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Plant volatile organic compounds: Emission and perception in a changing world

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Volatile organic compounds (VOCs) are produced by all kingdoms of life and play crucial roles in mediating the communication between organisms and their environment through emission and perception. Plants, in particular, produce and emit an exceptional variety of VOCs that together serve as a complex chemical language facilitating intra-plant, inter-plant, plant–animal, and plant–microbe interactions. VOC signals are perceived and decrypted by receiver plants; however, the emission, composition, distribution and effective range, as well as uptake of these infochemicals depend on temperature and atmospheric chemistry in addition to their physicochemical properties. Since both emission and perception are directly affected by ongoing climate change, research into these processes is urgently needed to develop mitigation strategies against this threat to plant communication networks. In this brief review, we highlight the recent advances about plant VOC emission and perception, emphasizing the effect of the current climate crisis on these processes. Despite some progress in understanding VOC emission and perception, significant gaps remain in elucidating their molecular mechanisms in plants.

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Importance of volatile organic compounds

Plants release over 10^9 metric tons of volatile organic compounds (VOCs) annually [1], diverting up to 40 % of the photosynthetically fixed carbon to their formation [2]. VOCs are low-molecular-weight lipophilic molecules with low boiling points and high vapor pressures at ambient temperatures and, based on their biosynthetic origin, primarily consist of terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives and amino acid derivatives. Emitted from all plant organs, VOCs play key roles in plant—animal and plant—microbe interactions as well as plant—plant communication and abiotic stress responses (summarized in Refs. [3—7]). In addition to benefiting plants directly, VOC-mediated interactions play a broader role in shaping surrounding ecosystems. By releasing VOCs, herbivore-infested plants not only reduce their own herbivory and trigger resistance in receiver neighbors, but also promote herbivore movement away from emitters, thus facilitating a more even distribution of the attackers within the local ecosystem [8]. In the atmosphere, plant-emitted reactive VOCs undergo rapid oxidation, leading to the formation of secondary organic aerosols that act as cloud condensation nuclei, thereby affecting atmospheric chemistry and climate [9]. In addition, biogenic secondary organic aerosol particles participate in plant—plant interactions and herbivore defense [*10], as they can deposit on plant surfaces and persist longer than the parent VOCs. Given their involvement in a wide range of biological processes, the chemical composition and quantity of plant-emitted VOCs are species-, organ- and tissue-specific, developmentally and/or temporally regulated, and depend on biotic and abiotic factors including light intensity, atmospheric CO_2 and ozone concentrations, temperature, relative humidity, and nutrient status.

Plant volatiles and climate change

Climate change, including the predicted increases in temperature, heatwaves, drought, wind speed, atmospheric CO_2, other greenhouse gases, and pollution, will impact natural and agricultural ecosystems. [11]. The increasing ambient temperature in particular, can either enhance or suppress VOC emission, and also alter the volatile spectrum. In principle, higher temperature greatly promotes VOC emission by accelerating molecular movement. This has been exemplified in recent years by elevated terpene emission from boreal wetlands of southern Finland [12] and peatland and alpine tundra in Scandinavia [*13]. However, when *Petunia axillaris* plants were acclimated at 35 °C for more than a week, smaller flowers and lower emission were observed, suggesting that, in addition to affecting general plant physiology, high temperature differentially impacts VOC emission [14]. On the other hand, when heat is combined with drought stress, it lowers stomatal conductance, leading to a convoluted effect on VOC emission from vegetative tissues that depends on the plant species and the physicochemical properties of the emitted compound(s) [15–17]. Furthermore, global warming will also affect plant interactions with their neighbors. Indeed, strawberry [18] and *Brassica rapa* [*19] flower emissions were diminished by increased temperature, making them less attractive to pollinators, though the reasons for reduced emission were not investigated. Beyond plant–pollinator interactions, global warming will also affect plant defense responses, including tritrophic interactions (reviewed in Ref. [20]). Remarkably, heat pre-treatment of potato plants enhanced emission of β-caryophyllene, a volatile sesquiterpene associated with herbivory defense response, and effectively repelled herbivores [21].

