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Review

Cracking the plant VOC sensing code and its practical applications

Gen-ichiro Arimura [1,*] and Takuya Uemura [1]

Volatile organic compounds (VOCs) are essential airborne mediators of interactions between plants. These plant–plant interactions require sophisticated VOC-sensing mechanisms that enable plants to regulate their defenses against pests. However, these interactions are not limited to specific plants or even conspecifics, and can function in very flexible interactions between plants. Sensing and responding to VOCs in plants is finely controlled by their uptake and transport systems as well as by cellular signaling via, for example, chromatin remodeling system-based transcriptional regulation for defense gene activation. Based on the accumulated knowledge about the interactions between plants and their major VOCs, companion plants and biostimulants are being developed for practical applications in agricultural and horticultural pest control, providing a sustainable alternative to harmful chemicals.

Highlights

Plant–plant (interplant) interactions via volatile organic compounds (VOCs) emitted by plants confer antiherbivore capabilities on the plants receiving these VOCs.

Interplant interactions occur with both conspecific and heterospecific neighboring plants, relying on VOCs emitted by herbivore-damaged plants as well as unique or constitutively emitted compounds such as isoprene and fragrant grass VOCs.

VOCs are taken up through stomata and diffuse across mesophyll cells in leaves. The mechanisms underlying cellular recognition and uptake of VOCs, likely involving receptors and transporters, are not well understood.

Chromatin remodeling and transcriptional regulation are the basis for gene activation for defense responses in VOC-receiving plants.

VOC-emitting companion plants and VOC biostimulants may provide sustainable agricultural and horticultural technologies.

Multiple potentials of plant signaling mediated by VOCs

VOCs play a critical role as airborne cues (infochemicals) that allow plants to interact with other organisms over both short and long distances. Typically, when a plant is damaged by herbivorous pests, it releases VOCs that can be detected by nearby, healthy plants, resulting in their increased resistance to pests [1–3] (Figure 1). This fascinating phenomenon of interplant interaction can be a defense strategy that allows plants to protect their populations from herbivorous pests. Even more curiously, it is not only the sense of smell that can detect VOCs, but also the other senses such as hearing, touch, etc. that plants can use to respond quickly and sensitively to their threats (Box 1).

Given the systemically acquired antiherbivore response of plants, it is reasonable to assume that information transfer via VOCs has evolved as an alternative to the transport system throughout the plant body. Particularly in plants such as giant trees and trailing plants such as legumes, VOCs may play an important role as mobile signals especially in long-distance signaling from damaged tissues to undamaged sites, in addition to the signaling via the vascular system [4–6]. Presumably, VOC cues originally responsible for such intraplant (within plant) interactions were detected by neighboring plants, and such detection evolved into interplant interactions. Therefore, even for interplant interaction, plants interact more with their relatives than with strangers, as exemplified by *Artemisia tridentata* plants, which can discriminate between the similar chemotypes of VOCs from genetically related individuals and from strangers to manage more effective defense [7–9].

In addition, some evidence has challenged the conventional thinking about interplant interaction via VOCs. As noted later, it has been observed that certain plant species respond to cues emitted by unfamiliar plants, suggesting that plants, including their heterospecific counterparts, may use as-yet-unknown VOCs to acquire their antiherbivore properties. In this context, VOCs such as green leaf volatiles (GLVs), which are released by most land plant species, including lycophytes [10], especially when plants are physically damaged, should play a role as herbivore danger cues even between non-kin plants. GLVs, including (*Z*)-3-hexenyl acetate, have been shown to affect plasma

[1]Department of Biological Science and Technology, Faculty of Advanced Engineering, Tokyo University of Science, Tokyo 125-8585, Japan

*Correspondence:
garimura@rs.tus.ac.jp (G. Arimura).

