

Effect of Plant Volatile Components on Honey Bee Flower Visitation: A Review

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ABSTRACT: Flower scents are pleasant and attractive odors naturally emitted by flowers. These scents are formed by the combination of different components in flowers, and the most common are volatile organic compounds, terpenes, esters, phenolic compounds, aldehydes and ketones, alcohols, and acids. Volatile odors in plants are chemical compounds produced either to protect the plants themselves or to support the pollination process. These odors can have various effects on insects. For example, some plant volatiles simulate unfavorable or harmful conditions for insects, while some plants use their odor to attract and trap insects. Other plants attract insects by emitting odors to encourage pollination. Insects use morphological and olfactory cues when foraging for food. Honey bees visit plants depending on whether they are attracted by the plant's volatile scents. The unique scents of flowers attract honey bees during which the bees inadvertently transfer pollen, thereby facilitating plant reproduction through pollination. In addition, honey bees are capable of learning diverse floral volatiles and retaining this information in their memory. In this way, they can return to the flowers of the same plants. However, certain adverse conditions can disrupt the volatile emissions of plants. Pesticides, air pollution, chemical contaminants, climate change, humidity, CO₂ levels, plant diseases, soil salinity, mineral content, pH imbalances, harmful insects or other organisms, as well as interspecific interactions, can all contribute to this disruption. Moreover, genetic diversity influences the capacity of plants to adapt to environmental stresses, and limited diversity may negatively affect the production of volatile compounds. To sustain pollination and, consequently, biodiversity, it is essential to address these adverse factors. Equally important is the identification of floral traits influencing bee visitation and the improvement of these traits through breeding programs or the development of enhanced plant varieties to support crop diversification.

Keywords: Honeybee, biodiversity, floral scents, plant volatile components, pollination.

Bitki Uçucu Bileşenlerinin Bal Arılarının Çiçek Ziyaretleri Üzerindeki Etkisi: Derleme

ÖZ: Çiçek kokuları, çiçeklerin doğal olarak yaydığı hoş ve çekici kokulardır. Bu kokular, çiçeklerdeki farklı bileşenlerin birleşimiyle oluşur ve en yaygın olanları uçucu organik bileşikler, terpenler, esterler, fenolik bileşikler, aldehytlar ve ketonlar, alkol ve asitlerdir. Bitkilerde bulunan uçucu kokular, bitkilerin kendilerini korumak veya tozlaşma sürecini desteklemek için ürettikleri kimyasal bileşiklerdir. Bu kokuların böcekler üzerinde çeşitli etkileri olabilir. Örneğin, bazı bitki uçucuları böcekler için hoş olmayan veya zararlı koşulları simüle eder ve bazı bitkiler böcekleri çekmek ve tuzağa düşürmek için kokularını kullanır. Bazı bitkiler tozlaşmayı teşvik etmek için koku sağlayarak böcekleri çeker. Böcekler yiyecek aramak için morfolojik ve koku alma ipuçlarını kullanır. Öte yandan bal arıları, bitkilerin uçucu kokularının onları çekip çekmediğine bağlı olarak bitkileri ziyaret eder. Çiçeklerin kendine özgü kokuları bal arılarını nektar toplamaya çeker, arılar da bu sırada polenleri taşıyarak bitkilerin üremesine yani tozlaşmaya yardımcı olur. Ayrıca bal arıları farklı çiçek kokularını tanır ve bu kokuları hafızalarında saklar. Bu sayede aynı bitkilerin çiçeklerine geri dönebilirler. Ancak bazı olumsuz koşullar bitkilerin uçucu kokularını bozabilir. Pestisitler, hava kirliliği, kimyasal kirleticiler, iklim değişikliği, nem ve CO₂ seviyeleri, bitki hastalıkları, toprak tuzluluğu, mineral içeriği, pH dengesizlikleri, zararlı böcekler veya diğer organizmalar ile bitkiler arası etkileşimler bu duruma neden olabilir. Ayrıca genetik çeşitlilik, bitkilerin çevresel streslere uyum sağlama kapasitesine etki ederek uçucu bileşiklerin üretimini olumsuz etkileyebilir. Tozlaşmanın ve dolayısıyla biyolojik çeşitliliğin sürdürülmesi için bu olumsuz faktörlerin ele alınması gereklidir. Benzer şekilde, arı ziyaretlerini etkileyen çiçek özelliklerinin belirlenmesi ve bu özelliklerin iyileştirilmiş ırk veya türler üzerinden geliştirilmesi, ürün çeşitliliğini desteklemek açısından önemlidir.

Anahtar kelimeler: Bal arısı, biyoçeşitlilik, bitkisel koku, bitki uçucu bileşikleri, tozlaşma.