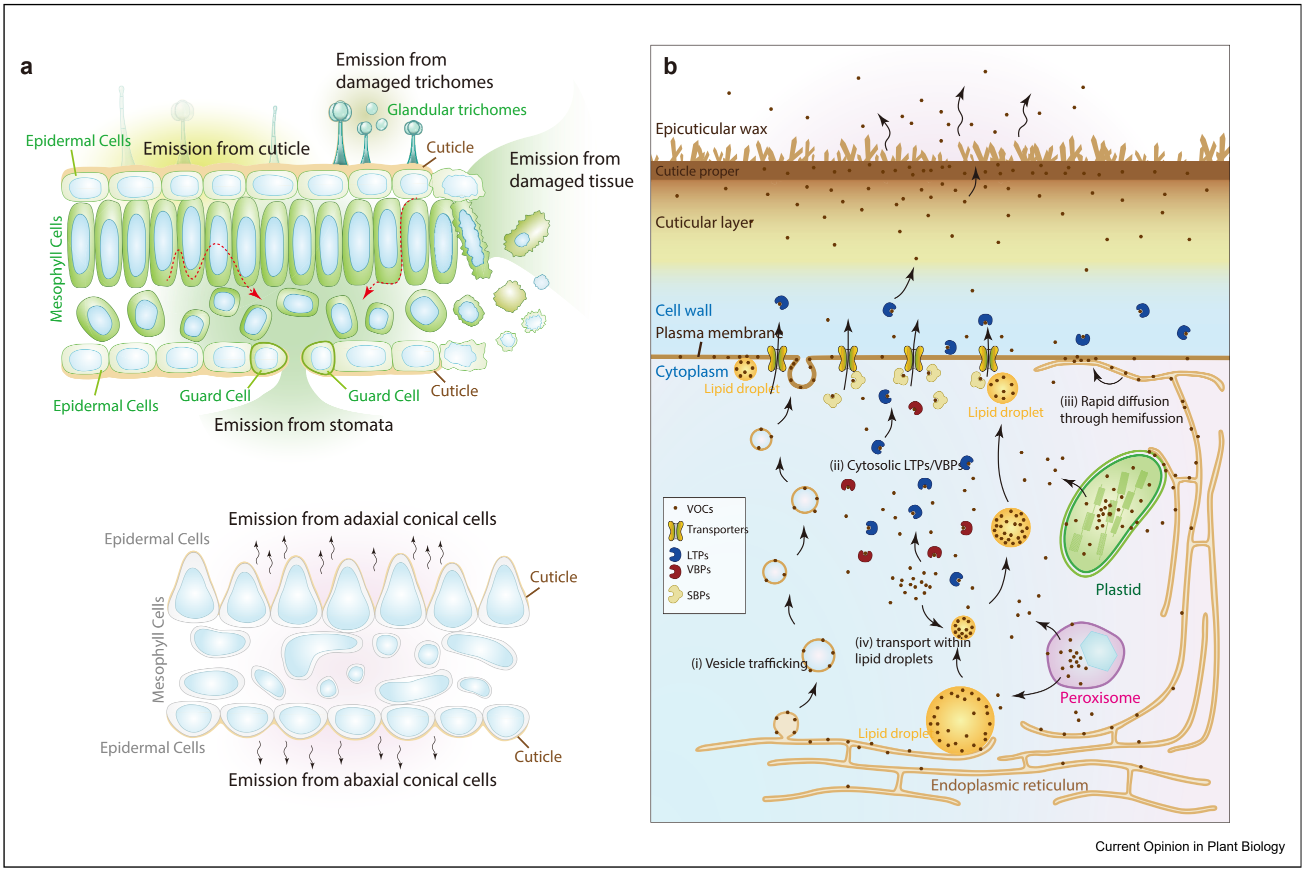
In addition to increasing temperature, airborne pollutants such as ozone and nitrate radicals will also impact ecological communities through chemical modifications of VOC molecules [22–24]. The spectrum of volatiles emitted by plants [25] and corresponding embedded information will be changed by direct chemical reactions of emitted compounds with atmospheric ozone [26]. Moreover, the distance over which VOC signals can be detected will decrease [27,28]. Indeed, oxidation by ozone and nitrate radicals changed floral scent composition and affected nocturnal visitations of *Oenothera pallida* by hawk moth pollinators [**29]. While some animals including insects may learn to respond to the altered volatile signals from plants [30], this global perturbation in VOC release could pose a major threat to ecosystems that depend on interactions of plants with neighboring organisms.