https://doi.org/10.1016/j.tplants.2024.09.005

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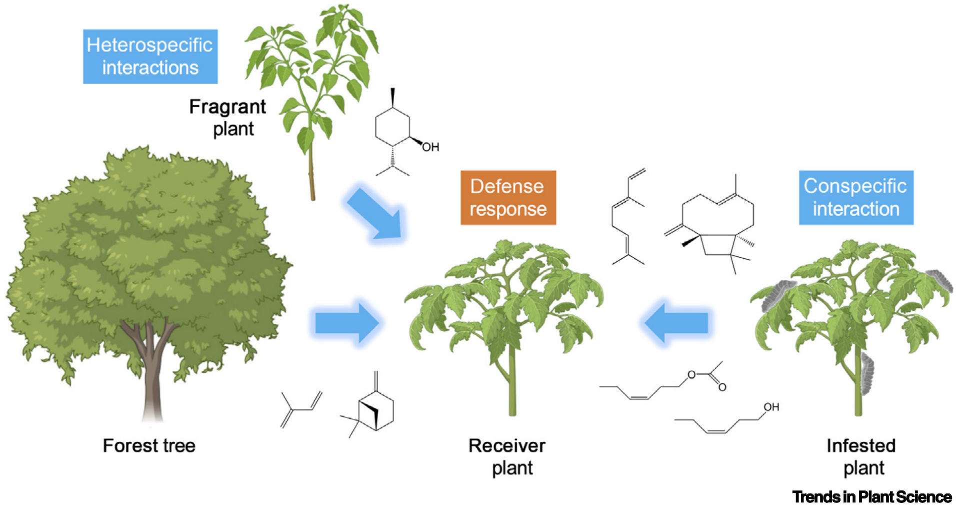

Figure 1. Multiple opportunities for plant–plant interactions mediated by plant volatile organic compounds (VOCs), resulting in enhanced defense properties in receiver plants. This figure was created in part with BioRender (https://app.biorender.com/).

membrane potential (*Vm*) variations and cytosolic Ca^{2+} fluxes in tomato leaf cells [11]. To date, GLVs including (*E*)-2-hexenal, (*Z*)-3-hexenal, (*E*)-2-hexenol, (*Z*)-3-hexenol, (*Z*)-3-hexenyl acetate, etc. have been shown to affect a wide range of plant taxa, such as arabidopsis (*Arabidopsis thaliana*), *Lolium temulentum*, tobacco (*Nicotiana attenuata*), tomato (*Solanum lycopersicum*), maize (*Zea mays*), lima bean (*Phaseolus lunatus*), and poplar (*Populus deltoides* × *nigra*) [2].

Terpenoids, also known as isoprenoids, which are among the more important types of VOCs, exhibit an impressive diversity of approximately 25 000 different structures [12]. Different plant species and families maintain distinctive terpenoid compositions [13]. These compounds are not only released when tissues are damaged, but are also emitted continuously from flowers and many aromatic plants. Of great interest is the fact that constitutively emitted VOCs, including terpenoids, can elicit responses in other plant species. For example, recent reports have shown that heterospecific plants exhibit enhanced defense responses to exposure to isoprene, which is emitted by deciduous broadleaf trees [14,15]. The same is also true for characteristic VOCs, including menthol, which is typically emitted by Lamiaceae [16,17]. Presumably, plants lack a precise olfactory system like that of animals (see later), but may sense and respond to VOCs based on their structural similarity to chemical compounds that the plants or their ancestors encountered through beneficial or detrimental interactions with various organisms.

Sensing of the VOCs that function in heterospecific interactions

A new function for isoprene

Isoprene is a C5 terpenoid emitted predominantly by deciduous broadleaf trees, including *Salix*, *Quercus*, and *Populus* species [18]. The global annual production of isoprene by plants has been estimated to be as high as 500 Tg, making this hemiterpenoid the most abundant plant-emitted VOC [19]. Isoprene allows plants to acquire tolerance to abiotic stress, hypothetically because it stabilizes the thylakoid membranes and scavenges reactive oxygen species (ROS) in plant tissues under stress conditions [20]. In addition to the antioxidant and membrane thermoprotective activities of this hemiterpenoid, it has been shown that isoprene-non-emitting plants activate a defense response when exposed to isoprene. For example, arabidopsis plants, which do not naturally produce isoprene, when exposed to pure isoprene or to a blend of VOCs including

Box 1. Plants not only smell, but hear and sense herbivores coming

Stressed plants release more than just chemicals, including VOCs. Tomato and tobacco plants have been shown to emit sounds in the airborne ultrasonic range of about 20–100 kHz when dried out or injured [77]. These sounds can potentially be detected by many mammals and insects from several meters away. Meanwhile, neighboring plants can also respond to these sounds [78,79]. For example, in response to the chewing sounds of insect larvae or the buzzing of a pollinating bee, the sounds are transmitted to the cells as vibrations and allow the plasma membrane tension and Ca^{2+} channel activity to increase. Inside the cells, Ca^{2+} can then be sensed by Ca^{2+} sensors that affect various signaling molecules, ultimately leading to defense responses [80].

