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REVIEW

Roles of flower scent in bee–flower mediations: a review

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Background: Bees and flowering plants associations were initially began during the early Cretaceous, 120 million years ago. This coexistence has led to a mutual relationship where the plant serves as food and in return, the bee help them their reproduction. Animals pollinate about 75% of food crops worldwide, with bees as the world's primary pollinator. In general, bees rely on flower scents to locate blooming flowers as visual clue is limited and also their host plants from a distance. In this review, an attempt is made to collect some relevant 107 published papers from three scientific databases, Google Scholar, Scopus, and Web of Science database, covering the period from 1959 to 2021.
Results: Flowering plants are well documented to actively emit volatile organic compounds (VOCs). However, only a few of them are important for eliciting behavioral responses in bees. In this review, fifty-three volatile organic compounds belonging to different class of compounds, mainly terpenoids, benzenoids, and volatile fatty acid derivatives, is compiled here from floral scents that are responsible for eliciting behavioral responses in bees. Bees generally use honest floral signals to locate their host plants with nectar and pollen-rich flowers. Thus, honest signaling mechanism plays a key role in maintaining mutualistic plant–pollinator associations.
Conclusions: Considering the fact that floral scents are the primary attractants, understanding and identification of VOCs from floral scent in plant-pollinator networks are crucial to improve crop pollination. Interestingly, current advances in both VOCs scent gene identification and their biosynthetic pathways make it possible to manipulate particular VOCs in plant, and this eventually may lead to increase in crop productivity.

Keywords: flowering plant, pollination, bees, flower scent, honest floral signal

Introduction

Animal pollinators are responsible for aiding over 80% of the world's flowering plants to reproduce, including 75% of all crops, and about 35% of the world's food crop (Klein et al. 2007; Potts et al. 2016). Among them, bees (Hymenoptera, Apoidea), are considered as the most important pollinator. They are characterized by their high degree of diversity, with about 20000 species worldwide (Michener 2007). Bees can be broadly grouped as either specialists or generalists depending on the diversity of floral resources they forage from. Specialist bees account 20%–30% bee species, collecting pollen from members of a single plant family or a genus (oligolectic) (Minckley and Roulston 2006), whereas most bees are generalist bees, which collect pollen from a broad variety of plant species belonging to various families (Cane and Sipes 2006). Honeybees, bumblebees and many mason bees, including *Osmia lignaria* are some of the bees that categorize under generalist (Chittka and Wells 2004; Lunau and Maier 1995).

Mutual coexistence between insects and flowering plants for over 120 million years has led to a mutual relationship where the plant serves as food and in return the insect help them with their reproduction (Bascompte 2019; Engel 2000; Poinar and Danforth 2006). Pollinators, particularly bees learn associations between floral features (scent, color, shape, texture, and other floral signals) and the reward (nectar and pollen), and use these effectively to locate their host flowering plants (Clarke et al. 2013; Muth et al. 2016; Whitney et al. 2009). For these interactions, each part has evolved differential adaption to enhance the performance (Fig. 1). Olfactory cues are often of major importance to bees to make flower choices, because olfactory cues are easily learned and remembered by pollinators (Wright and Schiestl 2009). Olfactory cues are also important when visual signal is limited, such as foraging on night-blooming

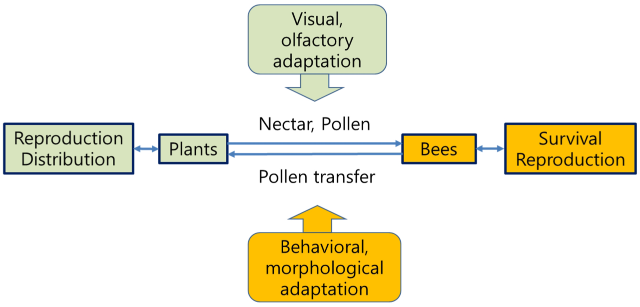


Fig. 1 Schematic diagram showing the interaction of bee-flower interaction and adaptation to enforce the interaction.

flowers and to locate their host plants from a distance (Raguso et al. 2003; Raguso and Willis 2002). In return, pollinators are equipped with behavioral and morphological adaptions to better serve the plant needs.

The notion that volatiles emitted by the plants mediate communication between plants and animals has long been acknowledged (Fraenkel 1959). The idea of volatile compounds mediation has been entertained since then by many other studies (Dötterl et al. 2014; Cheng et al. 2019; Knudsen et al. 2006). In general, flowering plants emit volatile organic compounds (VOCs), which are diverse and very complex. VOCs are lipophilic in nature, and possess high vapor pressure at ambient temperatures, as they are composed of low molecular weight. Indeed, plants belonging to 90 families have been reported to possess over 1700 individual volatile organic compounds (Knudsen et al. 2006). The composition of floral VOCs depend on many factors, including flower age, plant genotype, pollination status and others (Rodriguez-Saona et al. 2011; Klatt et al. 2013; Cheng et al. 2019). Previous studies showed that bees, especially honeybees and bumblebees, possess the capability to differentiate between individual and blends of VOCs (Laloi and Pham-Delègue 2004; Paldi et al. 2003; Wright et al. 2002).

Pollinators have a set of behavioral preferences, both innate and learned. Although naïve bees possess innate preferences for some floral signals, bees have a quick ability to learn association between volatile component(s) and food rewards (Milet-Pinheiro et al. 2013; Raguso 2008). Associative learning preference are largely beneficial for the pollinator because it has been credited to rapid floral diversification in both floral signals and floral rewards (Schiestl and Johnson 2013). Several studies over the years have indicated the importance of olfactory cues in bee-flowering plants interactions (Raguso 2008; Williams 1983). Bees possess one of the highest number of chemoreceptors (e.g., honey bees = 170; fruit flies = 62; mosquitoes = 79) in the insect kingdom that make them superior to recognize diverse floral odors (Robertson and Wanner 2006).