Mechanisms and key players in VOC emission

VOCs are emitted from above-ground organs into the atmosphere and from roots into the soil. While much progress has been made over the past decade on understanding how VOCs are released from aerial parts of a plant, our current knowledge on how they are exuded into the underground world is limited. In aerial parts, VOCs can directly vaporize into the environment from wounded sites caused by mechanical or herbivore damage (Figure 1a). Those emitted from intact cells often cross several subcellular barriers that may include intra-organellar space and their membranes, cytoplasm, plasma membrane, cell wall, and cuticle as the final barrier located at the interface between a plant and its aerial environment (Figure 1a). While VOCs could in principle diffuse across each barrier, mathematical modeling revealed that plant cells, if relying on simple diffusion alone, would need to accumulate detrimentally high levels of VOCs in plasma membranes in order to sustain high emission flux [31]. Using biochemical and genetic approaches and petunia flowers as a model system, it was shown that an ATP-binding cassette (ABC) transporter, PhABCG1, is involved in the active translocation of VOCs across the membrane during emission [32]. Such active transport is crucial in alleviating the toxic effects of overaccumulation of hydrophobic VOC molecules in membranes, and in driving directional emission. In addition to PhABCG1, which primarily transports benzenoid compounds, other transporters have been recently identified for monoterpenes like linalool and geraniol in scented orchids, *Phalaenopsis bellina* [*33] as well as for the sesquiterpene β-caryophyllene in *Artemisia annua* [34] and potentially *Brassica campestris* [35]. Considering the large number of distinct VOCs emitted from plant cells, it remains to be determined how this diverse suite of compounds is transported by relatively few predicted transporters in plant genomes. One hypothesis is that plants could use conformational dynamic substrate-binding proteins, interacting with ABC transporters, to provide the necessary substrate plasticity through multiple-conformation-activated export, mirroring ABC importers described in bacteria [36].

Crossing the hydrophilic cell wall is usually the penultimate step of VOC emission. This process is facilitated by non-specific lipid transfer proteins (LTPs), which are small proteins containing a hydrophobic cavity, that can bind and transport various hydrophobic compounds. It has been shown that heterologous overexpression of a tobacco LTP (NtLTP1) in orange mint can increase the size of glandular trichomes and enhance the secretion of monoterpenes into their storage cavities [37]. In petunia, cell wall localized non-specific LTP3 (PhnsLTP3) contributes to VOC emission through binding with benzenoid/phenylpropanoid VOC compounds and facilitating their diffusion through the cell wall [*38]. Additional potential mechanisms for regulating VOC emission include (Figure 1b) i) vesicle-mediated trafficking across the cytoplasm [39], ii) facilitated diffusion by cytosolic LTPs or other abundant VOC-binding proteins in the cytoplasm, iii) rapid diffusion through internal membrane hemifusion, and iv) transport within lipid droplets (LDs) known for their lipophilic micro-environment [40,41]. However, to date,

Figure 1



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Overview of plant VOC emission. (**a**) Schematic of VOC release from vegetative (upper) and floral tissues (lower). Red arrows indicate potential VOC movement through either plasmodesmata/symplastic or apoplastic pathways, black arrows indicate VOC release to the atmosphere. (**b**) Possible sub-cellular routes of VOC trafficking out of the cell. VOCs are synthesized in plastids, peroxisomes, and cytoplasm, as indicated by high density of VOC molecules in these areas. Arrows show direction of VOC movement. Abbreviations are as follows: LTPs, lipid transfer proteins; SBPs, substrate-binding proteins; VBPs, VOC-binding proteins.

the involvement and contribution of these different mechanisms remain to be further elucidated.

