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9. Effective Communication: Plant Volatiles in Chemical Signalling

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Abstract

Plants emit numerous volatile organic compounds (VOCs) to convey various types of information to multiple recipients through chemical signalling. The information carried by VOCs is crucial to the survival of an individual plant or a conspecific community. Plant VOCs attract pollinators and act as warning signals of imminent environmental stresses. Chemical signalling through the emission and reception of plant VOCs underlies plant–plant, plant-insect and plant-microbe interactions, all of which play pivotal roles in the maintenance of ecosystems. The aforementioned interactions can be effectively used in biocontrol and sustainable agriculture to reduce dependence on fertilizers, pesticides and weedicides.

Essential oils (EOs), which are a subset of VOCs, have been reported to provide chemical signals to tissues and organs of animals, including humans. The effects of EOs on the brains and nervous systems of animals are manifested not only as changes in gene expression and protein synthesis but also as neurogenesis and behavioural changes. For example, inhalation of rosemary EO resulted in the significantly improved working memory of participants in an experimental study. Consequently, EOs are excellent candidates for the treatment of dementia, depression and anxiety through complementary and alternative medicine.

In summary, plant VOCs can establish chemical signalling and induce behavioural changes in a myriad of life forms. The present review article explores examples and applications of plant VOC–mediated chemical communication across the spectrum of life forms. It discusses the therapeutic potential of EOs as the primary treatment for anxiety and depression and attempts to identify the factors contributing to the universal nature of plant VOC–mediated chemical communication.

Keywords: Plant volatile organic compounds (VOCs), chemical signalling, essential oil, biocontrol

1. INTRODUCTION

The biosphere comprises multiple levels of the organisation. Chemicals constitute the language of communication within as well as among the levels of the organisation. The smooth functioning of the biosphere largely depends on chemical communication. Plants produce and emit a wide array of chemicals to communicate with other plants, microbes, phytophagous insects and herbivorous animals. Volatile organic compounds (VOCs) emitted by plants have received considerable scientific attention over the past few decades because of technological advancements and significant cost reduction in analytical methods such as gas chromatography and mass spectrometry (Dudareva *et al.*, 2004). A growing body of research shows that in plants, VOCs are semiochemicals that are involved in multiple crucial functions in addition to attracting pollinators and deterring herbivores. The use of plant VOCs for communication ensures fast and reliable transfer of specific and relevant information. For example, some VOCs that are emitted by the roots of some plants attract useful soil microbes (Scharf *et al.*, 2016) such as nitrogen-fixing bacteria. The floral VOCs of some plants exhibit antibacterial (Kerdudo *et al.*, 2017) or antifungal (Ambatkar and D'cruz, 2020) activity, which may be necessary to protect the reproductive parts of the flowers from microbes. Some plant VOCs are emitted to warn surrounding plants of the same or different species of imminent biotic and abiotic stresses. Plants usually emit several VOCs into the air around them. Stress-related VOCs are released in response to the following situations: pathogen attack, insect attack, mechanical damage, touch stress, heat stress, noxious chemicals, drought stress, salt stress and the presence of pathogenic soil microbes. A unique combination of VOCs may be emitted by plants depending on the stress encountered. Recipient plants have fine-tuned receptors that enable them to sense specific relevant VOCs from among the mixture in the air and correctly match their response with the upcoming stress (Ninkovic *et al.*, 2021).

Some of the typical components of plant VOCs are aldehydes, terpenoids and esters. Some VOCs are not perceived by the human olfactory system (Dudareva *et al.*, 2004). VOCs may be emitted by any part of a plant, such as the flowers, leaves, fruits, stem and roots. Furthermore, anatomical structures such as stomata and glands facilitate the volatilization of synthesized organic compounds under ambient natural conditions, particularly if the molecular weight of the compounds is less than 200 g/mol. (Karlsson, 2010). Several plant-derived terpenes are volatile under natural ambient conditions. The biosynthesis of terpenes, which represent the major constituent of plant VOCs, has been an active area of research because of the potential uses of terpenes in perfumes, flavours, and pharmacology. The biosynthesis of terpenes begins with the formation of a primary C5 unit called isopentenyl diphosphate (IPP). Next, IPP units undergo condensation to form terpenes consisting of 10, 15, and 20 carbon atoms. Finally, the newly formed terpenes are

modified by a group of enzymes known as terpene synthases to enhance their volatility through various reactions such as oxidation and acylation. Furthermore, terpene synthases can synthesize multiple products from a single substrate (Dudareva *et al*., 2004).

Plant VOCs may be constitutive or inducible (Wong *et al*., 2020). The stresses encountered by a plant significantly affect the profile of emitted VOCs. Consequently, plant VOCs represent a highly dynamic aspect of plant physiology. Plant VOCs are involved in communicating the current physiological status of an emitting plant; consequently, environmental factors, plant age or maturity and diurnal cycles cause qualitative and quantitative variations in the VOC profile of plants (Karlsson, 2010). As a result, the chemical profiles of plants of the same species may vary considerably with environmental and physiological factors (Wong *et al*., 2020).

Apparently, the emission and reception of VOCs represent important evolutionary advancements in plants. Clearly, plants that could emit herbivore-repellent VOCs were more likely to survive herbivore attacks. Similarly, those plants that emitted VOCs for attracting pollinators improved their reproductive success. Just as VOC emission systems have evolved in plants, receptor systems have co-evolved in animals, particularly insects. Consequently, plants and insects have been exhibiting interdependence for millennia. Some phytophagous insects have evolved highly sensitive olfactory systems that are extremely specific to one or a few VOCs. The recognised odours are mainly biologically relevant molecules such as host plant-specific VOCs (Karlsson, 2010) that can assist the insects in locating host plants as well as assessing the stage of maturity of the plant.

