

Opinion

How do plants sense volatiles sent by other plants?

Francesco Loreto ^{1,2,*} and Sabato D'Auria ^{3,4,*}

Plants communicate via the emission of volatile organic compounds (VOCs) with many animals as well as other plants. We still know little about how VOCs are perceived by receiving (eavesdropping) plants. Here we propose a multiple system of VOC perception, where stress-induced VOCs dock on odorant-binding proteins (OBPs) like in animals and are transported to as-yet-unknown receptors mediating downstream metabolic and/or behavioral changes. Constitutive VOCs that are broadly and lifelong emitted by plants do not bind OBPs but may directly change the metabolism of eavesdropping plants. Deciphering how plants listen to their talking neighbors could empower VOCs as a tool for bioinspired strategies of plant defense when challenged by abiotic and biotic stresses.

Why do plants talk with other organisms?

Plants synthesize and release a diversity of **VOCs** (see [Glossary](#)) that are important for reproduction and defense [1], and in general to communicate with other organisms [2]. Much as in animals, communication does not always lead to a benefit to who sends the message: depending on who is listening, plants may gain (e.g., informing friends of their presence) or lose (e.g., informing enemies of their presence) from sending VOCs. It should be pointed out, however, that even when the emission of VOCs seems to be detrimental for the plant, it is likely that this cost allows benefits that should also be considered, or VOC emitters would be evolutionarily discriminated against.

Insects and generalist herbivores (including humans) are all able to sense plant VOCs through the presence of a complex molecular system comprising several protein transporters named **OBPs**. OBPs can capture VOC molecules and deliver them to **olfactory receptors (ORs)**. ORs activate the olfactory neurons, in turn responsible for the transduction of odorous stimuli into electrical signals that trigger in the receiving organism appropriate responses and choices ([Figure 1](#)).

Organisms receiving plant VOCs may be attracted or repelled. Attraction may lead to: (i) visiting the emitting plant, pollinating it, and being somehow rewarded [3]; (ii) foraging on the plant (e.g., in the case of herbivores [4]); or (iii) preying on or parasitizing the herbivore organisms feeding on the plant [5,6]. Repulsion generally causes the receiving organism to move away from the stinky cue sent by the plant [7,8]. VOCs are therefore the cornerstone on which the trophic relationships involving plants are built.

Plant VOCs may be emitted 'constitutively' or may be 'induced' by stresses. The straightforward evolutionary interpretation that VOCs allow plants to communicate with other organisms and thus improve plant fitness (e.g., deterring herbivores, improving reproductive success) is often tested to be true in the case of induced VOCs but may not apply to constitutive VOCs that are emitted lifelong. It may be argued that constitutive VOCs that are not induced by a stress or limited to a plant phenological stage represent a too-high metabolic and energetic cost for the plant, to be used only for communicating with other organisms. Numerous other physiological functions,

Highlights

Plants talk to other organisms and between themselves using volatile organic compounds (VOCs) as their alphabet. Interpreting the mysterious VOC voice is challenging scientists worldwide.

Listening to the messages sent by friends and foes requires a receptor system. Available reports indicate that plants may possess odorant-binding proteins (OBPs). OBPs transport VOCs to as-yet-undefined olfactory receptors (ORs) that activate the transduction pathway leading to VOC perception.

Nevertheless, plants lack neuronal cells and the anthropocentric system of odor perception may not fit their simple biology. Plants may not need OBPs and ORs, especially when sensing those constitutive VOCs that are not induced by stresses and do not carry information on imminent stress.

¹Department of Biology, University of Naples Federico II, Via Cinthia, 80126 Naples, Italy

²Institute for Sustainable Plant Protection, National Research Council of Italy (CNR-IPSP), Sesto Fiorentino, Italy

³Department of Biology, Agriculture, and Food Sciences, National Research Council of Italy (CNR-DISBA), Piazzale Aldo Moro 7, 00185 Rome, Italy

⁴Institute for Food Science, National Research Council of Italy (CNR-ISA), Avellino, Italy

*Correspondence: francesco.loreto@unina.it (F. Loreto) and sabato.dauria@cnr.it (S. D'Auria).



from antioxidant to hormone like, have been advocated for those constitutive VOCs that are largely and continuously emitted by plants, such as isoprene [9,10]. Whether constitutive and induced VOCs are also important in plant–plant communication is a perhaps more intriguing, but controversial, issue [2,11].