As a final barrier to VOC emission, the plant cuticle provides resistance and serves as a sink, or concentrator, for VOCs to modulate emission [42]. Passage of VOCs through the cuticle solely relies on diffusion and depends on both the thickness of the cuticular layer and its composition. Relatively higher cuticle thickness, in combination with the presence of thick cuticular nanoridges and accumulation of LDs inside the epidermal cells, all seem to contribute to elevated VOC internal pools and less emission in tuberose cultivar 'Calcutta Double' [43]. A similar effect might also be observed under drought conditions which lead to an increased thickness of the cuticle to minimize evaporation and water loss. Meanwhile, a reduction of cuticle thickness in petunia flowers, achieved by downregulating ABC transporters responsible for delivering wax precursors to the cell surface, has uncovered complex roles of cuticles in VOC detoxification, rhythmic emission, sensing, and feedback regulation of biosynthetic genes. [42]. *In vitro* and *in silico* analysis of a model cuticle formulated based on the epicuticular waxes of petunia flower petals revealed that cuticle composition, especially crystallinity, has a significant impact on cuticular permeability and VOC diffusion constants [44]. The effect of cuticle composition on volatile emission was further demonstrated in petunia flowers where suppression of *EPIDERMIS VOLATILE EMISSION REGULATOR*, an R2R3-MYB transcription factor regulating wax-related biosynthetic genes, increased emission of compounds with relatively low volatility [*45]. Overall, increases in plasma membrane and cell wall barrier resistance always reduce emission [32,*38], while cuticle composition and thickness have varying effects on emission [42,*45]. Considering that LTPs have broad substrate specificity and VOC movement through the cuticle occurs exclusively by simple diffusion, the specificity of volatile emission presumably depends on the selectivity of active transporters in the plasma membrane.

VOCs from flowers are emitted predominantly from adaxial and abaxial epidermal cells with a cuticle. In leaves, the cuticle also coats the stomatal apertures and sometimes covers the free inner epidermal cell surfaces of the substomatal cavity and intercellular spaces [46,47]. However, some leaf VOCs, for example, isoprene [48], are mainly produced in mesophyll cells, which lack a cuticular layer, and evaporate into the leaf air space before release to the atmosphere via stomata [49]. Sesquiterpene biosynthesis was shown to occur predominantly in vascular bundle sheath cells [50], while green leaf volatiles (GLVs) are produced throughout different cell types in the leaves [51]. Therefore, regardless of tissue and cell type, plant VOCs must cross the cytoplasm, plasma membrane and cell wall barriers to be emitted or stored in secretory structures. Depending on VOC biosynthesis within a tissue, VOCs may need to travel across several cells through plasmodesmata/symplastic or apoplastic pathways to reach the site of evaporation (Figure 1), although little is known about the involvement of either route. As a final gatekeeper over the release of VOCs within the gaseous part of a leaf, stomata can become a target of insect herbivores. Indeed, a salivary enzyme, glucose oxidase, secreted by the caterpillar *Helicoverpa zea* on tomato leaves can induce the closure of stomata within 5 min and the effect persists for at least 48 h. This stomatal closure leads to a further reduction in the emission of herbivore-induced plant volatiles, thus benefiting the herbivore [52]. Unlike aerial tissues, roots lack both a cuticle, which acts as a sink for VOCs and mitigates their toxic effects on cells, and stomata, which facilitate rapid release of VOCs into the environment. As a result, roots have likely developed a unique mechanism(s) for VOC release into the environment that has yet to be uncovered.