Essential oils (EOs), which are primarily odoriferous molecules, are derived from plant VOCs. Several EOs have been used extensively in traditional medicine and continue to be used in complementary and alternative medicine. Studies have shown that EO inhalation positively affects mood and memory (Moss and Oliver, 2012; Fung *et al*., 2021). EOs may be thought to convey chemical signals that elicit responses in animal tissues. The effects of essential oils on animal models and humans have been observed as changes in gene expression as well as behaviour. In particular, inhalation of EOs effectively elicits responses in the animal brain (Watanabe *et al*., 2015; Senturk *et al*., 2018; Karan *et al*., 2019; Ebrahimi *et al*., 2021). The gastrointestinal tract was reported to express receptors of odoriferous molecules in a recent study (Koyama and Heinbockel, 2020). The fact that the organs and tissues of animals, including humans, respond to EOs indicates possible co-evolution between animals and plants as well as the conservation of the ability to respond to chemical signalling by EOs. Furthermore, because microbes, plants, insects, animals and humans can all recognise and respond to chemical signals conveyed by plant VOCs, we can consider the possibility of plant VOCs being a universal chemical language. This review article explores some

examples of plant VOC–mediated chemical communication across the spectrum of life forms, discusses the therapeutic potential of EOs as a primary treatment for depression and anxiety, and attempts to identify the factors contributing to the universal nature of plant VOC–mediated chemical communication.

2. PLANT VOCS IN PLANT-MICROBE INTERACTIONS

The rhizosphere is the region of the soil in the immediate vicinity of the roots of a plant. It is a complex ecosystem and is the site of plant-microbe, plant-insect, and plant-plant interactions. The rhizosphere houses microbes that are advantageous to plants as well as those that are plant pathogens. Plant growth-promoting rhizobacteria (PGPRs) are a heterogeneous group of rhizosphere-colonizing bacteria that stimulate plant growth and prevent infection of plants by soil-borne pathogens.

Root exudates have been reported to play an important role in the plant-microbe interactions that occur in the rhizosphere (Neal *et al.*, 2012). Root exudates provide a carbon source for microbes, and some of the components of root exudates are signalling molecules that selectively attract some microbes towards a plant's roots while repelling some others (Badri and Vivianco, 2009). Microbial populations respond to root exudates through positive and negative chemotaxis. Organic acids, such as malic acid and citric acid, are important components of root exudates (Ling *et al.*, 2011) and regulate plant-microbe interactions (Yuan *et al.*, 2015). Root exudates are generally non-volatile and diffuse over short distances. However, in the rhizosphere, VOCs diffuse rapidly and effectively over long distances through the gas- and water-filled spaces in the soil matrix because of their lipophilic nature (Schulz-Bohm *et al.*, 2018).

The roots of numerous plants emit VOCs for communicating with soil microbes in the belowground environment (Ninkovic *et al.*, 2020). Plant-microbe communication results in either a symbiotic or commensal association. A study showed that the hydroponic application of the volatile ester γ-caprolactone chemotactically attracted the bacteria *Pseudomonas* and *Rhodococcus* to colonise potato roots (Cirou *et al.*, 2011). *Pseudomonas* (Frommel *et al.*, 1993) was reported to stimulate growth in potato plants, while *Rhodococcus* was reported to prevent soft-rot in potatoes (Latour *et al.*, 2013). Thus, VOCs clearly mediate communication and establish associations between plants and microbes.

Some root VOCs directly act as antibacterial agents and contribute to belowground plant defence (Ninkovic *et al.*, 2020), while some others act as signals emitted by plants to recruit and attract plant-beneficial microbes that assist the plants in containing or fight a pathogenic attack. A study on root VOCs emitted by *Carex arenaria* showed that soil bacteria, including *Paenibacillus* sp., *Collimonas pratensis*, and *Pseudomonas* sp., which were isolated from the rhizosphere of *C. arenaria*, exhibited positive chemotaxis in response to *C. arenaria* root VOCs. Furthermore, infection by *Fusarium culmorum* altered the root VOC profile of *C. arenaria* plants.

Both uninfected and infected plants emitted VOCs consisting of aromatic compounds (approximately 50%), such as benzonitrile or benzofuran, and esters (approximately 15%), such as γ-nonalactone or γ-decalactone; however, the root VOCs of the infected plants consisted of a higher percentage of alkenes and the monoterpene (Z)-limonene oxide than the uninfected plants. Moreover, the tested bacterium *Collimonas pratensis* showed increased migration towards root VOCs emitted by the infected plants (Schulz-Bohm *et al.*, 2018). *Collimonas* strains have been reported to produce antifungal compounds (Song *et al.*, 2015) against multiple soil fungi (Leveau *et al.*, 2010). Clearly, the VOCs emitted by the roots of the infected *C. arenaria* plants recruited and attracted *C. pratensis* into the rhizosphere for assistance in controlling the fungal infection. In addition, *Collimonas fungivorans* was reported to facilitate biocontrol of tomato foot and root rot caused by *F. oxysporum* f. sp. *radicis-lycopersici* (Kamilova *et al.*, 2007).

Plants secrete root exudates or release root VOCs to recruit suitable microbes from among the pool of soil microbiota; thus, a heterogeneous community of beneficial microbes is established in the rhizosphere. Some of the microbes colonise the roots. The positively chemotactic microbes are naturally tolerant to increasing concentrations of root exudates or root VOCs; alternatively, they adapt themselves accordingly. Hence, plant-microbe interactions in the rhizosphere have probably resulted in the co-evolution of plants and microbes. The bacteria that are repelled by the exudates are usually unsuitable or harmful for the plant (Badri and Vivianco, 2009; Hartmann *et al.*, 2009).

Biocontrol of plant diseases is an effective, chemical-free approach to pest management and disease control in crops. Furthermore, PGPRs are ideal candidates for biocontrol of plant diseases. PGPRs have been successfully applied on a commercial scale. The interactions between crop plants and PGPRs have become an area of active research because of their potential for use in biocontrol in agriculture (Zhang *et al.*, 2013). For example, *Bacillus amyloliquefaciens* SQR9 from the rhizosphere of *Cucumis sativus* prevented the invasion of the host plant by *F. oxysporum* f. sp. *cucmerinum* J. H. Owen (FOC). *B. amyloliquefaciens* competed with the fungal pathogen for the availability of nutrients and space (Xu *et al.*, 2013; Gu *et al.*, 2017). Similarly, *B. subtilis* in the rhizosphere of banana plants was reported to protect the host plants from *F. oxysporum* f. sp. *cubense* race 4 (FOC) (Zhang *et al.*, 2011). A recent review compiled data on the efficacy of different biocontrol agents in preventing *Fusarium* wilt in micropropagated banana plants. The biocontrol agents were administered as spore suspensions, bioformulations and organic amendments at different stages of development of the plants, namely the in vitro, nursery, transplantation and post-transplantation stages (Bubici *et al.*, 2019).