Why do plants talk with other plants?

Growing evidence shows that both constitutive and induced VOCs work as messages sent from emitting plants to eavesdropping plants (the ‘receivers’) in which VOCs influence gene regulation, metabolism, phenotype, responses to stress, and behavioral choices (Figure 2).

Interestingly, as for plant interaction with other organisms, the emitting plant does not always necessarily receive a reward for such a communication. For example, among plants releasing constitutive VOCs, the blend of VOCs emitted by tomato is clearly able to attract dodder (*Cuscuta* sp.), a parasitic plant that feeds on, and often kills, the emitting host [12]. By contrast, constitutive VOCs emitted by both leaves and roots are also frequently at the basis of other allelobiotic interactions; for example, triggering plant–plant allelopathy [13] and thus repelling neighboring plants with concurrent reward for the emitting plant, at least in terms of competition for resource availability.

In the case of VOCs induced by abiotic or biotic stresses, the message sent by the emitting plant may trigger different responses in the receiving plants. Most often, this is interpreted by receivers as an ‘alert’ message, **priming** or inducing defensive responses (e.g., [4,14,15]; reviewed in [11,16]). The message is apparently sensed both by kin and stranger neighbors [17], although it might work best on genetically similar plants [18]. Priming or induced reprogramming of the transcriptome generally helps receiving plants to cope with forthcoming stressors. Some classes of induced VOCs [e.g., green leaf volatiles (GLVs), terpenes] are known to produce an electrochemical signal that may even evoke ‘damaged-self signals’ [6]. Cases where VOCs induced and released by plants after a pest attack have made neighboring receivers more susceptible to the same pest have also been reported [19]. Priming salicylic acid (SA) defense at the expense of jasmonic acid (JA) defense is interpreted as a manipulation of plant defense, ultimately making receiving plants more vulnerable [19]. Perhaps JA depletion also favors a hypersensitive response, which overloads the defensive system, like cases of hypersensitivity to pathogens [20].

Pathways induced by abiotic or biotic stresses and producing VOC emissions that may be then used as signals or to prime defenses (Figure 3) include: the 12-OPDA pathway leading to the emission of methyl jasmonate (MeJA); the phenyl-propanoid pathway, which produces the volatile methyl salicylate (MeSA); the methyl erythritol phosphate (MEP) pathway generating volatile isoprenoids such as monoterpenes and hemiterpenes (with isoprene and some monoterpenes, however, also being emitted constitutively); the mevalonic acid pathway from which sesquiterpenes are made; the lipoxygenase (LOX) pathway that produces GLVs; and the pectin demethylation and esterification pathway producing methanol [9].

Plants talk, but how do they listen?

VOC-driven interactions are now appreciated as core modules of the ecological webs governing the behaviors of species and individuals, especially in a competitive/hostile environment. The capacity of some plants emitting VOCs to influence the metabolism and behavior of neighboring receiving plants has been repeatedly documented, as seen earlier. Nevertheless, the primary events in such elusive plant–plant communication – that is, how eavesdropping (receiving) plants perceive the VOCs sent by emitting plants – is as yet largely unknown. The issue has been raised several times in the past, conceding a substantial lack of knowledge about VOC perception by

Glossary

Messengers: extracellular (first messengers) or intracellular (second messengers) signaling molecules. First messengers (often also called signaling molecules; see following text) number in the thousands and are small or large organic compounds of diverse origin, including VOCs. First messengers bind receptors to deliver information from the surrounding environment and to start signal transduction mechanisms leading to cellular and organismal responses to stimuli.