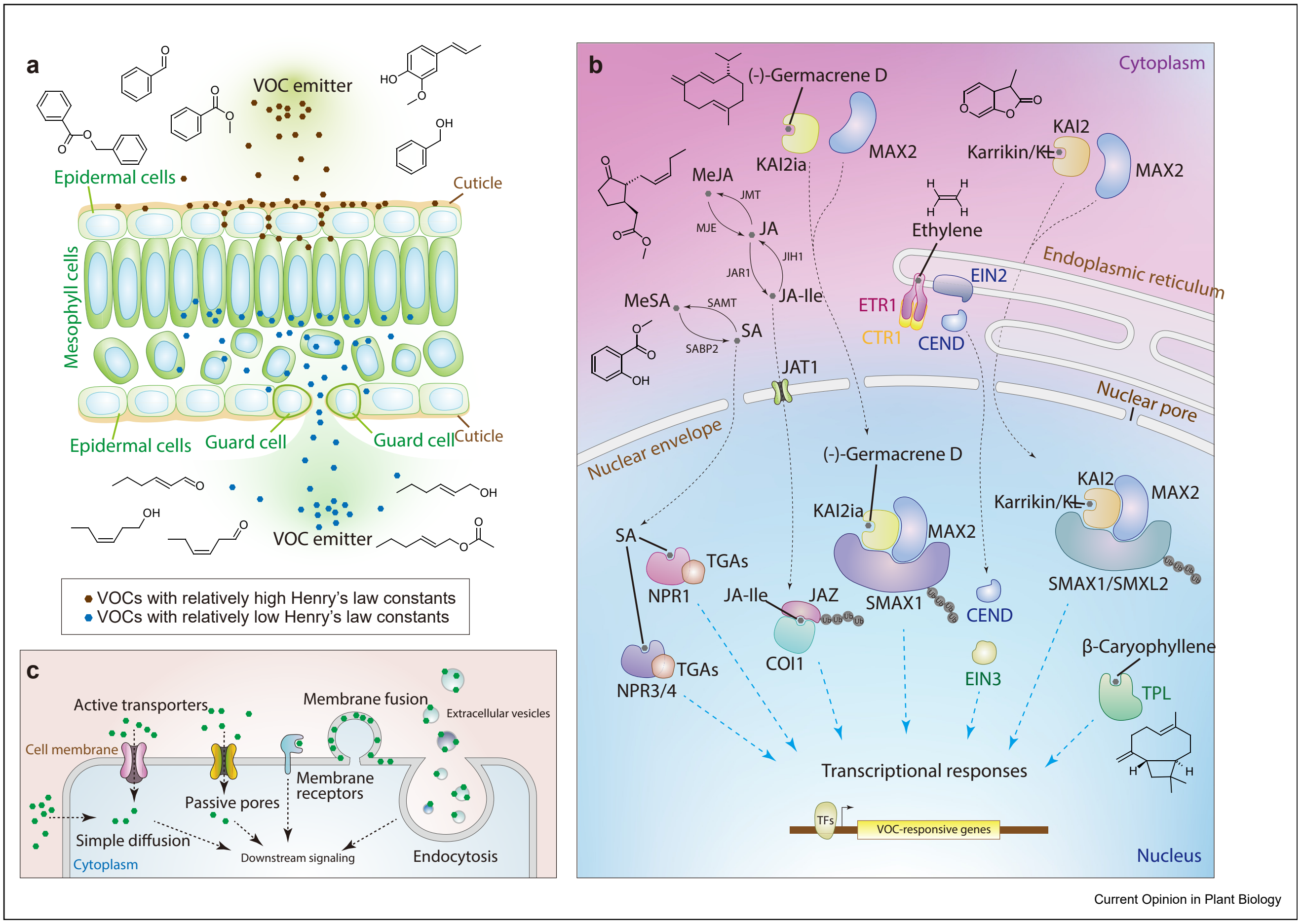
Uptake and perception of VOCs

Upon emission of VOCs by plants or other interacting organisms above- and belowground, the receiver plant must then perceive these diverse chemical signals and elicit the corresponding response(s) [53,54]. The perception of odorants in animals is well-studied and involves compound-specific or moiety-specific proteins, including membrane-bound G-protein coupled receptors [55—57]. However, while plants have related proteins, they appear to play different roles [58]. Signal perception in plants instead requires similar routes as emission in reverse [59], where multiple physical barriers must be crossed, and often involves further biochemical processing of the signal molecule.