In addition to the marked responses to touch of species such as the Venus flytrap (*Dionaea muscipula*) and the humble plant (*Mimosa pudica*), many plants can undergo gradual touch-induced morphological changes called thigmomorphogenesis. Jasmonate is required for the salient features of thigmomorphogenesis in arabidopsis, including a touch-induced delay in flowering and reduction in rosette size, as well as pest resistance induced by sensing repeated mechanostimulation [81]. Similarly, continuous leaf damage in lima bean enhances jasmonate accumulation at localized damage sites [82], suggesting that repeated herbivore contact and physical stimuli play a booster role in jasmonate signaling. In addition, plants that sense touch also activate jasmonate-independent signaling in which the calmodulin-binding transcriptional activators CAMTA1/2/3 cooperate to directly bind the promoters and activate gene expression of jasmonate-independent touch marker genes such as *TCH2* and *TCH4* [83].

Taken together, these and related findings have revealed that plants, like animals, have fascinating abilities to respond through various senses such as smell and hearing, allowing them to effectively protect themselves and their populations. Using these senses, plants can detect and respond to potential threats in advance or to encountered threats quickly, reacting to even a slight touch from a pest.

isoprene, released from grey poplar (*Populus* × *canescens*), exhibited resistance to *Pseudomonas syringae* infection, mediated by systemic acquired resistance (SAR) [14]. This was partly due to the transcriptional upregulation of genes for ethylene response factor (ERF) and WRKY transcription factors, as well as phenylpropanoid biosynthesis genes involved in stress tolerance [21]. Similarly, when arabidopsis and tobacco (*Nicotiana tabacum*) plants were transformed with an isoprene synthase, they modulated the transcript levels of genes involved in jasmonate-associated and stress tolerance gene expression as well as several growth regulators compared with their wild-type plants [15]. Thus, isoprene clearly serves as a cue for heterospecific interaction (Figure 1).

Notably, in addition to isoprene, many monoterpenoids are released in large amounts by forest trees such as conifers [22]. Given that monoterpenoids, including α-pinene, β-pinene, and camphene, induce ROS accumulation and the expression of salicylic acid- and SAR-related genes in arabidopsis [23], it is possible that monoterpenoids may also play an infochemical role in enhancing plant defense responses in forests (Figure 1).

Fragrant plant VOCs

The unique monoterpenoids of the mint family (Lamiaceae), including menthol and menthone, are rarely found in other plant species and have been commercialized as active ingredients for their insecticidal (repellent, antifeedant, and ovicidal) and antimicrobial efficacy against bacterial and fungal plant pathogens and insects [24]. Lamiaceae species accumulate huge amounts of VOCs in glandular trichomes, which are widely distributed in the aerial reproductive and vegetative organs [25].

It has been shown that the mint VOCs released from glandular trichomes are perceived by other plants and increase the antiherbivore capacity of these plants. When soybean (*Glycine max*) and komatsuna (*Brassica rapa* var. perviridis) plants were grown in close proximity to mint [candy mint (*Mentha* × *piperita* cv. Candy) or peppermint (*M.* × *piperita*)] plants, their defensive properties were enhanced [16,17]. However, when soybean and komatsuna plants were grown in close proximity to various other mint species, their defensive properties were not enhanced, suggesting that the VOCs released by candy mint and peppermint possess activity as infochemicals responsible for interplant interactions. Among these VOCs, three monoterpenoids – namely: 1,8-cineole, menthone, and menthol – have been found to be predominantly responsible for inducing transcriptional activation of defense genes in soybean leaves [17].

In another scenario, soybeans showed reduced leaf damage and increased accumulation of isoflavones when exposed to VOCs such as α-pinene, β-myrcene, and limonene released during mechanical damage of tall goldenrod (*Solidago altissima*) [26]. Similarly, leaves of maize plants exposed to VOCs released by wounded goldenrod and mugwort (*Artemisia indica*) showed elevated levels of salicylic acid and increased resistance to armyworm (*Mythimna separata*) larvae [27]. Also, intact molasses grass (*Melinis minutiflora*), a perennial mat grass of the Panicoideae with a strong odor, induces both direct and indirect defense responses in neighboring maize plants [28].