TABLE 1: Efficacy of biocontrol agents preventing Fusarium banana wilt in micropropagated plants (Bubici *et al*., 2019)

Biocontrol agent	Percentage of control (efficacy)
Pseudomonas spp.	79
Endophytes and *Trichoderma* spp.	70
Arbuscular mycorrhizal fungi, *Bacillus* spp. and non-pathogenic *Fusarium* strains	42–55

Climate change and the exponential increase in the demand for agricultural produce have necessitated sustainable agricultural practices. The use of plant-microbe interactions to stimulate crop growth and the adoption of biocontrol methods to manage plant diseases constitute important aspects of sustainable agricultural practices. The optimal use of plant-microbe interactions in agriculture can considerably reduce the need for chemical fertilizers and pesticides. The use of naturally occurring rhizobacteria to increase crop production would be an appropriate strategy because it would help to maintain the balance of the soil ecosystem.

3. PLANT–PLANT INTERACTIONS

VOCs enable plants to communicate with one another rapidly over long distances in homogeneous and heterogeneous plant communities. The ability to emit and receive signals in the form of VOCs provides plants with a survival advantage. VOC-based communication directs the rapid adaption of plants to changes in their surroundings and considerably improves their fitness (Ninkovic *et al*., 2020). Consequently, plants invest energy and resources in the biosynthesis of VOCs, emission of VOCs, development of structures for VOC perception and maintenance of cellular signalling pathways to respond rapidly to VOC-mediated signals.

Generally, aboveground VOCs that are emitted by the leaves and flowers of a plant can warn conspecific plants in the vicinity of impending herbivore attacks or environmental stresses. (Ninkovic *et al*., 2020) Some floral VOCs convey highly specific signals that regulate growth and development in conspecific plants in the surrounding area. An experimental study showed that floral volatiles can synchronize flowering in conspecific plants (Burdon *et al*., 2015). The synchronized flowering of conspecific plants considerably increases the overall reproductive success of a species in a given area (Burdon *et al*., 2015), which is advantageous to a plant species, particularly if it is under abiotic stress.

Plants release large quantities of VOCs into the surrounding air. Consequently, plants have evolved receptors that are fine-tuned to some crucial VOCs to enable them to sift out relevant signals from noise. However, occasionally, the noise may carry information that may improve the survival of unrelated plants in the surrounding. In heterogeneous plant communities, some non-target plants may also respond to the

information conveyed through VOCs by a plant to other conspecific plants. Non-target plants receive cues, while the target plants receive signals from the released VOCs. Cues are signals that are not intended for the receiving plant, whereas signals are specifically sent to inform receiving target plants. The effects of interaction between a plant and its environment are reflected in inducible VOC emissions. Hence, inducible VOCs provide accurate information of a plant's current physiological status, while constitutive VOCs provide information of genetic identity. Seedlings of the parasitic plant *Cuscuta pentagona* can identify their preferred host plant, *Lycopersicon esculentem,* from among other plants by detecting and recognizing the constitutive VOCs of the host plant, which includes characteristic compounds such as β-phellandrene and β-myrcene (Ruyon, Mescher and De Moraes, 2006). However, a plant attacked by phytophagous insects will be induced to produce and emit jasmonic acid and methyl jasmonates that can warn surrounding plants of the presence of phytophagous insects.

Tactile stimulation in maize plants was demonstrated to induce quantitative changes in VOC profile and gene expression within a few minutes of stimulation. The VOC emission levels of the stimulated plants were significantly higher than those of the unstimulated control plants. Furthermore, higher concentrations of specific aldehydes and terpenes were detected in the emissions of the treated plants than in those of the control plants (Markovic *et al*., 2019). Moreover, the untreated neighbouring maize plants sensed the changes in the VOCs emitted by the stimulated plants and received airborne signals of an impending tactile stimulus; consequently, they responded by exhibiting similar gene expression patterns as the stimulated plants. In the aforementioned study, the stimulated plants modified their VOC profile, which warned the neighbouring plants and primed them in advance.

Plants must rapidly process information conveyed by VOCs and exhibit a response that matches the impending stress. Delayed or erroneous responses to VOC-based stress signals can cost plants dearly. Hence, plants have systems to receive and process information conveyed by VOCs. These detection systems are fine-tuned to a few selected components or a blend of VOCs and their relative proportions. Some plants emit herbivore-induced plant volatiles (HIPVs) when attacked by herbivores. HIPVs are not usually released by undamaged plants (Mumm and Dicke, 2010), and the presence of HIPVs indicates a notable change in physiological state, and consequently, VOC profile. Qualitative and quantitative changes in VOC profiles are rapidly detected by target plants, which respond appropriately. Stresses such as herbivore attacks and drought alter the composition of floral volatiles. (Ramos and Sheiestl, 2020). Typically, plants that are damaged by herbivore feeding emit jasmonates, such as jasmonic acid and methyl jasmonate, to warn surrounding plants of herbivores and induce the expression of plant defence genes for protection (Engelberth *et al*., 2003). The overall effect

is that the plant becomes less attractive to herbivores and less liable to herbivore-induced damage.