VOCs produced by the plants may have a wide variety of biological activities, such as antibacterial, antifungal (Hammer et al. 2003; Huang et al. 2012) and repellent activities against florivores (Junker et al. 2011). Given the vital role of effective pollination to many important crop yields, the pollinators of such crops are also linked to their VOCs of the floral scents. To this end, in this review, we compile fifty-three VOCs that mediate between bees and their flowering plant host.

Literature collection

In this review, an attempt is made to collect all relevant papers from three scientific databases (Google Scholar, Scopus, and Web of Science database), covering the period from 1959 to 2021. The following search terms were used: "flower scent", "bee pollination"; "bee-flower scent interaction", "flower volatile composition"; "honest floral signal". Additional articles were also identified from the first search reference lists. From this search, we listed 53 VOCs compounds (Table 1) from 107 published papers.

Results

Flower scents

Bees in general pollinate a wide variety of plants that differ in floral morphology (size, shape), color, and scent. Understanding of floral scents are key in bee-plant pollination network as bees heavily rely on floral scents to locate their host plants (Endress 1996; Proctor et al. 1996). Flowers can emit a variety of odor blends, which can be learned and recognized by their visiting pollinators (Dobson 2006). Flowering plants are well recognized to actively emit specific floral scent signals to attract pollinators (Knudsen et al. 2006; Williams 1983). In this review, an attempt is made to compile fifty-three volatile organic compounds (Table 1) from floral scent that are responsible for eliciting behavioral responses in bees. These VOCs belongs to different class of compounds, mainly terpenoids, benzenoids and volatile fatty acid.

Terpenoids

Terpenoids comprise structurally diverse and the largest class of plant secondary metabolites present in all living organisms, particularly in flowering plants (Pichersky and Raguso 2018). In addition to attracting pollinators, terpenoids also play crucial role in plant's defense against herbivorous (Abbas et al. 2017). Terpenoids presented over 50000 well known naturally produced compounds across all kingdom of life (Belcher et al. 2020). Isopentenyl diphosphate and dimethylallyl diphosphate, the two building blocks for terpenoid biosynthesis, are generally synthesized via two pathways: the mevalonate pathway (Liao et al. 2016) and the 2-*C*-methyl-D-erythritol 4-phosphate pathway (Rohmer 1999) (Fig. 2). Terpenoids are largely biosynthesized and stored in plant tissues with specialized structures such as secretory cavities, resin canals, latex canals,

Table 1 Some floral plant and their volatile organic compounds that elicit response in bees

Volatile organic compounds	Plant source	Bee species	References
2-phenylethanol (18)^{B}; 4-oxoisophorone (44)^{C}; (*3E,6E*)-α-farnesene (45)^{T}; (6Z,9Z)-heptadecadiene (28)^{F}; (*8Z*)-heptadecene (29)^{F}; Nonanal (30)^{F}	*Actinidia deliciosa* (kiwifruit)	Honeybees (*Apise mellifera*)	Tatsuka et al. 1990; Twidle et al. 2015
α-farnesene (41)^{T}; *p*-anisaldehyde (42)^{B}; Acetophenone (43)^{B}; Phenylacetaldehyde (40)^{B}	*Brassica rapa*	Bumble bee (*Bombus terrestris* L.)	Knauer and Schiestl 2015
β-ocimene (1)^{T}; (*E,E*)-α-farnesene (45)^{T}; 1*H*-indole (38)^{N}; 2-phenylethyl acetate (12)^{B}; 2-phenylethanol (18)^{B}; 6,10,14-trimethyl-2-pentadecanone (31)^{F}; Benzaldehyde (23)^{B}; Linalool (2)^{T}; Phenylacetaldehyde (40)^{B}	*Brassica* spp.	Honeybees (*Apise mellifera*)	Kobayashi et al. 2012
1,6-dioxaspiro[4.5]decane (33)^{S}; E-7-methyl-1,6-dioxaspiro[4.5]decane (34)^{S}; E-2-methyl-1,7-dioxaspiro[5.5]undecane (35)^{S}; E-7-ethyl-1,6-dioxaspiro[4.5]decane (36)^{S}	*Campanula trachelium*	Campanula-specialist bee (*Chelostoma rapunculi*)	Milet-Pinheiro et al. 2013
1-octanol (19)^{F}; 2-phenylethanol (18)^{B}	*Campomanesia phaea*	Nocturnal bees (*Megalopta* spp.; *Ptiloglossa* spp.)	Cordeiro et al. 2017
p-anisaldehyde (42)^{B}; Benzaldehyde (23)^{B}; Phenylacetaldehyde (40)^{B}	*Cirsium arvense* (Canada thistle)	Honeybees and *Lasioglossum*	Theis 2006
1,2,4-trimethoxybenzene (46)^{B}	*Cucurbita* spp.	*Peponapis pruinosa* (North American squash bee)	Andrews et al. 2007
β-ocimene (1)^{T}; β-pinene (11)^{T}; Linalool (2)^{T}	*Gongora* spp.	Orchid bees (Euglossini)	Hetherington-Rauth and Ramírez 2016
p-methoxyanisole (24)^{B}	*Hydrocleys martii* (aquatic plants)	Oligolectic bees (*Protodiscelis palpalis)*	Carvalho et al. 2014
Benzyl acetate (13)^{B}	*Masdevallia lehmannii*	Euglossine bees	Gerlach and Schill 1991
2-tridecanone (25)^{F}; Diacetin (27)^{G}; Heptanoic acid (26)^{F}	*Lysimachia* spp.	*Macropis fulvipes* (Oil-collecting bees)	Schäffler et al. 2015
cis-3-hexenyl acetate (32)^{F}; Linalool (2)^{T}; Methyl salicylate (16)^{B};	*Medicago sativa* (alfalfa)	Honeybees (*Apise mellifera*)	Henning and Teuber 1992
E,E-farnesol (3)^{T}; *E,E*-farnesyl hexanoate (9)^{T}; Nonanoic acid (10)^{T}	*Ophrys sphegodes* (spider-orchid)	Solitary bee (*Andrena nigroaenea)*	Ayasse et al. 2000; Schiestl and Ayasse 2001
β-ocimene (1)^{T}; Linalool (2)^{T}	*Paullinia cupana* (guarana)	Nocturnal bee (*Megalopta* spp.)	Krug et al. 2018
Protoanemonin (39)^{L}	*Ranunculus* spp.	Chelostoma bees	Dobson and Bergström 2000
β-ocimene (1)^{T}; 2-phenylethyl acetate (12)^{B}; 2-phenylethanol (18)^{B}; Methyl 2-methoxybenzoate (47)^{B}; Methyl 4-methoxybenzoate (48)^{B}; Methyl nicotinate (38)^{N}	*Raphanus sativus* (radish)	Honeybees (*Apise mellifera*)	Kobayashi et al. 2012
1,4-dimethoxybenzene (24)^{B}	*Salix* spp.	Oligolectic bee (*Andrena vaga)*	Tollsten and Knudsen 1992; Dötterl et al. 2005