Thus, it is clear that certain fragrant plant VOCs, together with tree-emitted isoprene and monoterpenoids, can act as infochemicals in heterospecific interactions. However, these observations can also be interpreted as being due to direct effects of the herbivore response as a result of ‘passive associative resistance’ [29,30], when the captured VOCs from the neighboring plants are adsorbed on the leaf epicuticular wax surfaces of the receiver plant, camouflaging the natural odors of the receiver plant and repelling the specialist herbivores. However, the dose of VOCs rereleased from the receiver plant is not always high [28,31], and their effects on other organisms are expected to be very low.

Current insights into *in planta* VOC recognition machinery

In planta VOC sensory system

The overall possible model of the VOC uptake, transport and signaling machinery in receiver plants is shown in Figure 2. Considering the structure of the leaf, it appears that plants should have the potential to readily respond to VOCs by absorbing them into the leaf internal tissues through stomata via the gas exchange process, rather than through the epidermis covered by a cuticle that acts as a physical barrier. This idea is based on the hypothesis that VOC levels rapidly reach equilibrium between the gas phase and the cellular phase, leading to facilitated VOC uptake into cells via metabolic processes [32]. Increased stomatal conductance facilitates the uptake of volatile ketones and aldehydes [33]. By contrast, closed stomata have been shown to prevent the entry of GLVs, including (*Z*)-3-hexenol, into exposed maize plants [34].

Aratani *et al.* monitored the spatiotemporal dynamics of sensory transduction of VOCs emitted by mechanically damaged plants in receiver arabidopsis by visualizing rapid increases in cytosolic Ca^{2+} concentration ($[Ca^{2+}]_{cyt}$) using a wide-field imaging approach [35]. This tissue-specific Ca^{2+} imaging technique visualized the rapid Ca^{2+} signal propagation throughout the leaf in various cells (epidermal, mesophyll, guard, and vasculature cells) in real time on exposure to GLV aldehydes such as (*Z*)-3-hexenal and (*E*)-2-hexenal. GLV-induced $[Ca^{2+}]_{cyt}$ increases in guard and mesophyll cells preceded those in epidermal cells. These results were confirmed by a pharmacological approach using mutants defective in stomatal closure, suggesting that stomata-mediated VOC uptake plays a critical role in the rapid VOC responses. However, it is unclear whether the Ca^{2+} signals observed in the epidermal cells were propagated from the mesophyll cells or whether they resulted from GLVs penetrating the cuticle layer and directly affecting the epidermal cells. Furthermore, such a mechanism based on stromatal uptake of VOCs contrasts with the observation in maize leaves that young leaves, despite their low stomatal conductance, were much more sensitive to (*Z*)-3-hexenyl acetate [36]. Such a superior response might be dependent on a greater ability to promote jasmonate signaling in young leaves. Taken together, these results suggest that VOCs primarily enter the plant body through stomata, while the activation of the resulting defense responses in leaf cells is independent of VOC uptake levels. Rather, this activation depends on the physiological