Emitted volatiles diffuse through the atmosphere and/or soil until encountering a receiver plant where, in aerial tissue, they accumulate in the waxy cuticle depending on the physicochemical properties of the volatile and/or enter through the stomata [59—*61] (Figure 2a). Particularly for VOCs with low Henry's law volatility constants, such as indole, methyl salicylate (MeSA) and fatty acid derived GLVs, entry through the stomata is essential to ensure signal perception in leaves. Indeed, the opening of stomatal apertures was required for indole- and (*Z*)-3-hexenyl acetate-induced defense priming in maize [*61]. Stomatal closure prevented GLV-induced production and emission of volatile defense-related terpenoids [*62], further emphasizing the importance of environmental conditions on GLV perception, like night and drought, both of which lead to stomatal closure. Once GLVs enter the stomata, defense responses can be propagated in the form of calcium signaling that rapidly spreads across the leaf and elicits defense priming through transcriptional changes [**63]. This signaling perception appears to be compound-specific and moiety-specific and requires the presence of an aldehyde group on the GLV. Of the emitted compounds from wounded Arabidopsis, only (*Z*)-3-hexenal, a product of hydroperoxide lyase, and its isomer (*E*)-2-hexenal induced concentration-dependent local calcium signals. Moreover, GLVs can be converted into bioactive downstream compounds. In tomato, (*Z*)-3-hexenol emitted from herbivore-infested plants is taken up by receiver plants, where it is glycosylated into an active defense compound (*Z*)-3-hexenyl β-vicianoside [64]. Recently, it has been shown that this conversion involves two steps with a novel UDP-arabinosyltransferase catalyzing the formation of the final product [**65]. In addition to serving as volatile signals between plants, GLVs, like other metabolites, can be transported internally through the xylem by transpiration-driven bulk flow. Obtained in lower aerial parts directly via stomata or produced from 3-hexenal [66], (*Z*)-3-hexenol was transported through the xylem to upper aerial tissue, where it induced the production of defense-related terpenoids and jasmonic acid [67]. Therefore, stomatal apertures are critical regulators for the uptake of airborne VOCs with low Henry's law constants that readily partition into the aqueous phase within the plant [*61,67] where they are directly perceived, metabolized into active compounds, or transported elsewhere. Ongoing climate change, including shifts in atmospheric chemistry and increasing drought frequency, will impact stomatal conductance, thus perturbing the perception and response(s) of plants to crucial VOC signals. This is especially true for GLVs that signal herbivory, potentially leading to long-term effects on pest resistance and food security.

Following uptake through stomata or the cuticle, VOCs are generally thought to be perceived by compound-specific receptors, which are likely distinct from those seen in olfaction for animals [68,69]. The most well-characterized volatile signal receptors in plants are