In the belowground environment, root VOCs play a crucial role in plant-plant interaction. An experimental study that used sensitive equipment to detect root VOCs demonstrated that the roots of young plants are actively involved in VOC-mediated communication. They actively scan their surroundings to identify conspecific and non-conspecific plants (Elhakeem *et al*., 2018). The composition of root volatiles varies with the phenotype and sex of the plant. Root volatiles carries genetic information. Consequently, root VOC detection systems can sense the degree of relatedness between themselves and adjacent plants. Jasmonic acid was reported to be a component of root VOCs in wheat plants (Kong *et al*., 2018). VOC detection by the roots of a plant enables it to recognize whether adjacent seedlings are self, non-self, or kin. Usually, self and kin are conspecific plants; hence, their growth may not be inhibited. Studies have shown that plants such as rice and soybean exhibit allelopathy. The roots of allelopathic plants emit growth-inhibiting VOCs to retard the development of adjacent non-conspecific plants to reduce competition for shared resources (Wong *et al*., 2020). However, plants have been reported to emit growth-promoting VOCs if they are surrounded by conspecific plants (Ninkovic *et al*., 2020).

VOC-mediated aboveground plant-plant interactions can be used effectively in agriculture to reduce crop losses due to biotic and abiotic stresses, such as herbivory and drought stress, respectively. Experimental studies are needed to identify the responses of different crops to various stress-related VOCs. The findings of these studies will assist in the development of strategies to enable crops to resist herbivory, which in turn can prevent crop losses. Furthermore, the use of specific VOC components that warn plants about upcoming abiotic stresses, such as high temperature and drought, will improve the resilience of crops to these stresses. Moreover, information on root-VOC-mediated inhibition of plant growth (allelopathy) can be used to develop strategies that enable crops to control the growth of weeds in their vicinity. Thus, VOC-mediated plant-plant interaction, whether in the aboveground or belowground environment has potential for use in sustainable agriculture because it can reduce dependence on insecticides and weedicides.

4. PLANT-INSECT INTERACTIONS

Plants and insects have co-existed for millennia and co-evolved because of their mutual dependence. Plants and insects rely heavily on VOCs for communication. VOCs may be emitted from the flowers, leaves or roots of plants. An important aspect of plant-insect interaction is entomophily or insect pollination. Plants depend on insects to carry pollen from the flowers of one plant to those of the same plant or of another conspecific plant. In return, plants provide the pollinating insects with food as well as sites to hide, mate and deposit eggs (Karlsson, 2010).

The interaction between flowering plants and flower-visiting insects has played a pivotal role in establishing terrestrial ecosystems (Patrício-Roberto & Campos, 2014). Plants have evolved various visual attractants for their pollinators, such as brightly coloured flowers, modified leaves, and conspicuous structures, to improve their chances of pollination. However, to attract pollinating insects over long distances of several hundred metres, plants use an array of VOCs (Bouwmeester *et al*., 2019). VOCs have high vapour pressures under normal ambient conditions and diffuse rapidly through the air (Karlsson, 2010). Furthermore, in plant-insect signalling, colours cannot be used as highly specific signals because insects exhibit limited sensitivity towards subtle colour differences. However, because insects possess numerous olfactory neurons, complex combinations of plant VOCs can be used for specific signalling (Bouwmeester *et al*., 2019). The VOCs emitted by plants, particularly flowers, provide pollinators with highly specific information of the genetic identity as well as the current physiological status of the emitting plant. Clearly, plants invest energy in the biosynthesis and emission of VOCs for attracting pollinators to improve their reproductive success.

Co-evolution results in optimal interaction and maximizes benefits for both partners in mutualistic associations. For example, some plant VOCs are structurally similar to or identical to the hormones of pollinators to ensure that they are detected by the target insects' olfactory system; subsequently, the information sent by the plant is processed in the insect's central nervous system. The processed information enables insects to identify the emitting plant as a potential food source or mating site. Some plant VOCs can act as deterrents that enable certain insects to avoid the emitting plant altogether (Bruce, 2005). VOCs can elicit physical responses, such as foraging behaviour, mating behaviour and oviposition, in their pollinators. Furthermore, the presence of host plant VOCs was reported to improve the responsiveness of some phytophagous insects to their respective sex pheromones. An experimental study compared the lending rates (for mating) between two groups of male moths *(Sodoptera exigua).* The first group was exposed to only a sex pheromone, while the second group was exposed to the same pheromone in the presence of benzaldehyde and linalool from the host plant (cabbage). The moths in the second group exhibited significantly higher lending rates than those in the first group (Deng *et al*., 2004). Notably, some plant VOCs can elicit different behavioural responses in different insects depending on whether they are pests that invade the emitting plant or natural enemies of the pests. Consequently, VOCs from a single plant may cause avoidance behaviour in its pest, while simultaneously attracting the pest's natural enemies (Bruce *et al*., 2015).

Some phytophagous insects exhibit sex-dependent differences in the receptiveness of signalling compounds. For example, the female turnip moth has a higher sensitivity to low concentrations of plant VOCs than

the male moth, but it cannot sense pheromones; however, the male moth can sense plant VOCs as well as pheromones.

Studies have shown that the specificity of VOC-based signals for communicating with pollinators is affected by the ratio of its constituents (Bohman *et al*., 2018b) as well as the isomeric form of optically active components (Bohman *et al*., 2018a). Changes in the ratio of the constituents of plant VOCs have been experimentally demonstrated to attract different target insects. For example, the orchid *Caladenia crebra* is pollinated by a thynnine wasp. The active VOC emitted by *C. crebra* is a blend of four methylthiophenols. A blend of two of these compounds in the ratio 10:1 attracts the legitimate pollinator *Campylothynnus flavopictus*; however, if the ratio is altered to 1:1, wasps of an undescribed *Campylothynnus* species are attracted to the orchid (Bohman *et al*., 2017; Bouwmeester *et al*., 2019). Maintaining the specificity of signals meant for pollinators is necessary for plants to prevent frequent visits by nectar thieves and larcenists that consume floral nectar but do not necessarily pollinate the flowers they visit.

Many phytophagous insects have evolved highly sensitive and selective olfactory systems. Their olfactory neurons are tuned to a small number of chemical compounds (Bruce, 2005) produced by plants or other insects to minimize the effects of background noise and facilitate rapid processing of information about food availability and suitability, predator presence and the sexual status of potential mates (Karlsson, 2010).