Multitrophic interactions: the system by which organisms interact at multiple levels to forage and feed, typically starting with herbivore insects feeding on plants and progressively involving carnivores feeding on herbivores and hyperparasitoids (higher-order predators). VOCs are often central cues allowing the perception and location of food across the trophic scale.

Odorant-binding proteins (OBPs): small (10–30 kD) soluble proteins present in many vertebrates and in insects and which are believed to have a role in olfactory perception. OBPs are thought to increase the solubility of hydrophobic odorant volatiles. They bind the VOC at its entry port in the organism and deliver it to ORs often embedded in the cellular membranes of sensory neurons. Alternative functions for OBPs, however, have been suggested, from acting as a buffer against changes of odors to participating to anti-inflammatory responses. OBPs are mainly lipocalins, structurally characterized by the presence of six α -helix cysteine domains connected by three disulfide bridges. Despite this structural affinity, OBPs are divergent across and within species, with only 8% of residues conserved among species.

Olfactory receptors (ORs): a multigene family of class A rhodopsin-like receptors located in OR neuron cell membranes (e.g., cilia or epithelium in vertebrates, antennae in insects). When activated by the odor transported by OBPs, ORs undergo structural changes, bind G protein-coupled receptors, and, by opening ion (Ca^{2+} or Na^{+}) channels, create the action potential that trigger nerve impulses transmitting odor-driven information to the brain.

Plant communication: the multiple ways (including VOC emission, soil symbioses, release of exudates) that plants

plants (e.g., [2,6,21]). Since the discovery that the hormone ethylene (a VOC itself) can be perceived by plants through a dedicated **receptor** [22], it could be hypothesized that a receptor system must be present for all volatiles. While it is clear that plants can respond to chemical signals including VOCs, the nature of the VOC-sensing system in plants is unclear. Do plants have a receptor system that is mediated by transporters (OBPs), such as in vertebrates, or do plants sense VOCs through a totally different mechanism? Three different hypotheses are discussed in the following sections and illustrated in [Figure 4](#) (Key figure).

A first hypothesis is that plants possess a VOC-sensing system that is mediated by receptors. It is reasonable to think that, like in animals, proteins are used by plants as transporters that bring VOCs to receptors with some degree of specificity ([Figure 2](#)). There have been at least three cases in which the presence of OBP-like protein receptors was postulated in plants, all involving induced VOCs.

The methyl ester of JA (MeJA) is the volatile produced by the cooperation of three leaf organelles degrading linolenic acid (an unsaturated fatty acid) into the 12-OPDA pathway. MeJA is an important signaling molecule, induced by biotic and abiotic stresses, and is able to activate secondary (defensive) metabolisms in stressed plants [23]. After the discovery of an arabidopsis COI1 mutant unresponsive to JA [24], it was found that COI1 protein assembly with a jasmonate ZIM-domain JAZ protein family (COI1–JAZ) is a high-affinity receptor protein for the bioactive JA [25]. When JAZ proteins are degraded, transcription factor (TFs) are simultaneously released, which activate downstream genes and the defensive metabolites.

The methyl ester of SA (MeSA) is another important volatile involved in plant systemic acquired resistance (SAR). MeSA is produced by the phenyl-propanoid pathway on catabolism triggered by stress events. The SA-binding protein 2 (SABP2) OBP is an esterase belonging to the α/β -fold hydrolase superfamily with strong preference for MeSA. It binds SA with high affinity, inhibits MeSA esterase activity, and helps to convert biologically inactive MeSA into active SA [26].

Remarkably, in the case of both MeJA and MeSA, putative OBPs have been reported to operate in the same plants exposed to stress (within-plant signaling) but not in eavesdropping plants (between-plant signaling). It would be important to further test whether these OBPs are involved in plant–plant communication via MeJA and MeSA.