INTRODUCTION

Flowering plants have evolved a variety of metabolites to enable plant-pollinator interactions (Wong *et al.*, 2023). Plants produce sugars, amino acids, volatile organic compounds (VOCs) and secondary metabolites (SMs) to attract pollinators and provide defense (Slavković and Bendahmane, 2023). Among these metabolites, VOCs occupy an important place (Mas *et al.*, 2020a; Ma *et al.*, 2021). VOCs play a critical role in the interaction between plants and pollinators (Liu *et al.*, 2022b; Langford *et al.*, 2023). Through VOCs, plants communicate not only with pollinators but also with herbivores, pests, other plants and microorganisms (Bouwmeester *et al.*, 2019; Lo *et al.*, 2024). These chemical signals help plants regulate their growth, development, defense, distribution and their life cycle (Bouwmeester *et al.*, 2019). The VOCs secreted by flowers are complex and species-specific mixtures that vary depending on plant genotype, pollination status, age, season and phenology (Mas *et al.*, 2020a; Ma *et al.*, 2021). Insect-pollinated flowers have been found to release more and diverse VOCs compared to wind-pollinated flowers (Farré-Armengol *et al.*, 2015). Moreover, the peak secretion of volatile compounds coincides with the hours when pollinators are most active, suggesting that these compounds play a critical role in orienting pollinators (Gabriel *et al.*, 2009; Ma *et al.*, 2021). VOCs are compounds with low molecular weight that are easily evaporated and are synthesized from different parts of the plant. They are divided into three main groups according to their biosynthesis pathways: terpenoids, phenylpropanoids/benzenoids and fatty acid derivatives. Terpenoids are the most common VOC group and synthesized via mevalonic acid (MVA) and methylerythritol phosphate (MEP) pathways. Phenylpropanoids/benzenoids are derived from the amino acid phenylalanine while fatty acid derivatives are synthesized in chloroplasts and composed of unsaturated fatty acids. In addition, some nitrogen- and sulfur-containing compounds are also thought to play a role in pollinator attraction, although there is limited information about this topic (Lo *et al.*, 2024). Secondary metabolites (SMs) can directly influence the behavior of pollinators, for example, some compounds can interact with the nervous system of pollinators, altering their foraging behavior. Alkaloids and phenolic compounds can enhance pollinator memory and increase foraging efficiency, while flavonoids

support pollinator health through their antioxidant properties. At the same time, alkaloid and phenolic compounds can protect the plant against nectar thieves (Slavković and Bendahmane, 2023).

The amount and diversity of VOCs emitted by flowers can vary due to environmental conditions (biotic and abiotic factors) (Lo *et al.*, 2024). These factors can reduce the reproductive success of the plant, affecting both the health of the plants directly but also indirectly through its ability to attract pollinators. For example, buckwheat plants under drought stress bloom less and produce less nectar per flower; and although the sucrose content in the nectar is lower, the total sugar content and the amount of pollen per flower remain unchanged. In addition, although the total amount of volatile compounds emitted by flowers did not change, they secreted more (Z)-3-hexenol, isobutyraldehyde, 2-methylbutanal and 3-methylbutanal compounds, and the number of pollinators visiting drought-affected plants decreased, especially the visitation rate of bumble bees, honey bees and flies decreased significantly (Rering *et al.*, 2020).

Although vision is essential for pollinator orientation to flowers, olfaction appears to be a more determining factor (Kunze and Gumbert, 2001; Ma *et al.*, 2021). VOCs shape pollinators' foraging preferences, helping them to attract to specific flower species (Liu *et al.*, 2022b; Langford *et al.*, 2023). Different chemical signals emitted by flowers can influence the behavior of pollinators (Knudsen *et al.*, 2006; Ma *et al.*, 2021), their foraging preferences (Su *et al.*, 2022), and certain floral characteristics may be more attractive to some pollinators (Mas *et al.*, 2020a) and support plant reproduction (Abbas *et al.*, 2017; Démarets *et al.*, 2024). This may also improve pollination performance.