Insects, like the potato tuber moth, which feed entirely on plants belonging to the family Solanaceae (Karlsson, 2010) are called specialist herbivores. The potato tuber moth is a common pest on potato and tomato crops in India. Some specialist herbivores have been reported to synchronize their life cycles with that of the plant to ensure that each stage in the insect's lifecycle obtains optimal nutrition or adequate shelter on the target plant (Thiel *et al*., 2020).

An attack by herbivores or mechanical damage alters the VOC profile of plants. In fact, any biotic and abiotic stresses can change the VOC profile of a plant (Ninkovic *et al*., 2020) qualitatively or quantitatively. For example, under stress, the total amount of VOCs emitted from the flowers far exceed that emitted from the leaves (Ibrahim *et al*., 2010) probably because the emitting plant would attempt to reproduce before succumbing to the imminent stress (Burdon *et al*., 2015).

An indirect method by which plant VOCs protect plants from insect herbivores is by attracting another type of insect that is either a predator of the herbivore or naturally aggressive towards it. After the herbivore attacks, the plant typically emits VOCs that inform the predator of the presence of its prey (the herbivore) (Mortensen, 2013). This method of defence is often referred to as tritrophic defence because it involves members from three levels in the food web. An experimental study on *Phaseolus lunatus* showed that *P. lunatus* plants attacked by the mite

Tetranychus urticae emitted VOCs that attracted *Phytoseiulus persimilis*, which is a predator of *T. urticae*. Furthermore, the wounded *P. lunatus* induced neighbouring unharmed *P. lunatus* plants to emit VOCs that attracted *P. persimilis* as a defensive step against a possible attack by the mite *T. urticae*.

Herbivory has exerted enormous selection pressure on plants. Consequently, plants have evolved numerous strategies, including the emission of herbivore-deterring VOCs as well as of VOCs that attract the natural enemies of the attacking herbivores. These dual strategies enable plants to minimize losses caused by attacks by herbivores, survive and reproduce successfully. The use of plant VOCs to deter phytophagous insects has considerable potential in sustainable agriculture. A recent study described the development of a genetically modified wheat variety that expressed genes coding for the enzymes *(E)*-β-farnesene synthase (EβfS) and the precursor farnesyl diphosphate synthase (FPPS). The sesquiterpene hydrocarbon *(E)*-β-farnesene or (Eβf) is an alarm pheromone in multiple species of pest aphids, such as *Sitobion avenae* and *Rhopalosiphum padi*. Eβf was reported to cause dispersion of aphids and exhibit aphid-repellent activity. Moreover, Eβf was shown to promote foraging behaviour in the natural enemy or parasitoid of the aforementioned aphids, namely *Aphidius ervi*. The results showed that the transgenic wheat plants emitted significantly higher levels of Eβf than the non-transgenic plants. The emitted VOCs containing Eβf caused a visible alarm response in colonies of *S. avenae* and *R. padi*. The aphid pests spent significantly less time on the transgenic plants than on the non-transgenic plants. The emitted Eβf also promoted foraging behaviour in *A. ervi* on the transgenic plants, which eventually dissuaded the aphids from attacking the transgenic plants (Bruce *et al*., 2015).

The integration of apiculture into mainstream agriculture and promotion of rearing of pollinating insects other than bees, such as hoverflies, can significantly improve crop productivity (Doyle *et al*., 2020). The potential of plant VOCs as attractants for pollinators can be harnessed to boost agricultural production and reduce the use of chemical fertilizers. Experimental studies to determine the optimal ratios of component VOCs that promote pollination are warranted. Similarly, the identification of environmental cues that alter the composition of plant VOCs is necessary.

The use of transgenic crops that can be induced to emit sufficiently high concentrations of pest-repelling VOCs against an imminent pest attack can considerably improve crop production. The use of VOC-based pest-repellent strategies may reduce the use of pesticides in agriculture. Although the use of VOC-based strategies in agriculture appears to be environmentally friendlier and more beneficial than current practices, a thorough assessment of the probable ecological effects of the introduction of new pollinators as well as the effects of repelling or deterring crop pests on farmlands and their surrounding areas is necessary before implementing VOC-based strategies.

5. PLANT–LARGE HERBIVORE INTERACTIONS

Plants have developed structural and chemical defence methods to protect themselves from large herbivores. Structural defence methods include modification of the stem, leaves and stem epidermis that give rise to thorns, leaves and prickles that effectively deter cattle and herbivorous wild animals. The aforementioned strategies do not involve VOCs. Some common examples of plants that use this defence method are bougainvillea, citrus plants and roses. Some other plants have developed chemical methods of defence. These plants produce and store large quantities of secondary metabolites such as tannins and alkaloids in their leaves to reduce their acceptability to large herbivores. Wattles store tannins in their leaves to deter herbivores. Some plants like poison ivy store inflammation-causing substances in their leaves to prevent herbivory (Mortensen, 2013).

6. ESSENTIAL OILS AND SIGNALLING IN ANIMAL AND HUMAN BRAINS

Essential oils (EOs) may be considered a subset of plant VOCs (Mihaescu *et al*., 2021) because EOs represent the fraction of plant VOCs that can be perceived by the human nose as fragrant odours. EOs are mainly obtained by distilling EO-rich plant material. EOs may be obtained from the flowers, leaves, stems, roots, fruit or seeds of an EO-bearing plant because any part of a plant may synthesize fragrant compounds. EOs are primarily composed of monoterpenes and sesquiterpenes, although aldehydes, esters, alcohols and aromatic hydrocarbons also contribute to the fragrance and therapeutic properties of EOs (Worwood, 1996). EOs are mixtures of low-boiling and low–molecular weight (≤300 Da) compounds with high vapour pressures at 760 mmHg; hence, they diffuse rapidly through the air.