Table 1 Continued

Volatile organic compounds	Plant source	Bee species	References
β-pinene (11)^T; Limonene (49)^T	*Salvia* spp.	*Lasioglossum* spp.; *Xylocopa violacea*	Giuliani et al. 2020
1,8-cineole (20)^T; 2-phenylethyl acetate (12)^B; Benzyl acetate (13)^B; *p*-cresol (50)^B; *p*-cresyl acetate (51)^B; Methyl benzoate (14)^B; Methyl cinnamate (15)^B; Methyl salicylate (16)^B; Vanillin (17)^B	*Stanhopeinae* spp.	Orchid bees (Euglossini)	Williams and Whitten 1983
Anethole (52)^B	Synthetic compounds	Honeybees (*Apise mellifera*)	Allsopp and Cherry 1991
Benzyl acetate (13)^B; Eucalyptol (20)^T; Eugenol (21)^B; Methyl salicylate (16)^B; Skatole (22)^B; Vanillin (17)^B	Synthetic compounds	Nocturnal bee (*Megalopta aegis; Megalopta amoena; Megalopta guimaraesi*)	Knoll and Santos 2012
(*E*,*E*)-farnesol (3)^T; (*Z*)-citral (4)^T; Geranic acid (5)^T; Geraniol (6)^T; Nerol (7)^T; Nerolic acid (8)^T	Synthetic compounds	Honeybees (*Apise mellifera*)	Williams et al. 1981

Structure numberings are in parenthesis. Class of compounds are also represented by letter in superscript: B, benzenoids; C, cyclohexenones; F, volatile fatty acid derivatives; L, lactone; N, nitrogen containing compounds; S, spiroacetals; T, terpenoids

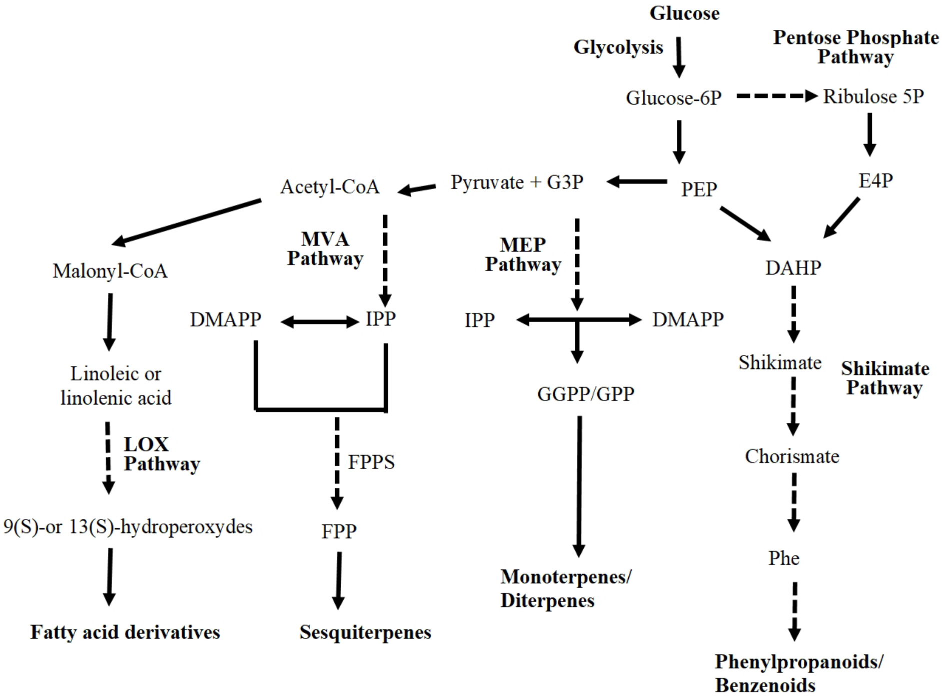


Fig. 2 Schematic representation of the floral scent biosynthesis pathways. Dotted arrows represent multistep pathways, and bidirectional arrows indicate reversible reactions. MVA, mevalonic acid; MEP, methylerythritol phosphate; LOX, lipoxygenase; PEP, phosphoenolpyruvate; G3P, glyceraldehyde-3-phosphate; E4P, erythrose 4-phosphate; DMAPP, dimethylallyl pyrophosphate; FPPS, farnesyl pyrophosphate synthase; FPP, farnesyl pyrophosphate; GGPP, geranylgeranyl pyrophosphate; GPP, geranyl pyrophosphate; IPP, isopentenyl pyrophosphate; DAHP, 3-deoxy-D-arabinoheptulosonate-7 phosphate; Phe, phenylalanine. Modified from the article of Ramya et al. (2017).

glandular trichomes (Holopainen et al. 2013).