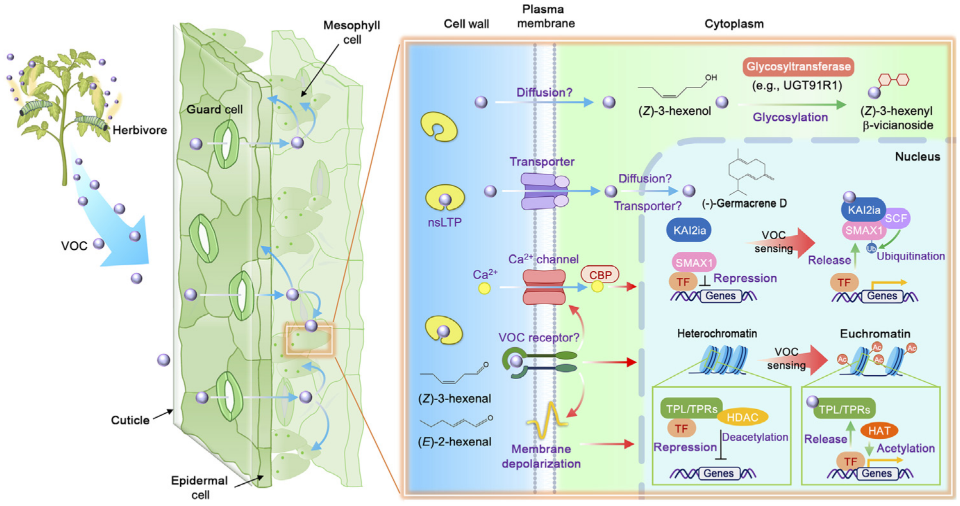

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Figure 2. Working model of the volatile organic compound (VOC) uptake, transport, and signaling machinery in receiver plants. VOCs emitted by herbivore-damaged or VOC-rich neighboring plants readily enter through stomata and diffuse within the leaf mesophyll of a receiver plant. VOCs can immediately affect guard cells and mesophyll cells, eliciting rapid VOC responses, while the effect on epidermal cells is delayed due to the presence of the cuticle. To cross the aqueous cell wall region, nonspecific lipid transfer proteins (nsLTPs) can carry VOCs for their effective trafficking. Once they reach the surface of the plasma membrane, a number of VOC molecules can be taken up into the cytoplasm either by the activities of transporters [e.g., ATP-binding cassette (ABC) transporters] or by diffusion without such assistance. VOCs may then be transported further into the nucleus to bind to regulatory factors and promote gene activation. In the case illustrated here, VOC alcohols, including (*Z*)-3-hexenol, are subjected to glycosylation in the cytoplasm, as shown in tomato [53]. Green leaf volatile (GLV) aldehydes such as (*Z*)-3-hexenal and (*E*)-2-hexenal induce membrane perturbation (e.g., membrane depolarization, Ca^{2+} influx) [35]. This process may be mediated by the perception of VOCs by as-yet-uncharacterized specialized receptors and the subsequent opening of Ca^{2+} channels through signal transduction. Elevated cytosolic Ca^{2+} levels then activate calcium-binding proteins (CBPs), such as calcium-dependent protein kinases and calmodulins, to transduce cellular signals [84]. In the VOC-receiving state, the transcriptional machinery for terpenoid hydrocarbon (i.e., β-caryophyllene)-responsive genes is repressed by TOPLESS (TPL) and TOPLESS-related (TPR) repressors, which act by interacting with the associated transcription factors (TFs) and with histone deacetylases (HDACs) to maintain a heterochromatic state. Presumably, in response to VOCs, TPL/TPRs are removed from the transcriptional machinery, resulting in the activation of the corresponding genes. Histone acetyltransferase (HAT)-mediated histone acetylation (Ac) then triggers transcriptional activation or priming. In another scenario, another terpenoid hydrocarbon [i.e., (–)-germacrene D] is transported to the nucleus and/or cytoplasm, binds to KAI2ia, and promotes the degradation of the transcriptional repressor SMAX1 via a SCF complex-dependent ubiquitin (Ub) proteasome system in petunia pistil cells [47]. This leads to the release of specific TFs and ultimately activates the downstream signaling pathway involved in floral development. However, it remains unclear whether this system is common to VOC-induced plant defense responses. Blue, red, and green arrows indicate the movement of substances, the activation of signal transduction, and enzymatic reactions, respectively. This figure was created in part with BioRender (https://app.biorender.com/).

capacity of the leaf cells; that is, the sensitivity to VOCs and the response of both intracellular and intercellular signaling.

The innate response of plants to atmospheric VOCs has been observed in over 30 plant species [3], and the results indicate that VOC response capabilities are likely to vary among species [37].

VOC-specific plant sensory systems

The longstanding question of whether plants, like animals, possess an ‘olfactory’ system capable of detecting subtle structural differences in VOCs has intrigued researchers [3,32]. Few molecules analogous to the mammalian and arthropod odorant receptors (ORs) in the G protein-coupled receptor (GPCR) family have been characterized in plant species [38]. Nevertheless, exposure to GLV aldehydes such as (*Z*)-3-hexenal and (*E*)-2-hexenal has been shown to induce rapid changes in $[Ca^{2+}]_{cyt}$ and membrane potential in arabidopsis, whereas structurally similar compounds such as *n*-hexenal, GLV alcohols, and GLV alcohol esters failed to stimulate Ca^{2+} signaling [35]. These observations suggest that the GLV aldehydes may specifically activate cellular signaling via VOC sensors such as plasma membrane-localized receptors that couple to the Ca^{2+} channel in a manner similar to the mammalian and arthropod olfactory systems. Animal ORs induce the production of cAMP as a second messenger in response to VOCs, resulting in cyclic nucleotide-dependent Ca^{2+} channel-mediated Ca^{2+} influx and subsequent membrane depolarization in olfactory cells [39].