Although EOs can be administered either through inhalation, topical application, or ingestion, inhalation is the most common route for administration and is considered most effective. The effectiveness of EO inhalation may be attributed to the volatility of EOs (Fung *et al*., 2021). EOs delineate a chemical language that is recognized and processed by the mammalian brain. When EOs are inhaled, they initiate numerous signalling events in the nervous system, including the brain. Some of the mechanisms of the action of EOs include regulation of monoamine levels and promotion of neurogenesis (Fung *et al*., 2021). The overall results of EO signalling are manifested as therapeutic effects such as stress relief and anxiety reduction (Malcolm and Tallian, 2017) as well as physiological effects such as restoration of elevated blood pressure and respiratory rate to normal levels.

EOs have been reported to elicit a wide variety of responses in the brain (Watanabe *et al*., 2015; Senturk *et al*., 2018; Karan *et al*., 2019; Ebrahimi *et al*., 2021). Recent studies involving human volunteers have shown that several EOs, particularly when inhaled, activate a different region of the brain because of the anatomical proximity between the

nose and brain. Odoriferous molecules, such as EOs, stimulate the limbic system, which consists of the amygdala, hippocampus and hypothalamus (Moss and Oliver, 2012; Fung *et al*., 2021). In the human brain, the limbic system is responsible for memory, mood, learning and emotion. Neurophysiological and brain mapping studies have been conducted on human volunteers to determine which brain regions are activated on receiving different olfactory signals. The olfactory cortex comprises the piriform cortex, olfactory tubercle, and entorhinal cortex, and each of these regions projects information and signals to various components of the limbic system. Olfactory signals are unique because they can project information to the olfactory region in the brain without involving the thalamus. Olfactory signals are conveyed through the ipsilateral axon directly to the piriform and orbitofrontal cortex, which are involved in the identification of odour and integration of olfactory information. Hence, odour perception, memory, emotion and endocrine function share direct, specific and highly intricate connections in the human brain (Fung *et al*., 2020).

Inhaled EOs have been reported to reach the brain in three possible paths of which two involve the olfactory system, while one involves the respiratory system. Inhaled EOs may attach themselves to olfactory chemoreceptors on olfactory sensory neurons within the nasal epithelium and relay signals to the olfactory lobes and connected regions of the brain. Alternatively, small inhaled EO molecules are thought to directly penetrate various brain areas through the network of olfactory neurons and initiate a cascade of events at the cellular and molecular levels. However, if inhaled EOs enter the respiratory system, they diffuse and dissolve in the respiratory epithelium, dissolve in the bloodstream, and travel to the brain. EOs can cross the blood-brain barrier (BBB) because of their small size and lipophilicity (Fung *et al*., 2021).

Irrespective of the path of entry of EOs into the human body, several EOs have been reported to increase the rate of neurogenesis, regulate neurotransmitter levels, activate brain regions and alter blood chemistry (Xu *et al*., 2015; Ayoub, 2017; Xiong *et al*., 2018). The overall result of the action of EOs is notable changes in mood and emotional state. Some cells in the gastrointestinal tract (GIT) and skin express receptors of odoriferous molecules although the GIT and skin are both entirely composed of non-olfactory tissue. Furthermore, some of the non-olfactory receptors in the GIT and skin are activated by odoriferous molecules. (Koyama and Heinbockel, 2020). Hence, exposure to odoriferous molecules, such as EOs, results in complex effects involving multiple organ systems in humans. The therapeutic effects of EOs may result from the action of one constituent or the synergistic action of multiple constituents (Fung *et al*., 2021).

The therapeutic uses of EOs have recently been gaining importance. Aromatherapy has become a recognized method of achieving and maintaining wellness. Furthermore, complementary and alternative

medicine recommends the use of EOs for the effective treatment of various conditions and diseases, ranging from depression to cancer (Worwood, 1996). Moreover, aromatherapy treatments for relaxation and rejuvenation have become an important part of tourism and the hospitality business.

Several studies have assessed the effectiveness of EO-based treatments in reducing anxiety, stress and depression-like symptoms in mouse and rat models (Fung *et al*., 2021). In animal studies, standardized tests, such as the forced swim test (FST) (Yankelevitch-Yahav, *et al*., 2015) and elevated plus maze (EPM) test (Walf and Frye, 2007), are used to assess the effectiveness of EO-based therapies in treating depressive-like and anxiety-related behaviour, respectively. By contrast, in studies involving human volunteers, the severity of depression and anxiety can be assessed using questionnaires or by conducting interviews to record subjective emotional states.

Over the past three decades, depression has become a common mental disorder worldwide and is considered the leading cause of disability (WHO, 2017). Similarly, the global prevalence of anxiety disorder has been increasing in recent years, and anxiety has become a primary mental health concern (WHO, 2017). In India, the prevalence of depression and anxiety disorders has increased steadily over the past two decades (Sagar *et al*., 2020), particularly in adolescents (Sagar and Selvakumar, 2021). Currently, prescribed medicines for both disorders are associated with withdrawal symptoms and dependency. Often, patients with depression and those with anxiety experience relief from their symptoms only many weeks after starting medication (Malcolm and Tallin, 2020); notably, delayed relief is a major contributor to non-compliance. Hence, patients now prefer therapies that are based on alternative or complementary medicine (Worwood, 1996).

Currently, the accepted hypothesis regarding the pathophysiology of depression is the 5-HT or serotonin hypothesis. According to this hypothesis, the signs and symptoms of depression result from 5-HT deprivation (Fung *et al*., 2021). Consequently, several studies on the effectiveness of EO-based therapy in alleviating the symptoms of depression have demonstrated the effects of EOs on the 5-HTergic system. A clinical study assessed the effects of an 8-week treatment involving inhalation of or therapeutic massage with a combination of lavender, sweet orange and bergamot EOs. The study population, which comprised community-dwelling elderly adults with depressive symptoms, was divided into two groups, namely the treatment group and the control group. The depressive symptoms of both groups were measured before the study by using the geriatric depression scale and patient health questionnaire-9 to obtain baseline information. Baseline 5-HT levels in the plasma were also recorded. After 8 weeks, the plasma 5-HT levels of the treatment group were significantly higher than the baseline levels. Furthermore, participants in the treatment group showed fewer depressive symptoms after treatment than at baseline (Xiong *et al*., 2018).