Floral scents of many flowering species are dominated by terpenoids (Fig. 3), which are known to attract generalist bees, including in *Chamaedora linearis* (Knudsen et al. 2001), *Ranunculus acris* (Bergström et al. 1995) and *Rubus idaeus* (Robertson et al. 1995). Among the terpenoids, *trans*-β-ocimene (1) is the most crucial VOC that serves as a general pollinator attractant (Farré-Armengol et al. 2017). It was also noted that 47.5% of the 291 plant species investigated was found to possess *trans*-β-ocimene (Farré-Ar-

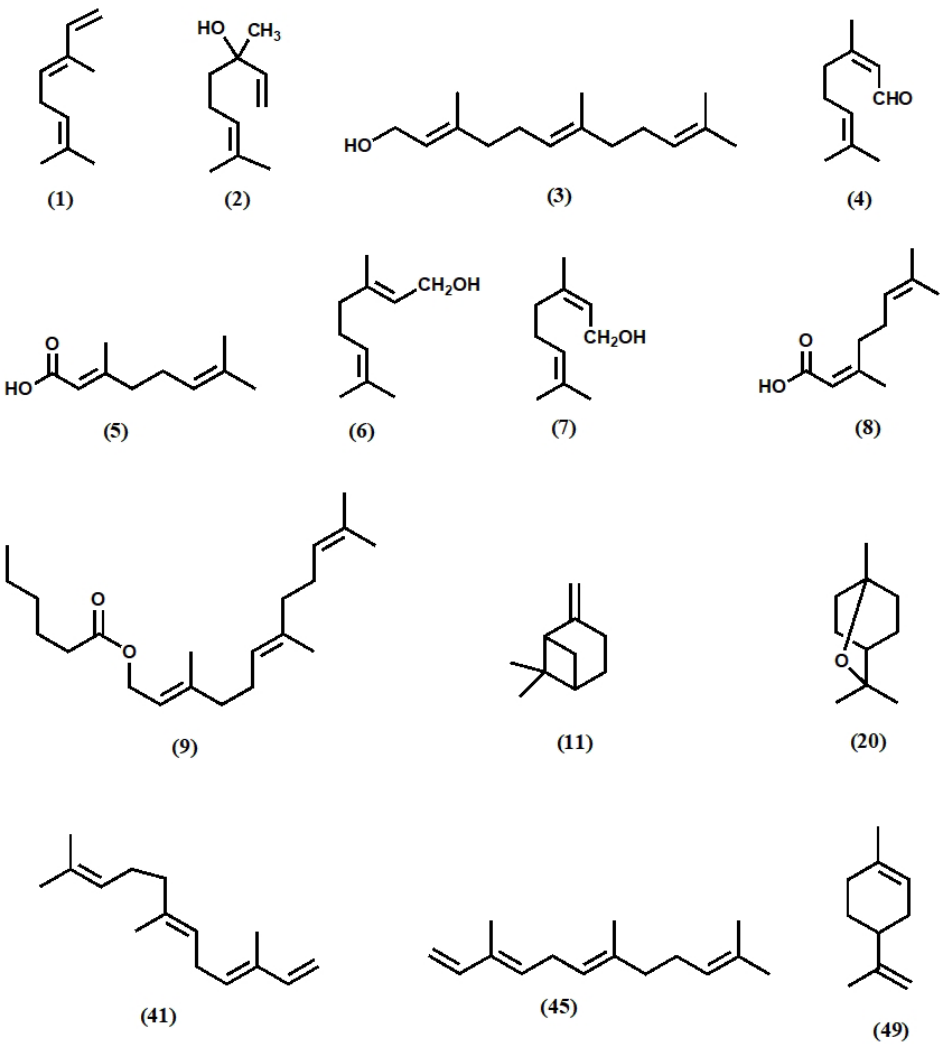


Fig. 3 Some of the commonest terpenoids from flower scents that trigger response in bees.

mengol et al. 2017). Both *trans*-*β*-ocimene (1) and linalool (2), which were among the most prevalent terpenoids produced by flowering plants, are linked to pollinator attractions, such as honeybees (Kobayashi et al. 2012), Euglossini bees (Hetherington-Rauth and Ramírez 2016), Nocturnal bees (*Megalopta* spp.) (Krug et al. 2018). Williams et al. (1981) demonstrated that each of the seven components of the Nasonov secretion ((*E*,*E*)-farnesol (3), (Z)-citral (4), geranic acid (5), geraniol (6), nerol (7) and nerolic acid (8)) attracted foraging honeybees individually, though their level of attraction varied. These compounds (3–8) are also among the most common compounds produced by plants.

Orchids of the genus *Ophrys* are well understood to employ sexual deception by emitting a chemical composition identical to that of female sex pheromones, and so males are deceived into attempting to mate with the flowers (Ayasse et al. 2000). Orchids are mostly pollinated by the male solitary bee *Andrena nigroaenea*, which are lured to the orchid by visual cues and volatile semiochemicals (Borg-Karlson 1990; Borg-Karlson and Tengö 1986). It was also noted that (*E*,*E*)-farnesyl hexanoate (9), (*E*,*E*)-farnesol (3) and nonanoic (10) acid from *Ophrys sphegodes* triggered antennae's response of males receptor (Ayasse et al. 2000). After pollination, it is interesting to note that *O. sphegodes* (also known as spider-orchid) marks itself with (*E*,*E*)-farnesyl hexanoate (9) to prevent the solitary bee *Andrena nigroaenea* from having duplicate visits (Schiestl and Ayasse 2001). *Gongora* spp. are common in angiosperm families and emit many diverse and complex VOCs. Among the many VOCs, *β*-ocimene (1), linalool (2) and *β*-pinene (11) are linked with the attraction of generalist pollinators including bees, flies and butterflies (Dobson 2006; Giuliani et al. 2020).