Figure 2



Overview of plant VOC uptake and perception. (**a**) Uptake of VOCs with different physicochemical properties via the cuticle or stomata. Representative chemical structures of compounds with high and low Henry's law constants. (**b**) Known VOC receptors and signaling pathways in plants. Methyl salicylate (MeSA) can be demethylated by SALICYLIC ACID BINDING PROTEIN 2 (SABP2) to SA [72,*73] which then moves to the nucleus, binds to the SA receptor NONEXPRESSOR OF PATHOGENESIS-RELATED GENES 1 (NPR1), enabling TGACG motif-binding transcription factor (TGA)-mediated transcription of responsive genes, and simultaneously suppresses NPR3/4 inhibition of TGAs [84]. In the reverse direction, SA can be converted to MeSA by salicylic acid methyltransferase (SAMT) [71]. Methyl jasmonate (MeJA) can be demethylated into jasmonic acid (JA) by MeJA esterase (MJE), conjugated by JASMONATE RESISTANT 1 (JAR1) to isoleucine forming jasmonyl-isoleucine (JA-Ile) that is transported into the nucleus by a JA transporter (JAT1) where it binds with a F-box protein CORONATINE INSENSITIVE1 (COI1) in complex with a JA-zinc-finger inflorescence meristem domain (JAZ) co-repressor. JAZ is then degraded, releasing transcription factors that induce changes in gene expression. JA-Ile in the cytoplasm can also be converted by JA-Ile hydrolase 1 (JIH1) back into JA that can be methylated into MeJA by JA carboxyl methyltransferase (JMT) (JA signaling reviewed in Ref. [85]). KARRIKIN INSENSITIVE 2 (KAI2) proteins perceive karrikins and/or unknown KAI2 ligands (KLs) [76], whereas KAI2ia from petunia perceives (–)-germacrene D [*80]. In both cases, ligand binding leads to Skp Cullin F-box (SCF) E3 ubiquitin ligase complex formation containing the F-box protein MORE AXILLARY GROWTH 2 (MAX2) and degradation of the transcriptional co-repressors SUPPRESSOR OF MAX2 1 (SMAX1) or SMAX1-like 2 (SMXL2) (reviewed in Ref. [78]). The perception of ethylene is quite complex (reviewed in Ref. [70]) and generally proceeds through Cu^{2+}-dependent binding of ethylene to ETHYLENE RESPONSE1 (ETR1) receptor in the endoplasmic reticulum (ER). This leads to conformational changes of ETR1 and sequestration or deactivation of CONSTITUTIVE TRIPLE RESPONSE1 (CTR1), followed by proteolysis of ETHYLENE INSENSITIVE 2 (EIN2). The released carboxyl end of EIN2 (CEND) migrates to the nucleus and activates EIN3 to promote transcription of target genes. TOPLESS-like proteins (TPLs), on the other hand are less explored; however, they are transcriptional co-repressors that interact with terpenoids, such as the sesquiterpene β-caryophyllene, and play a role in transcriptional response to VOCs [75]. Varied transcriptional regulation is depicted by blue dashed arrows and transcription factors are summarized as TFs. Possible targets of signal-dependent polyubiquitination (Ub) are shown. (**c**) Potential mechanisms for uptake of VOCs across plant cell membranes.