Honey bees are considered an excellent model organism for the study of cognitive abilities such as learning and memory. The processes of learning, information storage and memory are of great importance in bees, as these abilities are essential for them to collect nectar, learn the location of flowers and return to the hive (Frasnelli *et al.*, 2013). Despite having a small brain containing 960,000 neurons, the honey bee has become an important model organism in the life sciences, and especially in cognitive neuroscience, for its ability to perform complex cognitive tasks (Frasnelli *et al.*, 2014). Their antennae contain sensilla for odor detection, each sensillum

placodeum is innervated by 5-35 olfactory receptor neurons, and the response of the antennae to the same odor can differ between bee species (Zhao *et al.*, 2020). It has been found that the antennae of *Apis cerana* bees have a more developed sense of smell compared to *Apis mellifera* and respond more strongly to various floral volatile compounds (Jung *et al.*, 2014). In addition, pollen-collecting forager bees are more sensitive to odors than nectar collectors. It is reported that the increased ability of pollen-collecting forager bees to detect odors is linked to their enhanced odor perception at the antenna level. It is also emphasized that antennal responses to pollen odors lead to different neural activities in different forager bee species, which may be an adaptation that helps bees distinguish between different food sources (Moreno *et al.*, 2022).

Honey bees prefer their food by detecting only certain compounds in floral odors (Mas *et al.*, 2020a). Furthermore, bees can learn these odors and recognize flowers through their memory (Démarets *et al.*, 2022) and use their sense of smell to select flower scents that they have previously associated with quality food. They share information about the taste and quality of nectar through trophallaxis and location information through directional dances. Recent research shows that bees also carry some floral volatile compounds on their body surfaces (cuticles) (Mas *et al.*, 2020b). These compounds are thought to have been previously learned by bees and associated with quality food sources. This suggests that bees consciously prioritize certain odors in the foraging process and that odor cues play an important role in their communication. However, it has been found that prior exposure to odors can affect memory in young bees (3-5 days old), but this effect is no longer detectable at later ages (17-19 days old) (Ramírez *et al.*, 2016; Mas *et al.*, 2020a). In addition, caffeine and tea polyphenols found in tea plant (*Camellia sinensis*) leaves have been shown to improve the learning and memory abilities of honey bees (Gong *et al.*, 2021).

In this review, the effects of plant volatile compounds on honey bee foraging behavior are examined. Methods for assessing odor response, the interactions of honey bees with floral volatiles, and the environmental and biotic factors influencing both these compounds and bee behavior are comprehensively discussed.

METHODS FOR ODOR RESPONSE DETECTION

To understand how honey bees perceive floral volatile compounds, it is important to consider the methods used to detect and analyze olfactory responses. Therefore, the following sections describe the main techniques used to study bee olfaction.

Electroantennography (EAG):

Electroantennography (EAG) is a technique that detects and measures electrical signals from insect antennae (Byers and Jacobs, 2024) and is the most common method used to measure the detection of volatiles by insects (Schott *et al.*, 2013; Byers and Jacobs, 2024). This method was developed in 1953-1956 in studies in France and Germany and was used to measure the electrical response of insect antennae to odor. In the very first experiments, electrodes and oscilloscopes were used to examine the stimuli applied to the antennae, and then slow potential recordings were taken and the method was named ElectroAntennoGram (Syntech, 2015). In this technique, the insect's antennae are connected to electrodes and electrical signals generated upon response to volatiles are recorded. The nanovolt-level signals resulting from depolarization are filtered and amplified. For electrode connection, saline solutions or electrocardiogram gels are used. The disadvantage of EAG is that it requires highly pure compounds for accurate recordings, as it measures the responses of all antenna neurons simultaneously (Schott *et al.*, 2013). The olfactory sensitivity of honey bees can be assessed to different volatile compounds by measuring the electrical responses of their antennae using EAG, and even the neural activity triggered by the chemical composition of some odors can be distinguished at the antenna level (Moreno *et al.*, 2022). The response of the antenna to the voltage change indicates that the compounds are physiologically active, and these compounds, in their pure form or in mixtures, can be validated by behavioral tests (Byers and Jacobs, 2024). However, the EAG method does not show how odors are processed in the brain and cannot directly explain the behavioral responses of the insect (Schott *et al.*, 2013).

Gas Chromatography-Electroantennographic Detector (GC-EAD)

In order to overcome the disadvantages of the EAG method, volatile compounds can be separated by gas chromatography (GC). This separation is then combined with an EAG detection unit and the system is called a gas chromatography-electroantennographic detector (GC-EAD). Almost all volatile compounds can be separated using different chromatographic columns and temperature and pressure programs (Schott *et al.*, 2013). The detection of volatile compounds emitted by plants is usually achieved by combining gas chromatography and electroantennographic detection (GC-EAD) by measuring voltage changes in the antennae of insects that detect volatile compounds with their antennae. In GC-EAD analyses, the reproducibility of the method is limited as active signal identifications are not clear, making comparisons difficult and increasing the margin of error. Furthermore, plant volatile compounds may generate weaker responses compared to insect pheromones, although systems that sexually attract and pollinate insects can be an exception. Therefore, by analyzing GC-EAD data with a new signal processing method against baseline line drift and low signal:noise ratio in GC-EAD, the responses of hawkmoths and wild bees to flower volatiles were compared and it was found that this technique allows for a more sensitive study of plant-insect interactions (Byers and Jacobs, 2024).