Terpenoids are highly diverse in nature because a single terpenoid is susceptible to undergo several reactions (e.g., carbocation cyclization, rearrangement, and elimination reactions), lead to multiple products (Christianson 2018; Karunanithi and Zerbe 2019). It has been also demonstrated that the occurrence of multi-substrate terpenoids depend on the physiological and development status of plants. This suggests that terpene/terpenoids may be the plant's preference in response to fluctuations in the environment (Pazouki and Niinemets 2016).

Benzenoid compounds

Benzenoids, also known as phenylpropanoids, constitute the second largest class of plant VOCs (Knudsen et al. 2006). They are exclusively derived from the aromatic amino acid phenylalanine, which is synthesized via the shikimate/phenylalanine biosynthetic pathways (Yoo et al. 2013). Benzenoids are biosynthesized via the shikimate pathway, involving a sequence of seven metabolic steps beginning with the condensation of phosphoenolpyruvate and erythrose 4-phosphate to form chorismate, the precursor of the aromatic amino acids and many aromatic secondary metabolites (Fig. 2) (Peled-Zehavi et al. 2015; Tzin and Galili 2010).

Male bees in Euglossini widely pollinate flower species belonging primarily to the Orchidaceae family (Endress 1996). Among the common VOCs that eliciting response in euglossine bees were benzenoids (Fig. 4) from *Stanhopeinae* spp., such as 2-phenylethyl acetate (12), benzyl acetate (13), methyl benzoate (14), methyl cinnamate (15), methyl salicylate (16) and vanillin (17) (Andrews et al. 2007; Williams and Whitten 1983). Floral scents may be particularly effective in two scenarios—for plants pollinated at night when the floral resources are less visible and attraction from a distance (Krug et al. 2018). Bees are largely light sensitive and limited light levels or anything that obscure of visual cues can easily affect their foraging flights (Galen et al. 2019; Kelber et al. 2006) except nocturnal bees (Hopkins et al. 2000; Wcislo and Tierney 2009). For instance, a benzenoid (2-phenylethanol (18)) along with 1-octanol (19) emitted by a night flowering plant *Campomanesia phaea* (flowering period from 04:30 to 05:00 am) attracted night-active nocturnal bees (*Megalopta* and *Ptiloglossa* species) (Cordeiro et al. 2017). Moreover, benzyl acetate (13), eucalyptol (20), eugenol (21), methyl salicylate