The last case concerns the recent identification of a TOPLESS protein that specifically binds β -caryophyllene, a stress-induced sesquiterpene (sometimes also found as a constitutive component of the VOC blends, although in minimal amounts) active as a volatile signal for herbivores and carnivores in **multitrophic interactions** [27]. TOPLESS proteins are induced by THE *tpl* (TOPLESS) and *tpr* (TOPLESS-related) genes and interact as corepressors with TFs to modulate THE gene expression of hormone signaling (influencing auxin signaling) and stress responses (influencing JA signaling). Interestingly, their capacity to bind β -caryophyllene was tested with emitting and receiving plants (between-plant signaling) [28].

In all of these cases, it remains unclear whether the function of the plant OBP is similar to that of an animal OBP that binds and delivers the VOCs to an OR ([Figure 1](#)). Moreover, while the three examples mentioned previously may indicate that OBPs are present in plants, all other VOCs await the identification of suitable proteins that may bind and transport them.

A second possibility is that plants do not need OBP–OR systems to perceive VOCs. Three cases may be envisioned. (i) Plant OBPs act as *bona fide* ORs capable of triggering directly the cellular

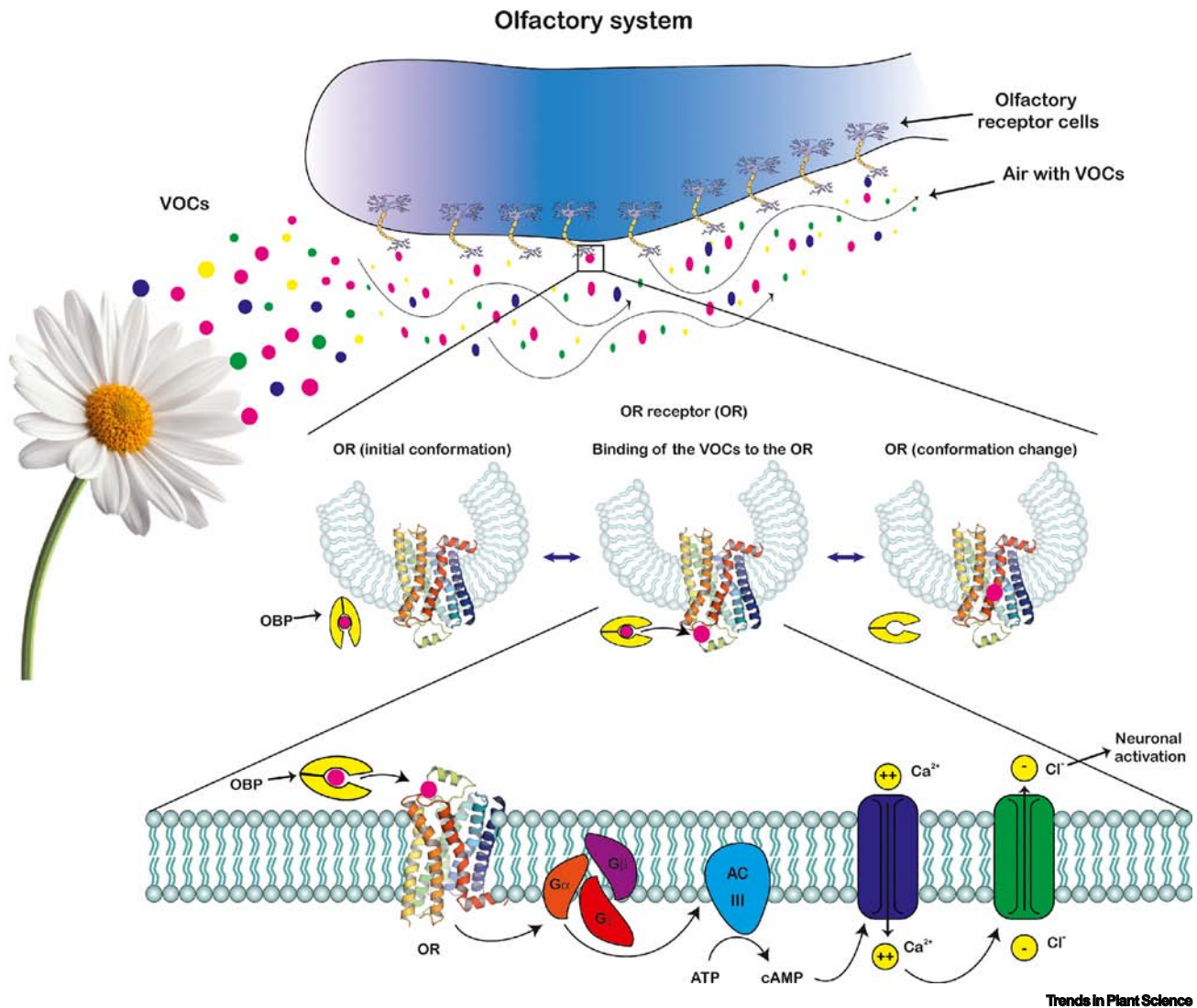
interact among themselves and with a wealth of other organisms including microbes, animals, insects, and fungi. VOCs are among the main tools allowing communication between emitting plants (emitters) and other plants (receivers, listeners, or eavesdroppers).