Single Sensillum Recording (SSR):

Electroantennography data are usually only presented qualitatively as “response present/absent” (Byers and Jacobs, 2024). Compounds that stimulate electrophysiological responses at the same level can produce different behavioral responses (Mas *et al.*, 2020a). Measurements with all antennae or all insects do not provide selectivity for individual volatiles and cannot determine which sensillum responds to particular compounds (Schott *et al.*, 2013). Therefore, it is not possible to make definitive behavioral inferences based on EAG data alone. For example, in one study, certain compounds such as linalool and phenylacetaldehyde caused the most pronounced feeding response in honey bees, whereas these compounds did not elicit the highest EAG responses (Mas *et al.*, 2020a). Single sensillum recording (SSR) allows measurement of the response of a particular

sensillum to specific compounds. In this method, a thin electrode is placed at or near the tip of the sensillum, while the ground electrode is attached to the base of the antenna or to the body. The advantage of SSR is that it provides high sensitivity by recording each signal in spikes. However, since the signal amplitude is low, measurements are sensitive to electromagnetic fields and vibrations and are usually made in a Faraday cage. There are up to five olfactory receptor neurons in a sensillum, which makes SSR a highly selective method. For accurate measurement, mechanoreceptors and irrelevant chemoreceptors must be excluded by using pure test substances. GC-SSR is a powerful technique for identifying odorant receptors and the active ingredients in pheromone mixtures (Schott *et al.*, 2013).

Honey bees direct their antennae towards the source of the odor when they respond positively, while they move in the opposite direction when they respond negatively (Gascue *et al.*, 2022). It has been determined that while the right antenna is more effective in short-term memory tests, the left antenna is more dominant for long-term memory recall processes (Frasnelli *et al.*, 2013; Frasnelli *et al.*, 2014). Bees have been found to use their right antenna more than their left antenna when managing social interactions (Frasnelli *et al.*, 2014). This suggests that sensory and social perception in bees may be linked to brain lateralization and that the right antenna plays a more dominant role in social interactions. In addition, Anfora *et al.* (2010) found that the right antenna of honey bees can remember odors or stimuli they have learned better than the left antenna, and that their right antenna gives a stronger EAG response than their left antenna, which means that their sensory sensitivity may be higher.

INTERACTION OF HONEY BEES WITH VOC'S IN PLANTS

Numerous studies have investigated how honey bees respond to floral volatile compounds emitted by different plant species. The following sections present selected examples from various plant groups to illustrate these interactions.

VOC's in Fruit Plants

Volatile compounds present in fruit species such as pear, melon, kiwi, loquat, blueberry, and strawberry can function either as attractants or deterrents for honey bees, thereby influencing their foraging preferences and pollination dynamics.

Both artificial pollination and pollination by honey bees are used in pear production (Lee *et al.*, 2017; Ma *et al.*, 2021). However, honey bees show less interest in pear flowers, especially when more attractive nectar sources such as rapeseed (*Brassica napus* L.) are present in the surrounding area. This is mainly because pear flowers have a low sugar content and produce very limited amounts of nectar. This translates into a low energy reward for the bees. In comparative studies, *Apis cerana cerana* was found to be a more effective pollinator of pear flowers than *Apis mellifera ligustica*. A total of 76 VOCs were detected in pear flowers obtained from Su, Ya and Xuehua cultivars, 21 of which were found to be common to all cultivars. Although 3-methyl-1-butanol and (+)-limonene were detected at high levels and elicited strong electrophysiological (EAG) responses in bees, they did not result in behavioral attraction. Therefore, offering scented sugar syrup can be recommended to draw bees to flowers and enhance pollination in pear orchards (Ma *et al.*, 2021).

Comparing local *Pyrus bretschneideri* and exotic *Pyrus communis* species, it was observed that bees were more attracted to *P. communis* flowers (64.37% for *Apis mellifera*; 62.10% for *Apis cerana*). *P. communis* flowers produced 27 and *P. bretschneideri* flowers produced 31 volatile compounds, 17 of which were common to both species. Electrophysiological analysis revealed that bees responded to 1-nonanol, linalool, methyl 2-hydroxy-3-methylpentanoate, methyl L-isoleucinate and α -farnesene compounds in both species. In addition, 8 compounds (methyl L-valine ester, benzaldehyde, 6-methyl-5-hepten-2-one, isophorone, 2-methyl octane, longicyclene, longifolene and caryophyllene) in *P. bretschneideri* flowers and 3 additional compounds (β -ocimene, 4-oxoisophorone and lilac alcohol D) in *P. communis* flowers were detected by bees (Su *et al.*, 2022). In a different study, it was determined that an average of 256 ng of volatile compounds were released per flower per hour from different pear cultivars. The most intensely released compounds were linalool, methyl benzoate and methyl 2-hydroxy-3-methylpentanoate. Bee antennae responded electrophysiologically to 17 of these compounds. Two new compounds ((E)-N-(2-methylbutyl)- and (E)-N-(3-methylbutyl)-1-(pyridin-3-yl)methanimine) were also discovered in this study (Lukas *et al.*, 2019).