In addition to the role of cannabinoid receptor type 2 (CB_2), a GPCR, in olfactory cells, CB_2 has been shown to play a role in the gastrointestinal tract by binding natural ligands, including the sesquiterpenoid β-caryophyllene, to its hydrophobic ligand binding pockets. These ligands act as agonists of the CB_2 receptor, resulting in anti-inflammatory effects by suppressing *de novo* synthesis of cytokines and mitogen-activated kinase activation [40]. Moreover, TRPM8, one of the temperature-sensitive cation channels, is known to be a receptor for menthol, which causes a cooling sensation in a subset of sensory nerves [41]. However, this applicability paradigm remains uncertain because, as described, plants most likely lack such sensory proteins [38,42,43].

We should also focus on a family of receptor-like kinases (RLKs) that act across the plasma membrane in a variety of cellular processes or in response to environmental cues [44]. For example, the brassinosteroid receptor (BRI1), which couples with BAK1, is known to activate calcium spikes via Ca^{2+}-conducting cyclic nucleotide-gated channel 2 (CNGC2) [45]. Since brassinosteroids are derived from squalene, a triterpenoid, it is plausible that certain low-weight volatile terpenoids may also be recognized by RLKs. To date, however, there is no empirical evidence in support of this hypothesis.

Alternatively, it is possible that direct VOC coupling in the cytoplasm and/or nucleus is responsible for downstream intracellular signaling after uptake into cells. To date, two intracellular factors that interact with VOCs in plants have been identified. One of them, the nuclear TOPLESS (TPL) corepressor, has been shown to bind to β-caryophyllene to induce gene expression responses in tobacco [46] (see later for more details). Furthermore, the karrikin-insensitive 2 receptor PhKAI2ia has been shown to interact with (–)-germacrene D, a sesquiterpenoid released from the floral tube, in petunia (*Petunia hybrida*) pistil cells; this leads to proteasomal degradation of the transcriptional repressor SMAX1 via the formation of the SCF E3 ubiquitin ligase complex, resulting in transcriptional activation of genes predicted to be involved in reproductive organ development, such as pistil development, and seed yield [47]. Given the fact that (–)-germacrene D is known to be one of the major herbivore-induced plant VOCs [48], this system may be responsible for interplant interactions related to plant defense responses. Overall, based on the aforementioned two findings, it is clear that sesquiterpenoid hydrocarbons are capable of nuclear and cytoplasmic import and interaction with intracellular regulatory factors.

VOC transport and metabolism system

The aforementioned fact that GLV aldehydes predominantly induce calcium spikes in arabidopsis leaves, whereas other VOCs such as (*Z*)-3-hexenol and β-caryophyllene do not [35], suggests that the VOC response may be determined not only by the membrane-bound receptor system that mediates Ca^{2+} signaling but also by a receptor-independent system. Extracellular release of floral VOCs has been shown to be facilitated by plasma membrane-localized ATP-binding cassette (ABC) transporters that are specifically expressed in petunia and orchid (*Phalaenopsis bellina*) petals [49,50]. Since some ABC transporters are reverse functional in both export and import directions [51,52], it is possible that plasma membrane-localized transporters may be involved in the cellular uptake of VOCs. Such VOC transporters exhibit broad affinities for VOC species [49], suggesting that a range of VOC molecules may be taken up into cells by only a few sets of the transporters.

In tomato, (*Z*)-3-hexenol is taken up by cells and can be glycosylated by the diphosphate glycosyltransferase UGT91R1 [53,54]. Glycosylation of (*Z*)-3-hexenol confers antiherbivore properties against the common cutworm (*Spodoptera litura*) in tomato plants in a jasmonate signaling-independent manner [53]. However, as described earlier, β-caryophyllene and (–)-germacrene D, sesquiterpenoid hydrocarbons, can trigger gene expression responses by binding to intracellular regulators [46,47], presumably without any chemical modification inside the cells.