those for ethylene, a gaseous phytohormone that functions as both an internal and inter-plant signal, and is perceived in the endoplasmic reticulum (reviewed in Ref. [70]) (Figure 2b). MeSA is another volatile plant signaling molecule that neighboring plants can perceive and respond to. Upon infection, plants produce salicylic acid (SA) that is converted to MeSA by SA carboxyl methyltransferase [71] and transported throughout the plant in the phloem. It is then demethylated back to SA by SA binding protein 2 (SABP2) and induces systemic acquired resistance to herbivory and pathogens [72,*73]. The same SABP2 acts as an odorant-binding protein-like receptor that perceives MeSA from neighboring aphid-infested plants and converts it to SA, leading to NAC2-mediated defense and priming against aphid attack [*73]. Additional plant 'odorant-binding proteins' [68] include a CORONATINE INSENSITIVE 1-jasmonate zinc-finger inflorescence meristem domain (JAZ) protein complex for jasmonates [74] and TOPLESS-like proteins for sesquiterpenes [75], both of which are primarily localized to the nucleus for paired perception of the signal and transcriptional regulation of responsive genes. KARRIKIN INSENSITIVE 2 (KAI2) α/β hydrolases [76] represent another group of VOC receptors and are paralogs of the D14 strigolactone receptors [77]. While the endogenous ligand for KAI2 receptors remains elusive, they are known to bind karrikins, VOCs derived from burning vegetation, and trigger an array of physiological responses (reviewed in Ref. [78]). KAI2s are partially localized in the cytoplasm and are trafficked by a yet unknown mechanism to the nucleus, where they can interact with their nuclear signaling partners [76,78,79]. Recently, a member of the intermediate clade of KAI2s from petunia, PhKAI2ia, was found to interact with the volatile sesquiterpene (−)-germacrene D that acts as a hormone-like signal for stigma development via a karrikin-like signaling pathway [*80]. As such, different signaling molecules can bind to distinct groups of KAI2 proteins to elicit corresponding responses. However, relatively few receptors are known to date (Figure 2b) for the large number of VOC signals perceived by plants [69], and it is not clear how many receptors are required, considering that they might have broad ligand specificity [68]. Since VOC receptors identified in plants do not appear plasma membrane-localized, their function may require the involvement of plasma membrane-localized olfactory receptors, transporters mirroring those involved in emission, and/or other uptake mechanisms facilitating efficient signal perception (Figure 2c). VOC perception is also commonplace in roots, where it is an essential part of plant—microbe interactions in the soil. However, little is known about the precise sensing and signaling mechanisms belowground, although they likely share similarities with the principles described for aerial tissues [54,81]. Further research is needed to overcome the lack of known receptors for numerous volatile signaling compounds as well as to uncover the factors involved in modulating distinct and diverse responses to these signals across different tissues and developmental stages.

Conclusions and open questions

VOC-mediated communication is heavily impacted by environmental factors that influence both the physiological processes within the emitter and receiver, as well as the physical parameters of the transmitted airborne signals. As global climate change profoundly impacts environmental factors, it directly affects inter-organism interactions in ecosystems, which depend on the emission, transmission, and perception of VOCs. To mitigate the far-reaching consequences of global change, it is urgent to gain a thorough understanding of not only the formation of volatiles, but also their release and modes of perception. Only a limited number of transporters involved in VOC emission and/or perception have been characterized to date, and it remains to be determined what governs the specificity or promiscuity of these proteins. Some VOC transporters may exhibit broad substrate specificity and accept numerous structurally similar compounds or those with common moieties, while others may show strict substrate selectivity. Similarly, only a small number of plant proteins have been found to act as receptors for VOCs, and the open question is how many receptors are needed for the perception of the whole suite of plant infochemicals. Ligand promiscuity will likely reduce the necessity of receptors for individual compounds, although this raises another question about the specificity of signaling and downstream responses. One possible scenario for signaling specificity with relatively few receptors includes unique protein—protein interactions upon binding to specific ligands. This can occur either through unique ligand-dependent conformational changes of the receptor itself upon binding, or a ligand can directly facilitate the formation of distinct protein complexes through interactions with multiple proteins. Alternatively, the receptor's ligand binding specificity can be shaped by its pre-existing interactions with other protein(s). A set of currently available techniques, including proximity labeling, traditional pulldown and co-immunoprecipitation/mass spectrometry, bimolecular fluorescence complementation and split-luciferase assays will help to uncover protein—protein interactions, if any, both in the presence and absence of candidate ligands. Another open question is how the perceived signals lead to specific downstream responses. The identification of transcriptional co-repressors and interacting transcription factors will reveal key players determining the response specificity. It should not be excluded that canonical biosynthetic enzymes may also act as 'pseudoreceptors' and immediately metabolize volatile ligands into the active signaling compound akin to SABP2 [*73] or methyl jasmonate esterase [82,83] and co-opt known signal transduction pathways. Other important unsolved questions include, but are not limited to, the contribution of the stomata versus cuticle for the uptake of VOCs as well as the impact of individual compounds compared to a blend of compounds in eliciting downstream responses. Overall, this knowledge will ultimately uncover new targets for metabolic engineering to fine-tune the plant VOC communication network for plant interactions with the surrounding environment and to overcome the adverse effects of climate change.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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