When the volatile compounds emitted from Xing-tian melon flowers were analyzed, a total of 77 different VOCs were detected. Most of these compounds were aldehydes. In EAG tests, honey bees showed strong neural responses to e-2-hexenal, e-2-octenal and 1-nonanal compounds. In behavioral tests, it was determined that especially e-2-hexenal and e-2-octenal compounds attracted bees more (Zhang *et al.*, 2022).

Kiwifruit flowers do not produce nectar, but both male and female flowers produce pollen that is attractive to bees (Goodwin *et al.*, 1993; Twidle *et al.*, 2015) and the plant is completely dependent on honey bees for pollen transportation (Estravis-Barcala *et al.*, 2024). GC-EAG analyses showed that honeybees were more likely to bind to nonanal, 2-phenylethanol, 4-oxoisophorone, 4-oxoisophorone, (3E,6E)- α -farnesene, (6Z,9Z)-heptadecadiene and (8Z)-heptadecene compounds in female kiwifruit flowers; whereas they showed a strong response to five of them (nonanal, 2-phenylethanol, 4-oxoisophorone, 4-oxoisophorone, (6Z,9Z)-heptadecadiene and (8Z)-heptadecene) in male flowers (Twidle *et al.*, 2015).

Apis cerana is an important pollinator of loquat flowers which bloom in early winter in China (Zhang *et al.*, 2023; Huang *et al.*, 2025). This action is associated with the ability of the olfactory system of bees to adapt to low temperatures. It was found that 4-methoxybenzaldehyde, (E)-ethyl cinnamate and methyl cinnamate compounds in loquat flowers showed strong binding affinity with the Odorant Binding Protein 2 (OBP2) and this binding was further enhanced at temperatures as low as 285 K (12°C) (Zhang *et al.*, 2023). In another study, low temperature conditions increased Chemosensory Protein 1 (CSP1) gene expression and CSP1 protein was shown to bind to these volatile compounds more strongly than OBP2 (Huang *et al.*, 2025).

In a study conducted in British Columbia, a total of 55 volatile compounds were identified in 11 different blueberry genotypes that require pollination by honey bees. Seven of these compounds were common to all genotypes (e.g. 3-hexen-1-ol acetate, linalool, bourbonene isomer, benzaldehyde, cinnamaldehyde and two isomers of cinnamyl alcohol). It was also observed that the volatile compound profiles emitted from flowers can vary depending on environmental conditions (Huber *et al.*, 2023).

A total of 38 different volatile compounds were released from the flowers of 'Red Face' strawberry variety. *Apis mellifera* was found to exhibit strong antennae (EAG) responses to compounds such as ethyl benzoate, (Z)-3-hexenyl propionate, (Z)-3-hexenyl acetate, benzeneacetaldehyde and melonal (Liu *et al.*, 2023).

VOCs in Vegetable Plants

Volatile compounds emitted from the flowers of carrot, radish, Chinese cabbage, and tomato play a decisive role in honey bee visitation, with certain compounds acting as attractants that enhance foraging activity, while others elicit avoidance responses and reduce floral attractiveness.

In New Zealand, three varieties of summer flowering vegetables (carrots, radishes and Chinese cabbage) were produced by male sterility. Eight different compounds from the flowers of these vegetables induced consistent electrophysiological responses in honey bees. Compounds benzaldehyde, nonanal, decanal, 2-aminobenzaldehyde in Chinese cabbage; phenylacetaldehyde, nonanal, methyl salicylate in carrot; and phenylacetaldehyde, nonanal, 2-phenylethanol, 4-oxoisophorone in radish caused responses. Especially nonanal and phenylacetaldehyde induced strong electrophysiological responses in all vegetables (Mas *et al.*, 2018). On the other hand, β -ocimene in high-yielding carrot varieties was found to increase nectar foraging by creating an attractive effect for honey bees. In contrast, α - and β -selinene compounds found in low-productive lines were found to reduce foraging by repelling bees (Quarrell *et al.*, 2023). Forty-six different volatile compounds were detected in tomato flowers (variety 4805Dahong). As a result of EAG tests, honey bees showed strong antennal responses to 1-nonanal, (+)-dihydrocarvone and toluene among the 16 compounds that were tested. Behavioral tests showed that 1-nonanal and (+)-dihydrocarvone induced avoidance behavior in honey bees. This was considered as an important factor reducing honey bee attraction to tomato flowers (Liu *et al.*, 2022a).