Even more curious is how VOCs get to the plasma membrane in plants after being absorbed. A similar phenomenon can be observed in the antennae of male insects, where odorant-binding proteins (OBPs) are responsible for transporting VOCs through the sensillar lymph to the olfactory cells [55]. In addition to lacking sensory proteins, including ORs, plants lack OBPs homologous to those of mammals and arthropods [56,57]; however, in high-viscosity cell walls, nonspecific lipid transfer proteins (nsLTPs) act for VOC transfer [58]. Such extracellular carrier proteins share a 3D structure that is formed by disulfide bonds and provides space for hydrophobic molecules [55,59].

Chromatin remodeling and transcriptional regulation system

The identification of intracellular factors that bind to VOCs and initiate signal transduction for defense responses has long been elusive. In this context, the involvement of TPLs as transcriptional corepressors interacting with caryophyllene analogs has been reported, as described earlier [46]. Overexpression of TPLs in tobacco cells decreases the expression of β-caryophyllene-induced genes, suggesting their role as transcriptional corepressors in response to β-caryophyllene. TPL and TOPLESS-related (TPR) can interact with transcription factors containing repression domains (RDs) with conserved amino acid sequences, such as DLNxxP, R/KLFGV, TLxLF, ERF-associated amphiphilic repression (EAR) domain with LxLxL amino acid sequences, or less-characterized motifs, resulting in the transcriptional repression [60]. Moreover, TPL and TPRs (e.g., TPR2) then control the jasmonate ZIM domain (JAZ) with EAR domain either directly or indirectly through NOVEL INTERACTOR OF JAZ (NINJA) or EAR motif-containing adaptor proteins (ECAPs), respectively [61,62]. Overall, this regulatory mechanism ensures the negative mode of gene expression in plants with VOC-unreceiving status, and VOCs are predicted to deconstruct this system to activate genes in receiver plants.

VOCs are known to act as agonists of regulatory factors in mammals. For example, 1,8-cineole and β-caryophyllene bind to and activate ligand-activated transcription factors such as liver X receptors (LXRs) and peroxisome proliferator-activated receptors (PPARs), respectively [63,64]. Both of these regulatory factors possess the ability to form heterodimers with the retinoid X receptor (RXR) to achieve binding and transcriptional activation in the target promoter region [65].

In addition, TPL/TPRs are known to recruit histone deacetylase 6 (HDA6) to deacetylate histones and repress gene expression during plant growth and development [66]. HDA6 represses ERF genes (*ERF8* and *ERF104*) in arabidopsis under normal conditions [67]. In response to β-ocimene, a number of histone acetyltransferases, such as HAC1, HAC5, and HAM1, regulate histone acetylation at these *ERF* genes, leading to transcriptional activation of the genes. This regulatory mechanism is critical in maintaining the medium-term response to β-ocimene, which lasts 5 days in arabidopsis. A similar trend of histone acetylation and the resultant transcriptional regulation of defense genes in response to VOCs has been observed in soybeans exposed to mint VOCs [17].

Taken together, the aforementioned findings indicate that it is likely that VOC hydrocarbons activate transcription by targeting a chromatin remodeling system containing TPL/TPRs and histone deacetylases in receiver plants. However, this model represents a consolidation of events found in different plant species (i.e., tobacco and arabidopsis) and with different VOCs (i.e., β-caryophyllene and β-ocimene). Future research efforts should focus on exploring the specific mechanism using a specific plant and VOC model to gain a deeper understanding.