Similarly, in an experimental study on mice, inhalation of compound anshen EO (a mixture of sandalwood, rose, aloe, lavender, frankincense, neroli and sweet orange EOs) improved sleep quality and increased 5-HT levels (Zhong *et al*., 2019). Furthermore, exposure to *Cananga odorata* (ylang ylang) EO, which is commonly used to relieve stress and anxiety and alleviate depression in humans, was reported to increase 5-HT levels in the hippocampus of mice (Zhang *et al*., 2016).

In addition to a reduction in 5-HT levels, changes in dopamine (DA) levels are crucial in the progression of depression. In the human brain, DA is responsible for the feelings of excitement, pleasure and euphoria. Several basic and clinical studies have shown that reduction in DA levels or DA reception occurs in depression. Notably, anhedonia, a condition in which an affected individual is unable to feel pleasure in normally pleasurable activities and exhibits a lack of interest in those activities, is considered a core symptom of depression. Anhedonia has been shown to be caused by low levels of DA (Fung *et al*., 2021). An experimental study on rats showed that vanillin (the main fragrant component and flavouring agent in vanilla) exhibited an antidepressant effect by increasing the levels of 5-HT and DA in the brain (Xu *et al*., 2015).

Over the past two decades, multiple studies on animal models of depression have revealed widespread suppression of neurogenesis (Malberg *et al*., 2000; Santarelli *et al*., 2003; DeCarolis and Eisch, 2010; Ruan *et al*., 2014; Lee *et al*., 2016; Ayoub, 2017). Lavender EO was reported to show antidepressant activity by preventing the suppression of neurogenesis. Furthermore, lavender EO was reported to promote the dendritic growth of immature neurons and maintain serum levels of a brain-derived neurotrophic factor (BDNF) (Sánchez-Vidaña *et al*., 2019). Lavender EO is likely to be effective in reducing the rate of neuronal degeneration in age-related conditions such as dementia and Alzheimer's disease. Promoting neurogenesis is a strategy that is being considered to treat or retard the progression of ageing-related degenerative conditions of the brain (DeCarolis *et al*., 2010). A study investigated the effects of aromatherapy by using lemon, rosemary, lavender and orange EOs in elderly patients with dementia and Alzheimer's disease. After the treatment period, all participants showed significantly improved cognitive function without any side effects (Jimbo *et al*., 2009). Inhalation of lavender EO increased BDNF levels in the hippocampus of rats exhibiting depression-like behaviour, which was induced using corticosterone (Sánchez-Vidaña *et al*., 2019; Lee *et al*., 2016).

The involvement of monoamine neurotransmitters such as 5-HT, DA and gamma-aminobutyric acid (GABA) in anxiety disorder has been frequently discussed in animal studies on anxiety. Many studies have shown that some EOs exhibit antidepressant and anxiolytic activities because they can interact with receptors of multiple monoamine neurotransmitters, which increases the levels of the neurotransmitters.

The anxiolytic effects of EOs in rats or mice have been demonstrated. The anxiety levels of the experimental animals were assessed using the EPM and open field test (OFT). Rats and mice show a natural preference for dark, enclosed spaces as well as a natural curiosity to explore new spaces. The EPM test allows researchers to observe how much time rodents spend in open and closed spaces or arms of the maze (Walf and Frye, 2007). Furthermore, rodents prefer to stay close to the walls of an unfamiliar open space. The OFT enables researchers to compare the time spent by rodents in the open area and near the walls. The locomotion of rodents in the open area is also assessed (Nordquist *et al*., 2017). Stress and anxiety, which modify behaviour, have been reported to suppress the natural curiosity of rodents. Consequently, the closed-arm time of stressed rodents increases in the EPM. Similarly, stressed rodents stay close to the walls and exhibit little locomotion in the OFT. The administration of anxiolytic drugs increases the open-arm time and locomotor activity in the EPM and OFT, respectively. Studies on rodents have shown that EOs of lavender, lemon and ylang-ylang increase open-arm time in the EPM and locomotor activity in the OFT (Komiya, Takeuchi and Harada, 2006; Chioca *et al*., 2013; Lee *et al*., 2016). Hence, lavender, lemon and ylang-ylang EOs exhibit anxiolytic activity.

A study involving human volunteers showed that lavender and chamomile EOs reduced depression and anxiety in older adults (Fung, Tsang and Chung, 2012). Inhalation of lavender EO during panic attacks was reported to reduce blood pressure and respiratory rate, which indicates its anxiolytic effect (Karan, 2019). Furthermore, patients who inhaled lavender EO before abdominal surgery reported less anxiety than the control patients.

Some EOs may alter cognitive performance. A recent study examined the effects of rosemary EO, which is rich in 1,8-cineole, on the cognitive performance in human volunteers. The volunteers were divided into treated and control (untreated) groups. Both groups were asked to perform serial subtractions to test three domains of cognitive function, namely working memory, executive function and sustained attention. The treated group was exposed to rosemary EO by using a diffuser in the testing cubicle. The treated group exhibited significantly higher performance than the control group. Thus, rosemary EO was concluded to improve cognitive function (Moss and Oliver, 2012).

Most studies on EO-based treatments used inhalation, which appears to be an easy, rapid and effective method of administration. Consequently, human olfaction must play a role in the maintenance of good health. The roles of human olfaction in nutrition, avoidance of potentially dangerous substances and mating have been studied in detail (Roberts *et al*., 2020). The role of human olfaction in preserving good health warrants additional research.

Clearly, EOs potentially provide an alternative to antidepressant and anxiolytic drugs. Furthermore, the use of EOs is unlikely to be addictive

or habit-forming if used over an extended period (Malcolm and Tallian, 2017). The ability of EOs to act as signalling molecules in the brain and bring about physiological and behavioural changes indicates their therapeutic value. The effectiveness of EOs in altering physiological and behavioural states explains the gradual and widespread acceptance of aromatherapy and the steadily growing demand for it.