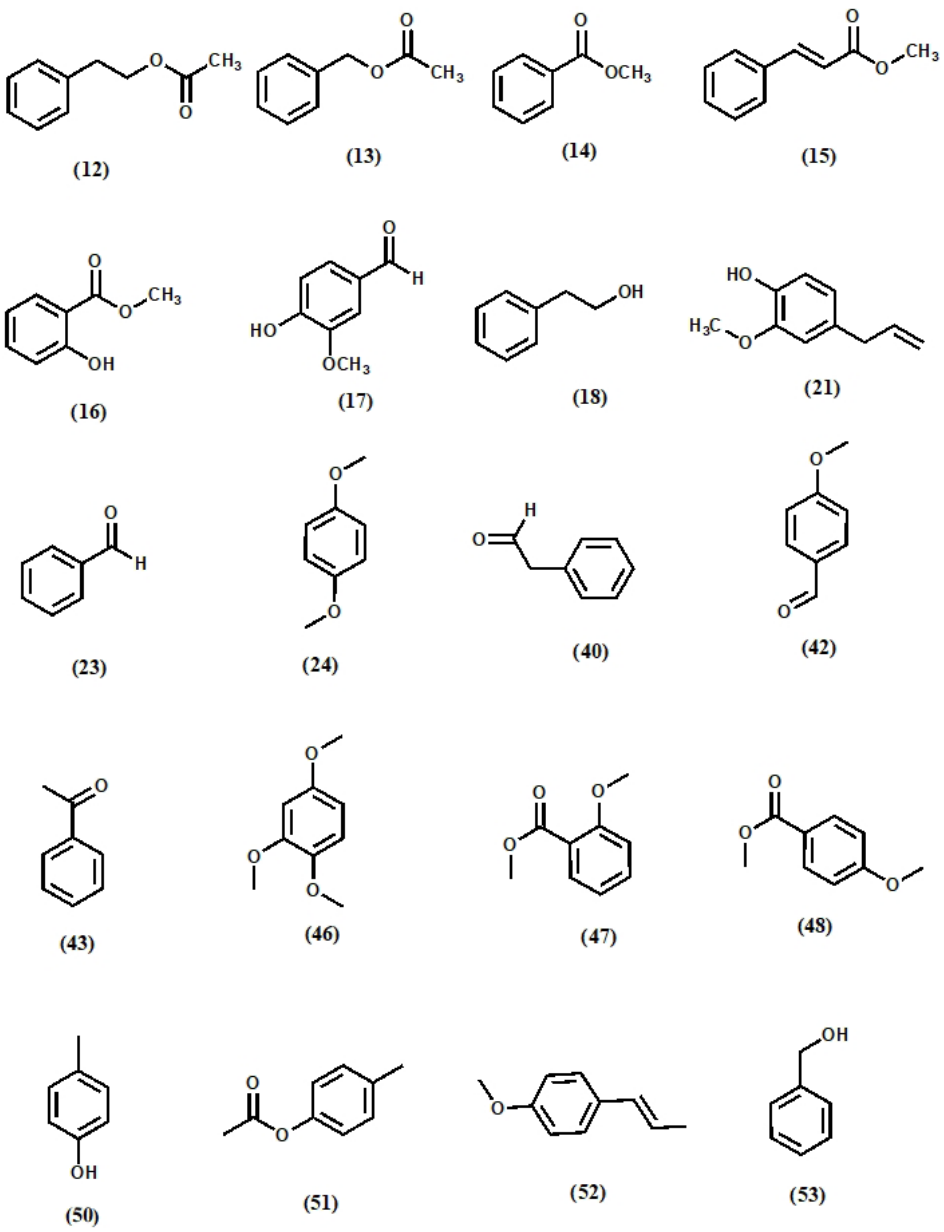


Fig. 4 Benzenoids from flower scents that elicit response in bees.

(16), skatole (22) and vanillin (17) also lured nocturnal bees, *Megalopta* bees (Knoll and Santos 2012; Krug et al. 2018; Wcislo and Tierney 2009). Indeed, benzaldehyde (23) and 2-phenylethanol (18) are the two predominant benzenoids of floral scents of many species (Farré-Armengol et al. 2017; Theis 2006).

Many different oligolectic bee species are usually attracted to the flowering species belonging to the genus *Salix* because of its pollen are easily accessible (Michener 2000; Newsholme 1992). 1,4-Dimethoxybenzene (24) emitted by *Salix* spp. are responsible for the attraction of the oligolectic bee *Andrena vaga* (Dötterl et al. 2005; Tollsten and Knudsen 1992). 1,4-Dimethoxybenzene (24) was also produced by the tiny flowers of *Notylia* spp. to attract the male euglossine bees (Gerlach and Schill 1991). It was reported that *p*-methoxyanisole, also known as 1,4-dimethoxybenzene (24) from *Hydrocleys martii* (aquatic plant) lure Oligolectic bees *Protodiscelis palpalis* (Carvalho et al. 2014). Synthetic compounds, such as anethole (52), also play crucial role in attracting honeybees (Allsopp and Cherry 1991).

Volatile fatty acid derivatives

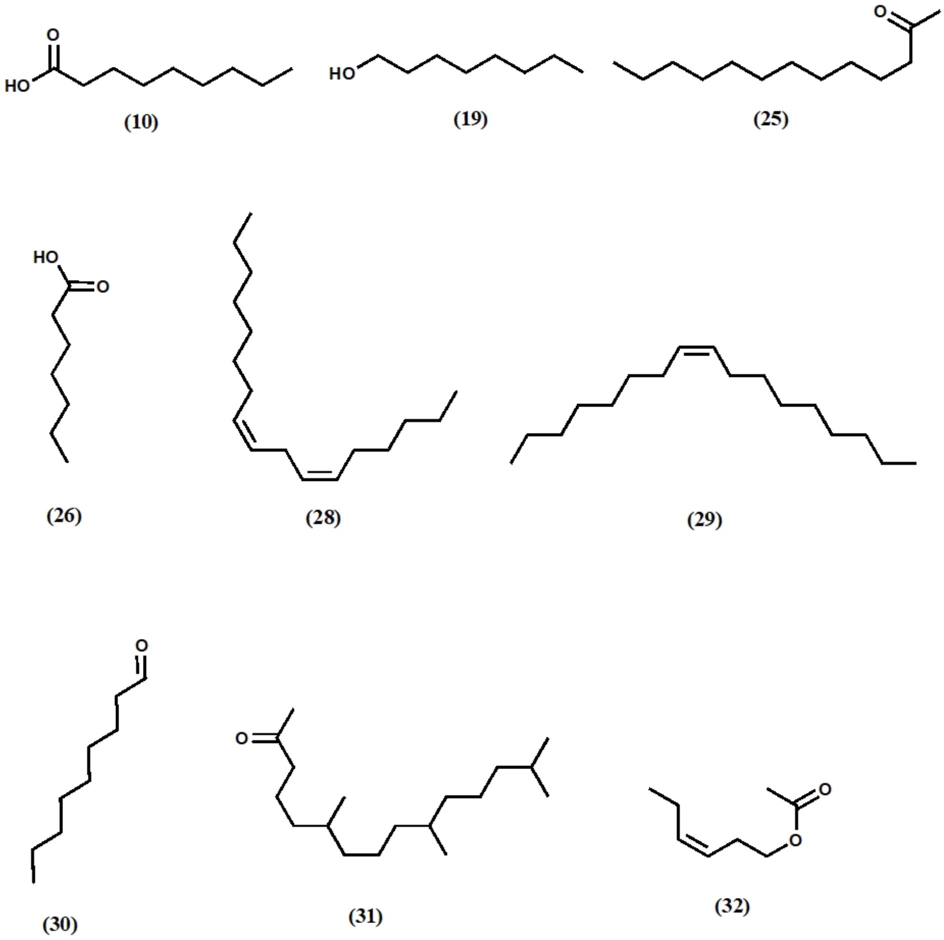
Fatty acid derivatives are the third largest class of flower VOCs (Fig. 5), which derive from the unsaturated C18 fatty acids (linolenic and linoleic) (Muhlemann et al. 2014). Volatile fatty acids are synthesized and relied on a plastidic pool of acetyl-CoA derived from pyruvate, the final product of glycolysis (Feussner and Wasternack 2002).

Most of the oil-producing flowers and their frequent visitors (flower-oil-collecting bees) are neotropical. Oil-collecting bee species, such as *Macropis* bees were frequently noticed to collect oil and pollen only from *Lysimachia* spp. as food for their larvae (Dötterl and Schäffler 2007). Interestingly, fatty acid derivatives (such as 2-tridecanone (25) and heptanoic acid (26) and glycerol derivative (diacetin (27)) from *Lysimachia* spp. are responsible for enticing *Macropis* bees (Schäffler et al. 2015).