Implementation of VOC use in agricultural and horticultural technology

Currently, chemical pesticides are widely used for crop protection, but their negative impact on the environment and the increasing demand for higher food productivity highlight the need for safer alternatives. Therefore, there is an urgent need for research on plant defense potentiators. VOCs play various roles in plants, such as protection against abiotic stress, suppression of pathogen growth, regulation of plant growth, attraction of natural enemies of pests, and stimulation of plant defense responses, as partly highlighted in this review. The use of VOCs offers sustainable strategies for defense and productivity in crops [68], leading to an environmentally friendly strategy to reduce dependence on pesticides and harmful chemicals. In this regard, the push–pull system in East Africa is promising [69] but there are still economic and political barriers to more widespread implementation of this approach. With this in mind, for an effective strategy to optimize interplant interactions in agriculture and horticulture, considering factors such as labor and cost, one effective strategy is to incorporate companion plants that emit consistent VOCs or to use odor sources that provide beneficial effects. For example, the use of companion plants such as mint, as described earlier, has proved to be effective in this regard. However, to achieve highly practical results, it is important to consider the optimization of a number of conditions and the use of appropriate plant taxa/genotypes, and another critical factor to consider is the ideal proximity to companion plants. Typically, interplant interaction is most effective at relatively short distances, ranging from a few tens of centimeters to a few meters [17,31,70–72]. Undoubtedly, as the distance between the VOC emitter and the receiving crop increases, the protective effect in the receiving crop would decrease. Therefore, it is advisable to place VOC emitters at appropriate distances and intervals. In addition, since the effects of VOCs on interplant interactions are dose dependent [11,35], physical conditions such as the biomass of VOC sources and, in some cases, wind direction and other natural conditions are also likely to affect the effective distance for interplant interactions.

The use of synthetic VOCs as an alternative to companion plants could be a viable solution to conserve valuable VOC sources, but there are potential concerns regarding cost and increasing restrictions on chemical pesticides [68]. In this regard, the concern of high cost could be solved by using low-cost synthetic VOCs and commonly used essential oils (EOs). For example, rose EO, which is rich in β-citronellol, potently activates the defensive property in tomato leaves [73] and is effective when diluted to extremely low concentrations (1×10^5 times dilution) and applied to potting soil as an aqueous solution, minimizing the amount needed.

It should be noted that high concentrations of VOCs can act as allelochemicals [74,75]; thus, plants in close proximity to the VOC source may experience growth inhibition. It should also be considered that high VOC concentrations can result in 'passive VOC interaction' for plant–herbivore interactions. It has been shown that sesquiterpenoids from neighboring broccoli (*Brassica oleracea*) plants are adsorbed on the epicuticular leaf wax of receiver plants and act as pest attractants, resulting in increased associative susceptibility of the receiver plant [76]. Moreover, under the current conditions of climate change, a third apparent risk is an increase in abiotic stresses, including the extreme sensitivity of plant VOC interaction to air pollutants, particularly ozone [76].

In conclusion, the potential implementation of companion plants and biostimulants for interplant interactions is being developed as agricultural and horticultural technologies. With some fine-tuning for the use of these technologies efficiently in actual fields in a convenient and cost-effective way, their realization in the near future is highly likely.

Concluding remarks

Demonstrating the ecological and evolutionary significance of 'VOC sensing' not only in conspecific (self or kin) but also in heterospecific (non-self or kin) interplant interactions remains a major scientific challenge. However, it would be extremely difficult to experimentally demonstrate a true plant fitness advantage in a heterospecific interaction involving defense mechanisms for oneself and one's population at plant evolutionary levels. Even in the case of conspecific interaction, some would argue that protecting a plant's community is a byproduct rather than a driving selective force. In this regard, it is currently unclear whether the heterospecific interaction has arisen proactively or passively, and perhaps it is a case-by-case situation.

The mechanisms of plant response to VOCs, such as the VOC-sensing and transport system and the activation of defense responses, are beginning to be elucidated. In addition to this knowledge, not only laboratory experiments but also multiyear and field trials in a variety of environments to assess the effectiveness, economics, and safety of this interaction strategy would greatly contribute to the understanding of the true biological and ecological significance of interplant interactions as well as their practical application (see Outstanding questions).

Outstanding questions

Is it possible for plants that are not closely related to interact with each other using VOCs? This question should be based on the definition of true interplant interaction, which requires a fitness benefit for both the sending and the receiving plant or for the receiving plant alone.

In the complex interaction between different species, what VOC cues are involved?

How do plants absorb VOCs and trigger defensive reactions on a cellular scale?

How can the concept of 'VOC sensing' as part of the interaction between plants be effectively applied to agricultural and horticultural pest control? What obstacles must be overcome to successfully implement this method?

Acknowledgments

This work was partially supported by Japan Society for the Promotion of Science (JSPS) KAKENHI (20H02951 and 24K01723 to G.A.; 24K18197 to T.U.), by Tokyo University of Science Research Grants to G.A. and T.U., and by a JSPS KAKENHI Grant-in-Aid for Transformative Research Areas (A) (24H02134) to T.U.

Declaration of interests

No interests are declared.

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