Lemon EO was reported to exhibit antidepressant activity in mice by altering levels of DA and 5-HT (Hao *et al*., 2013). People experiencing fatigue, lack of motivation and depression-like symptoms have been observed to benefit from the use of lemon EO during aromatherapy sessions (Worwood, 1996); moreover, clients with the aforementioned problems show a preference towards lemon EO. Empirical observations regarding EO preferences and mental states by aromatherapists can provide important information on the progression of conditions like depression. With sufficient information, aromatherapists may advise timely medical help and prevent the progression of depression in their clients. The question of whether the repeated preference of a specific EO to relieve specific symptoms of a medical condition indicates a predisposition to that clinical condition warrants research.

Globally, India is a major exporter of aromatic plants and their products; however, India's aromatic market share of 1.1% is being challenged by other exporters, such as China, Thailand and Cambodia. Increasing the annual production of aromatic plants will help to maintain and increase India's position in the global aromatic market (Sujatha *et al*., 2011) The cultivation of EO-bearing plants on agricultural land for intercropping may be beneficial to farmers considering the growing demand for natural EOs. The use of aromatic plants as intercrops in pear orchards was reported to effectively control pests on pear trees (Song *et al*., 2010). Areca nut plantations with intercropped *Cymbopogon flexuosus* showed a significant increase in yield per unit area. Moreover, the pH and organic content of the soil were maintained at optimal values because of intercropping. The cultivators also reported an additional income from sales of the aromatic plants (Sujatha *et al*., 2011). Some EO-bearing parts are hardy and adequately adapted for growth in arid regions; consequently, their requirement of water, pesticides and fertilizers is minimal (Kumar and Jnanesha, 2017). Various programmes, such as contract farming and guaranteed buy-back schemes, are being promoted by the Indian Government through institutions, such as the Central Institute of Medicinal and Aromatic Plants and Fragrance and Flavour Development Centre, to encourage Indian farmers to cultivate EO-bearing plants as a step towards meeting the domestic demand for aromatic or EO-bearing plants and increasing exports. The wide variety of climatic and soil conditions in India can be used effectively for sustainable commercial cultivation of numerous native and non-native EO-bearing plants with adequate consideration of the ecological effects of cultivating EO-bearing plants.

7. UNIVERSALITY OF PLANT VOC–MEDIATED CHEMICAL COMMUNICATION

The hypothesis underlying the present review article is that plant VOCs constitute a chemical language for universal communication and information exchange within the biosphere. At any given time, multiple lifeforms, of varying complexity, can simultaneously receive plant VOCs and process the information or signals conveyed by them. However, each receiving lifeform interprets the conveyed information in the context most relevant to its situation. Consequently, the VOCs emitted by a plant in response to an attack by a phytophagous insect can repel the herbivore while simultaneously attracting the predator of the herbivore. Chemically, plant VOCs are low-boiling and low-weight molecules; consequently, they diffuse rapidly through air and the soil matrix. Within living systems, the small size and lipophilicity of plant VOCs and EOs ensure swift diffusion into tissues, transport through blood and passage across the BBB. The chemical nature and molecular structure of plant VOCs (including EOs) are responsible for the universality of plant VOC-mediated communication.

A recent meta-analysis compared the VOCs produced by plant roots and soil microbes (bacteria and fungi). In total, 39 VOCs emitted by the roots of *Hordeum vulgare* (29 VOCs), *Arabidopsis thaliana* (8 VOCs), *Zea mays* (1 VOC) and *Vicia fabia* (1 VOC) were included in the study. The 39 VOCs included were grouped together on the basis of their biosynthesis and chemical classes. The 39 VOCs included 11 alcohols, 4 aldehydes, 2 aromatic compounds, 2 esters, 1 furan, 4 ketos, 1 organic acid, 2 sulphur compounds and 1 terpene. The results showed that numerous soil microbes produced VOCs that were also produced by plant roots. Furthermore, the bacteria *Proteobacteria and Firmicutis* sp. and the fungus *Ascomycetes* produce plant volatiles. The findings indicate the extent of intersection between plant and microbial volatiles Moreover, the findings support the possibility of the existence of a core set of VOCs that is common to plants and microbes (and possibly other lifeforms) that emit VOCs (Schenkel *et al*., 2015). VOCs are produced by the action of enzymes in specific biosynthetic pathways that can be traced back to responsible genes. Hence, the emission of identical VOCs by plants and microbes reflect genetic similarities that may have been conserved during the course of evolution. Furthermore, the emission of identical VOCs provides evidence of the universality of plant VOCs as signalling chemicals in the living world.

Some phytophagous insects like bark beetles sequester monoterpenes from the volatile compounds produced by their host plants as building blocks to synthesize their own pheromones because of the chemical and structural similarity between the monoterpenes and pheromones (Martin *et al*., 2003). Thus, signalling molecules synthesized in a plant system can be taken up by an insect system, probably modified, and reused as signalling molecules. This phenomenon also indicates the universality of plant VOCs as a means of chemical communication.

Numerous studies have demonstrated behavioural changes in phytophagous insects caused by plant VOCs. Similarly, EOs have been shown to cause behavioural changes in animal models of anxiety and depression as well as in human volunteers with the aforementioned conditions. Although the behaviour varies with the lifeform, the underlying mechanisms of action are likely to share similarities despite the differences in the complexity of the systems of insects and mammals.

8. CONCLUSION

Plant use VOCs to communicate and share information with various lifeforms in the biosphere and initiate behavioural changes in them. Plant VOCs represent a chemical language that is recognized and processed by multiple lifeforms of varying complexity. Plant VOCs that are involved in plant–plant, plant-microbe, and plant-insect interactions have tremendous potential for use in biocontrol and sustainable agriculture. If used appropriately, plant VOCs may reduce the dependence of agriculture on chemical fertilizers, pesticides and weedicides. Similarly, EOs provide effective and non-addictive treatment options for depression and anxiety. Although currently, EOs are mainly used in supplementary treatment, a growing body of experimental evidence indicates the potential of EOs as a primary treatment for depression and anxiety. Hence, strategies to promote large-scale commercial cultivation of EO-bearing plants need to be developed. Finally, the universal nature of chemical communication through plant VOCs and EOs appears to be attributable primarily to their small size and lipophilicity.

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