Several previous studies also demonstrated that volatile fatty acid derivatives such as (*6Z*,*9Z*)-heptadecadiene (28), (*8Z*)-heptadecene (29) and nonanal (30) (*Actinidia deliciosa*; [Tatsuka et al. 1990; Twidle et al. 2015]), 6,10,14-trimethyl-2-pentadecanone (31) (*Brassica* spp.; [Kobayashi et al. 2012]), *cis*-3-hexenyl acetate (32) (*Medicago sativa*; [Henning and Teuber 1992]) are capable of attracting honeybees.

Rare volatile organic compounds

Flowering plants are known to emit wide range of VOCs from being relatively rare to common. In general, specialized pollinators are attracted to flowering plants emitting



(10) (19) (25)

(26) (28) (29)

(30) (31) (32)

Fig. 5 Volatile fatty acid derivatives from flower scents that elicit response in bees.

rare VOCs (Fig. 6). One good example is *Campanula trachelium*, a flowering plant, which emits spiroacetal volatile compounds (33–36) to attract Campanula-specialist bee (Milet-Pinheiro et al. 2013). Likewise, *N*-containing compounds such as methyl nicotinate (37) (*Raphanus sativus*) and 1*H*-indole (38) (*Brassica* spp.) were also reported to have positive responses to honey bee's antenna (Kobayashi et al. 2012). Diacetin (27) (a volatile acetylated glycerol) from *Lysimachia* sp. was also found to be a crucial signal in the *Lysimachia*-*Macropis* pollination system by eliciting strong antennal responses in oil-collecting bees (*Macropis* bee) (Schäffler et al. 2015).

Mostly hydrocarbons produced by *Ophrys* flowers are active in triggering behavioral response in the male pollinators (mostly the solitary bee Andrenidae) (Ayasse et al. 2000; Borg-Karlson 1990; Kullenberg 1973; Paulus and Gack 1990). The newly-emerged of solitary bee *Chelostoma florisomne* is enticed by the pollen of *Ranunculus* sp., which emits a rare lactone of γ-hydroxyvinylacrylic acid, protoanemonin (39) (Dobson and Bergström 2000). In addition to bee attractant, protoanemonin (39) was also reported to possess antifungal activity (Martín et al. 1990).

Honest flower signals

In plant-pollinator relationship, pollinators prefer to visit flowering plants with honest floral signals that correlate positively with the reward status (food amount) (Bolstad et al. 2010). Honest signals could be either olfactory, visual, size, shape or any floral signal of the flower. In fact, pollinators are mostly guided to their host flowering plants by innate preferences or their ability to learn association between VOCs and food rewards (Arenas and Farina 2012; Raguso 2008).

There are several cases where bees make their decision to visit flowers based on the amount of the volatile components released by the flowers, and their association with the reward (Dobson et al. 1999; Dötterl and Jürgens 2005; Mena Granero et al. 2005). For example, level of phenylacetaldehyde (40) in *Brassica rapa* is associated with the number of visitation by the bumble bee (*Bombus terrestris*) (Knauer and Schiestl 2015). Similarly, the level of diacetin (27) in *Lysimachia* sp. is linked to the number of visitation by the oil-collecting bees (*Macropis* bee) (Schäffler et al. 2015). Other floral signals can also serve as honest signal, such as coloured nectar (Hansen et al. 2007) and the size of the gland secreting reward in *Dalechampia schottii* (Bolstad et al. 2010). Synthetic phenylacetaldehyde appeared to attract large numbers of bees in a trap that aimed at capturing moths (Meagher 2002). In general, pollinators naturally prefer to navigate flowers with high level of honest floral VOC signals (Majetic et al. 2009; Parachnowitsch et al. 2012), indicating that pollination services can be elevated by producing more honest flower scent signal. For instance, four VOCs (α-farnesene (41), *p*-anisaldehyde (42), acetophenone (43), phenylacetaldehyde (40)) emitted by *Brassica rapa* L. are well documented to lure bumblebees for pollination (Knauer and Schiestl 2015). However, phenylacetaldehyde (40) only serves as an honest signal by associating high amount of this compound with their corresponding proportions of pollen and nectar. In another

