and ZN – in a relatively small number of plant species under several families is listed separately in this review. The distribution of the phenylbutanoids varies greatly within a species according to growth stage or locations or physiological stage as well as time of day, especially among floral parts. The natural role of the phenylbutanoids as antimicrobial and pollinating agents have been highlighted. Particularly, their vital role as floral synomones to exclusively attract Dacini fruit fly males as potential pollinators for many daciniphilous orchid species. More research should be conducted to fully understand the biochemical, physiological and chemoecological basis, mediated by individual or combination of phenylbutanoid attractants, so that we can improve the pest management techneques of those destructive pest species. It will further enlighten the true mutualistic interactions between plants and insects, especially between certain Dacini fruit fly species, pest and/or non-pest, and the daciniphilous *Bulbophyllum* species, often endangered due to deforestation, in the natural tropical forest/jungle ecosystems.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of Interest The authors sincerely declare that there is no conflict of interests.

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