Priming: the phenomenon by which exposure to a stimulus influences the response of the organism to successive stimuli. Primed plants show earlier, stronger, and faster responses and increased resistance/tolerance to stresses. VOCs may play an important role as priming stimuli because of their capacity to quickly reach plant parts distant from their place of synthesis.

Receptors: molecules that bind a signaling compound and help to transfer the signal to internal signaling pathways. Receptors are generally embedded in membranes and allow transmembrane diffusion of the signals via proteins (G protein-coupled receptors), ion-channel opening, or enzyme activation. While membrane receptors generally carry large signaling molecules, small gaseous molecules that easily diffuse through membranes (e.g., VOCs) are more typically bound by cellular receptors.

Signaling molecules: molecules activating responses at the cellular and organismal level in receiving organisms. Often also named first messengers (see previous text) or ligands, signaling molecules bind specific receptors, which deliver them to where they initiate signal-transduction pathways. Signaling molecules differ in nature and may have differing physicochemical properties. Some VOCs may act as gaseous signaling molecules.

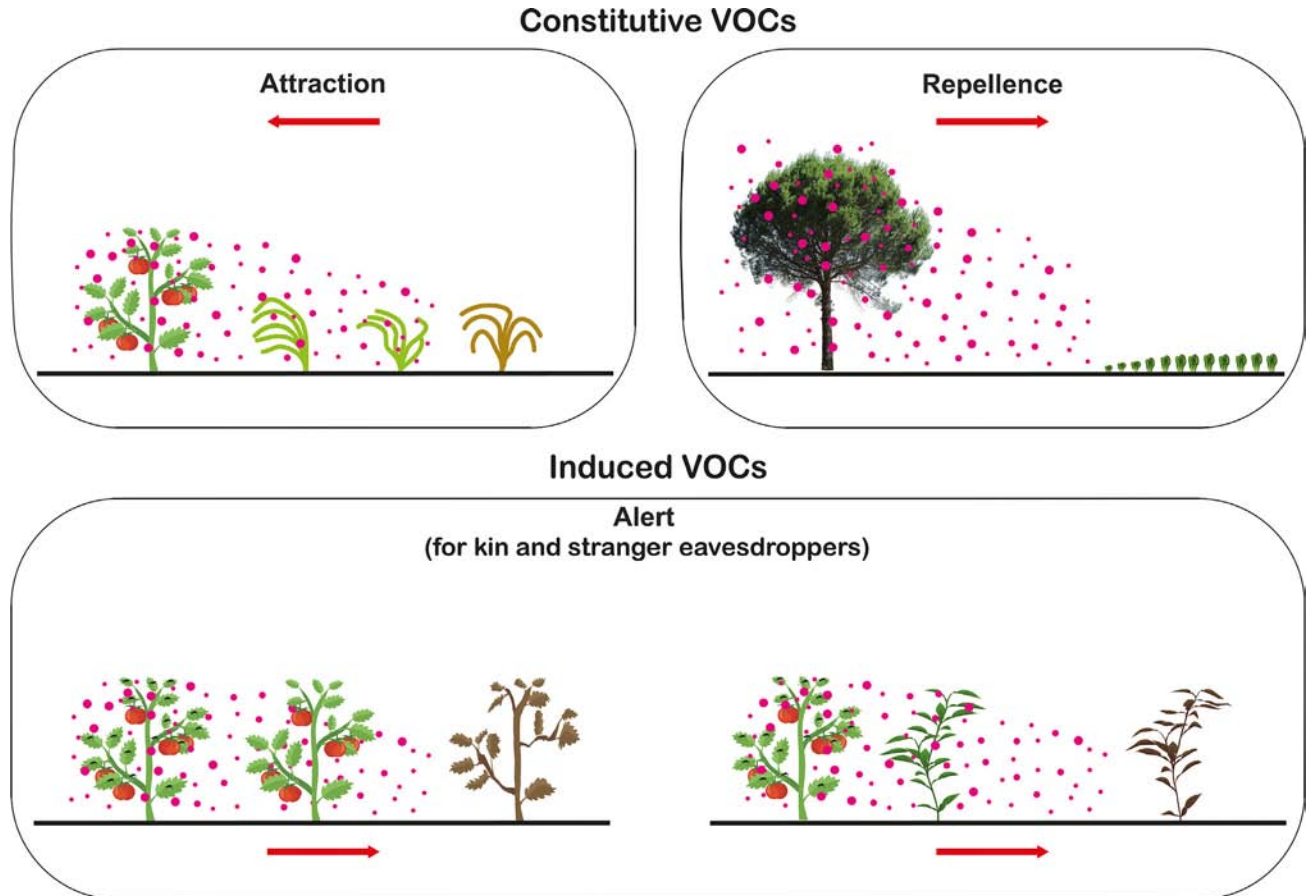
Volatile organic compounds (VOCs): volatile molecules produced in their thousands by diverse metabolic pathways ([Figure 4](#)) in almost all plant tissues above and below ground (from flowers to roots). Constitutive VOCs (e.g., foliar isoprene) are emitted continuously by plants, whereas induced VOCs are elicited by stresses or during specific developmental stages of plants (e.g., methanol). A few VOCs can be both constitutive and induced in specific plant taxa (e.g., monoterpenes). VOCs allow plants to communicate with other organisms and may have other functions ranging from antioxidants to signaling.