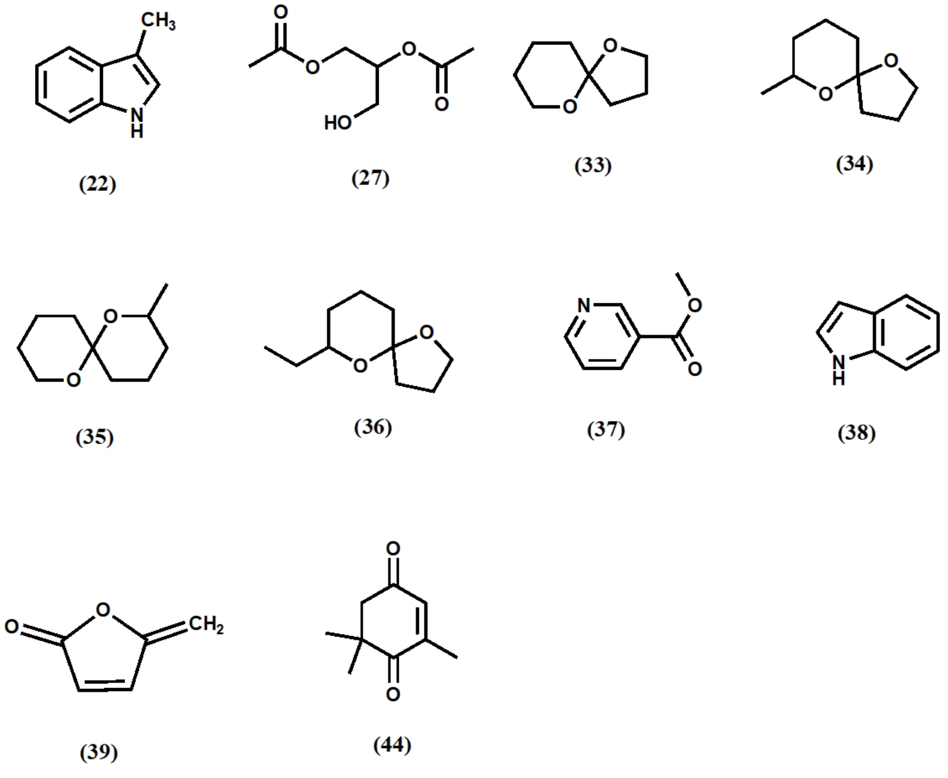


Fig. 6 Compounds belonging cyclohexanone, lactone, *N*-containing compounds and spiroacetals from flower scents that trigger response in bees.

example, (*E*,*E*)-farnesol (3) alone and a mixture of citral (4) and (*E*,*E*)-farnesol (3) from *Ophrys* lutea were found to be highly attractive and elicited a few long-lasting behavioral events to many *Andrena* species (Borg-Karlson and Tengö 1986).

Nectar-depleted flowers can also emit distinct volatiles to repel pollinators and non-pollinator herbivores (Galen et al. 2011). The *Orchid Ophrys* sphegodes emits (*E*,*E*)-farnesyl hexanoate (9) to avoid the solitary bee *Andrena nigroaenea* from having mutltiple visits (Schiestl and Ayasse 2001). Therefore, flowers regulate their emission of attractant and repellent chemicals to maintain a balance between nectar supply and demand.

In fact, flowering plants are rich with secondary metabolites. Terpenoids (such as *trans*-*β*-ocimene (1), linalool (2), limonene (49)) and benzenoids benzaldehyde (23), benzyl alcohol (53) and 2-phenylethanol (18) have been reported to occur in floral scent in more than half of the families of seed plants (Cseke et al. 2007; Knudsen et al. 2006). These compounds mostly serve as attractants to generalist bees. In a study conducted by (Henning and Teuber 1992) indicated that linalool (2), methyl salicylate (16), and *cis*-3-hexenyl acetate (32) from *Medicago sativa* L. (alfalfa) elicited a strong honeybee antennal response. Linalool (2) and methyl salicylate (16) appeared to increase honeybees' visitation to alfalfa. In contrast to linalool (2) and methyl salicylate (16), *cis*-3-hexenyl acetate (32) had the opposite effects. Thus, it was suggested that alfalfa yields could be increased through genetic manipulation by selection of alfalfa variety rich with linalool and methyl salicylate, but not *cis*-3-hexenyl acetate (32) (Henning and Teuber 1992).

Over the years, several attempts have been made to modulate plant VOCs profiles and their effect on insect behavior. Numerous strategies have been implemented, such as by the modification of existing pathways, or by blocking the competing pathways or by introducing new gene(s) (Lange and Ahkami 2013). One success story of the strategy is that plant defense mechanism was highly improved by producing the volatile patchoulol along with additional sesquiterpene products in transgenic tobacco, overexpressing Pogostemon cablin patchoulol synthase (Wu et al. 2006).

Conclusions

Floral scents are composed of hundreds of diverse and complex volatile molecules. Understanding the function of these floral scent alone (Pichersky and Raguso 2018) or in synergy with other floral signals (e.g., visual cues) (Kunze and Gumbert 2001; Raguso and Willis 2002) is crucial in plant–pollinator mediations. Flowers generally use honest floral signals, and bees are able to correlate floral signals with nectar and pollen-rich flowers (Howell and Alarcón 2007). Thus, honest signaling mechanism plays a key role in maintaining mutualistic plant–pollinator associations (Knauer and Schiestl 2015). It was also indicated by previous studies that flowers with high level of floral VOCs can improve pollination service (Majetic et al. 2009; Parachnowitsch et al. 2012). For instance, field trials with flower scent manipulation to increase honeybee's visitation to kiwifruit flowers led to some success (Pinzauti 1990; Tsirakoglou et al. 1997). Thus, crop production may be improved through genetic manipulation of the floral scent (Henning and Teuber 1992; Kobayashi et al. 2012; Twidle et al. 2015).

Given the role of chemical communication in plant-pollinator interactions, understanding and identification of VOCs from floral scent are crucial in improving crop pollination. Interestingly, current advances in both VOCs scent gene identification and their biosynthetic pathways make it possible to manipulate particular VOCs in plant. Thus, this eventually may lead to increase in crop productivity.

Abbreviations

DAHP: 3-Deoxy-D-arabinoheptulosonate-7 phosphate
DMAPP: Dimethylallyl pyrophosphate
E4P: Erythrose 4-phosphate
FPPS: Farnesyl pyrophosphate synthase
FPP: Farnesyl pyrophosphate
G3P: Glyceraldehyde-3-phosphate
GGPP: Geranylgeranyl pyrophosphate
GPP: Geranyl pyrophosphate
IPP: Isopentenyl pyrophosphate
LOX: Lipoxygenase
MEP: Methylerythritol phosphate
MVA: Mevalonic acid
PEP: Phosphoenolpyruvate
Phe: Phenylalanine
VOCs: Volatile organic compounds

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Authors' contributions

DB reviewed and wrote the manuscript. CJ designed, analyzed and edited the manuscript. All the authors approved the manuscript.

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Availability of data and materials

All data reviewed in this study are available from the corresponding author on request.

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Not applicable.

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Competing interests

The authors declare that they have no competing interests.

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