VOC's in Oil Crops

Volatile compounds emitted from *Jatropha curcas* and sunflower flowers influence honey bee foraging behavior, with certain aldehydes and alcohols eliciting strong antennal responses.

Jatropha curcas (L.) is an important biodiesel tree that contains abundant seed oil and can be used as a

renewable energy source. This species reproduces by windless pollination. *Apis cerana* is a common and effective pollinator of the *Jatropha curcas* tree and the antennae of *Apis cerana* show high sensitivity to aldehydes such as decanal, hexanal, nonanal and octanal, and alcohols such as linalool and 3-hexenol (Luo *et al.*, 2013). While more than 100 VOCs were detected in the analysis of sunflower extract, 24 compounds (1-pentene-3-ol, 3-methyl-1-butanol, trans-2-hexenal, 1-hexanol, cis-thujenol, 1,8-cineole (eucalyptol), 4-thujanol (trans-sabinene hydrate), myrtenal and myrtenol, unknown, 2,3,3-trimethyl-epoxy cyclopentyl acetaldehyde, bomyl acetate, unknown, unknown, β -elemene, vanillin, branched c10 methyl ester, germacrene d, propiovanillone, caryophyllene oxide, sesquiterpenic alcohol, 4-hydroxy-2-methoxy cinnamaldehyde, unknown, tetradecanol, hexadecanoic acid) were found to induce significant EAG responses in honey bees (Thiery *et al.*, 1990).

VOCs in Other Flowers

Volatile compounds emitted from the flowers of *Elsholtzia rugulosa*, *Jacquemontia pentanthos*, *Cymbidium kanran*, and Mānuka (*Leptospermum scoparium*) play a crucial role in mediating honey bee foraging behavior. Specific sesquiterpenes, monoterpenes, aldehydes, and other floral volatiles act as attractants, enhancing pollinator visitation.

β -caryophyllene and β -elemene in *Elsholtzia rugulosa* (Lamiaceae) were found to be attractive to *Apis cerana* (Zhang, 2018). It was also determined that the color and volatile components of the flowers are important for *Apis cerana* in its preference for *Jacquemontia pentanthos* flowers. The petals of the flowers contain ultraviolet light absorbing regions that help bees find nectar and a compound called β -caryophyllene is emitted from these flowers and *Apis cerana* reacts to this compound. Behavioral tests have shown that honey bees similarly prefer β -caryophyllene and α -humulene (Abraham *et al.*, 2018).

Cymbidium kanran is a rare plant protected in China and registered in the World Genetic Conservation Plant Registry. *Apis cerana* is the most effective pollinator of this plant. Research has shown that *C. kanran* flowers attract bees not by their color, but by their scent. Volatile compounds released at different stages of flowering such as hexanal, heptanal, octanal, 2-pentyl

furan, 4-methyl-2-pentanone and 1,4-cyclooctadiene play an important role in attracting pollinators (Luo *et al.*, 2024).

Mānuka (*Leptospermum scoparium*), native to New Zealand, grows naturally in the North and South Islands of the country and is an important part of the ecosystem. The mānuka honey obtained from this plant has strong antimicrobial properties due to methylglyoxal (MGO) derived from dihydroxyacetone (DHA) in its nectar and significant differences in terms of some unique compounds. A total of 34 different volatile compounds were identified, of which 14 were sesquiterpenes, 11 were monoterpenes, four were aldehydes, three were green leaf volatiles and the remaining two were isoamyl acetate and β -ionone. In general, the most released compounds from mānuka plants are monoterpenes, followed by sesquiterpenes (Effah *et al.*, 2022). Among the floral odors, nonanal was found to be of particular interest to bees in 12 different plant species pollinated by honey bees (Liu *et al.*, 2022b).

FACTORS INHIBITING THE DETECTION OF VOC IN PLANTS AND VOC ODORS IN HONEY BEES

While VOCs play a crucial role in plant-pollinator communication, several abiotic and biotic factors can disrupt this interaction. This section outlines key stressors that impair the production, detection, or interpretation of floral scents by honey bees.

Air Pollution

Air pollution can affect the mechanism of interaction between plants and insects. Harmful air pollutants such as ozone can alter the structure of VOCs emitted by plants (Dötterl *et al.*, 2016; Dubuisson *et al.*, 2022). This can make plants difficult to detect by insects (Blande, 2021; Langford *et al.*, 2023) and can cause the degradation of airborne VOCs, leading to the formation of new chemical compounds and secondary organic aerosols (Blande, 2021). Gaseous and particulate pollutants such as carbon monoxide (CO), carbon dioxide (CO₂), nitrogen oxides (NO_x), ozone (O₃), sulfur dioxide (SO₂) and particulate matter (PM_{2.5}/PM₁₀), as well as associated heavy metals (HMs) (Pinto-Zevallos *et al.*, 2025) and micro/nanoplastics (MPs/NPs) (Shah *et al.*, 2023; Pinto-Zevallos *et al.*, 2025) can negatively affect these interactions (Pinto-Zevallos *et al.*, 2025). Selenium, which can be lethal at high concentrations, impairs bee

learning and memory even at low doses, negatively affecting bee foraging and hive maintenance. As a result, selenium exposure can harm the health and productivity of honey bee colonies (Burden *et al.*, 2016). Different O₃ levels can alter plant-pollinator relationships by affecting floral VOC release by plants and the persistence of these compounds in the atmosphere. The response of antennae differs according to the chemical structure of VOCs and O₃ levels (Démarets *et al.*, 2024). O₃-induced oxidative stress negatively affects the sense of smell in the honeybee brain (Démarets *et al.*, 2022). For example, O₃ decreases the antennal responses of honey bees to (Z)-3-hexenyl acetate, but does not alter the responses to linalool and 2-phenylethanol (Dötterl *et al.*, 2016). Flowers of lavender (*Lavandula angustifolia*), a plant native to the Mediterranean, showed no significant change in VOC emissions when exposed to high levels of O₃ for short periods. However, a decrease in the amount of terpenes and an increase in new compounds (carbonyls, carboxylic acids) were observed as a result of interaction with O₃. These changes may cause pollinators to have difficulty in recognizing lavender flowers in areas with high ozone pollution and may negatively affect plant-pollinator interactions (Dubuisson *et al.*, 2022).

Pesticides

Bees exposed to pesticides also have reduced antennal responses. Exposure to sublethal concentrations of the neonicotinoid insecticide thiacloprid can negatively affect odor perception, learning ability and memory-related behaviors in honey bees (Ke *et al.*, 2023). Exposure to sublethal doses of fluvalinate significantly reduced the odor responses of honey bees in EAG (Lim *et al.*, 2020). Exposure of bee colonies to pesticides such as Imidacloprid and Thiacloprid may affect antennal responses to apple (*Malus domestica* L.) flower volatiles (Favaro *et al.*, 2022). This indicates that bees exposed to neonicotinoids are negatively affected in the short term in their ability to detect odor and are less effectively able to evaluate environmental signals (e.g. food sources or communication with the colony).

In addition, studies report that drugs applied in the hive can also affect the memory of bees. Tau-fluvalinate, amitraz, coumaphos and formic acid applications caused memory loss in bees, while thymol did not show this effect. Low doses of acaricides did not affect the

expression of genes associated with memory and development, while effects were observed at high doses. Furthermore, low doses of thymol, formic acid, amitraz and coumaphos increased the expression of the defensin-1 gene. However, this effect of thymol may be related to the immune system. In conclusion, the effects of acaricides on memory differ and formic acid was found to be more harmful (Gashout *et al.*, 2020).

The incidental exposure of honey bee colonies to pesticides is a major problem in agriculture and beekeeping. Current methods to prevent bee exposure to pesticides suggest applying pesticides in the evening when bees are foraging or before flowering. However, in addition to these methods, additional measures are needed to reduce bee losses (Larson, 2017). Another approach is the use of chemical deterrents to make bees less likely to interact with pesticide products (Larson, 2017; Pires *et al.*, 2020). For this purpose, pheromones (e.g. Nasonov's pheromone, geraniol, nerol, citral, 2-heptanone, isoamyl acetate), chemicals such as piperidine and DEET (98% active ingredient; N,N-diethyl-meta-toluamide) have been effectively used to keep bees away from sprayed products (Larson, 2017). Benzaldehyde and methyl anthranilate acted as repellents in electroantennographic and behavioral responses in Africanized honey bees (Pires *et al.*, 2020). Heterocyclic amines (HCAs) have also been found to be an effective method to keep foraging honey bees away from certain agricultural crops (Larson *et al.*, 2021).

Drought

Buckwheat plants under drought stress bloom less and produce less nectar per flower, and although the sucrose content in the nectar is lower, the total amount of sugar is stable and there is no change in the amount of pollen per flower. In addition, although the total amount of volatile compounds emitted by flowers did not change, they secreted more (Z)-3-hexenol, isobutyraldehyde, 2-methylbutanal and 3-methylbutanal compounds, and the number of pollinators visiting drought-affected plants decreased, especially the visitation rate of bumble bees, honey bees and flies decreased significantly (Rering *et al.*, 2020).

Diseases, Fungi and Microorganisms

Apple flowers infected with *Erwinia amylovora* release repellent volatile compounds such as methyl salicylate,

making them less attractive to honey bees (Cellini *et al.*, 2019). As viral loads of various pathogens such as deformed wing virus (DWV) and its variants increase in bees, olfactory sensitivity decreases and gene expression of some olfactory proteins (OBP) decreases (Silva *et al.*, 2021). Entomopathogenic fungi can be effective in controlling insect pests both through direct application and by living in plant tissues. In melon plants treated with *Beauveria bassiana*, this fungus internally colonized the plant and spread to the flowers. These plants flowered earlier, produced more pollen and secreted higher levels of volatile compounds that attract pollinators such as D-limonene and benzeneacetaldehyde than the control group (González-Mas *et al.*, 2023).

The microorganisms living in nectar can change the overall odor of the flower with the scents they produce and this can affect the flower preferences of bees (Rering *et al.*, 2018a; Rering *et al.*, 2018b). In a study conducted by collecting 1170 flower samples from 28 different nectar-producing plant species native to California, the odors produced by microorganisms living in nectar could be detected by honey bees and bees preferred flowers according to these odors. Fungal compounds such as 2-ethyl-1-hexanol and 2-nonanone were especially remarkable for bees. In addition, the yeast *Metschnikowia reukaufii* was found to be the microorganism producing the most attractive odors for bees (Rering *et al.*, 2018a).

CONCLUSIONS AND RECOMMENDATIONS

Recent studies have detailed the chemical composition of volatile organic compounds (VOCs) released from the flowers of various plant species with high economic value in agricultural production and examined their behavioral and electrophysiological effects on different bee species. These studies show that plant species-specific VOC profiles significantly influence the interaction with the olfactory systems of pollinating insects, especially honey bees such as *Apis mellifera* and *Apis cerana*. However, environmental conditions (e.g. temperature, presence of competitive floral resources and seasonal variability) and morphological and physiological differences among bee species also significantly shape responses to these chemical signals. Flowers of some plant species, despite their low nectar content, can attract pollinators due to specific VOC compounds, whereas some species, despite their high VOC production, are not preferred by bees. These

findings suggest that the effects of floral odors on bee attractiveness should be considered not only in terms of chemical content but also in an ecological context. Accordingly, understanding the potential of floral VOCs to drive pollinator behavior provides an important knowledge base for both the development of sustainable pollinator management strategies and applications to increase fruit yield.

Plant breeding programs emphasize the need to focus on improving floral traits to attract honeybees more effectively. In order to increase agricultural productivity and promote pollination, it has been suggested that optimizing the floral scent of plants by synthetic means could be an effective method to attract pollinators (Mas *et al.*, 2018). For instance, by analyzing the floral odors of two different almond cultivars (*Prunus dulcis*, cv. Guara and Viu; both cultivars are self-compatible), the odors that attract bees were identified. Honey bee colonies fed with a combination of these odors, the “Almond Imitation Odor” (AM)-benzaldehyde, R-(+)-limonene and (±)-linalool mixture-sucrose solution, were observed to be more active than colonies fed with unscented food. These colonies collected more pollen and showed significant increases in foraging activity and pollen storage rates (Farina *et al.*, 2023). In a similar study, an

artificial scent similar to the natural scent of kiwi flowers was added to sugar syrup and given to bees. Bees that were fed in this way collected more kiwi pollen than those fed with sugar syrup alone. These findings suggest that artificial scents can create olfactory memory in bees and, when combined with a sugar reward, can specifically direct bees to kiwi flowers. This method has the potential to direct bees even to plants that do not produce nectar (Estravis-Barcala *et al.*, 2024).

These findings suggest that artificial flower scents can be an important tool in shaping the behavior of bees and improving pollination processes. Especially in non-nectar-producing plants, guiding bees with such odors indicates a great potential for increasing agricultural productivity. This could be an important strategy to increase the productivity of natural pollinators and support sustainable agricultural practices. Moreover, considering the role of volatile compounds in different plants and environmental factors, it seems that plant-bee interaction needs to be studied in more depth. Such research could lead to more effective pollination management in agriculture in the future.

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