Trends in Plant Science

Figure 1. Schematic representation of the c-AMP-mediated transduction pathway operating in the sensory cilia of olfactory neuron receptors in vertebrates. The odorant molecules emitted by plants in volatile organic compound (VOC) form are captured by the odorant-binding proteins (OBPs) that transport VOCs to olfactory receptors (ORs) localized on the cell membrane. The first magnification shows the sequence of events leading to the discharge of the VOC (identified by the red circle) from the OBP and the subsequent binding to the OR. The second magnification shows the conformational change of the OR on VOC binding, which prompts the formation of a second messenger (e.g., cAMP via adenylyl cyclase). The formation of c-AMP triggers a signal-transduction pathway that results in the appropriate neuronal response by means of changes in the ion concentrations on the two sides of the membrane.

response. It is unclear how this may successfully deliver the signal to the transduction pathway and this possibility is not discussed further. (ii) VOCs are directly bound to ORs that are embedded in membranes. The presence of ORs without OBPs transferring the volatile to them is unrepresented in higher organisms but has been reported in invertebrates, where ORs are directly connected to an embryonal neuronal system. For example, in the widely investigated nematode *Caenorhabditis elegans*, no OBP was found, but volatiles are sensed by seven-transmembrane G protein-coupled receptors (7TM GPCRs) acting as ORs and located in the sensory cilia of chemosensory neurons exposed to the external environment [29]. However, plants do not have a *bona fide* neuronal system and it remains unclear whether they have classic ORs, which transduce the signal but do

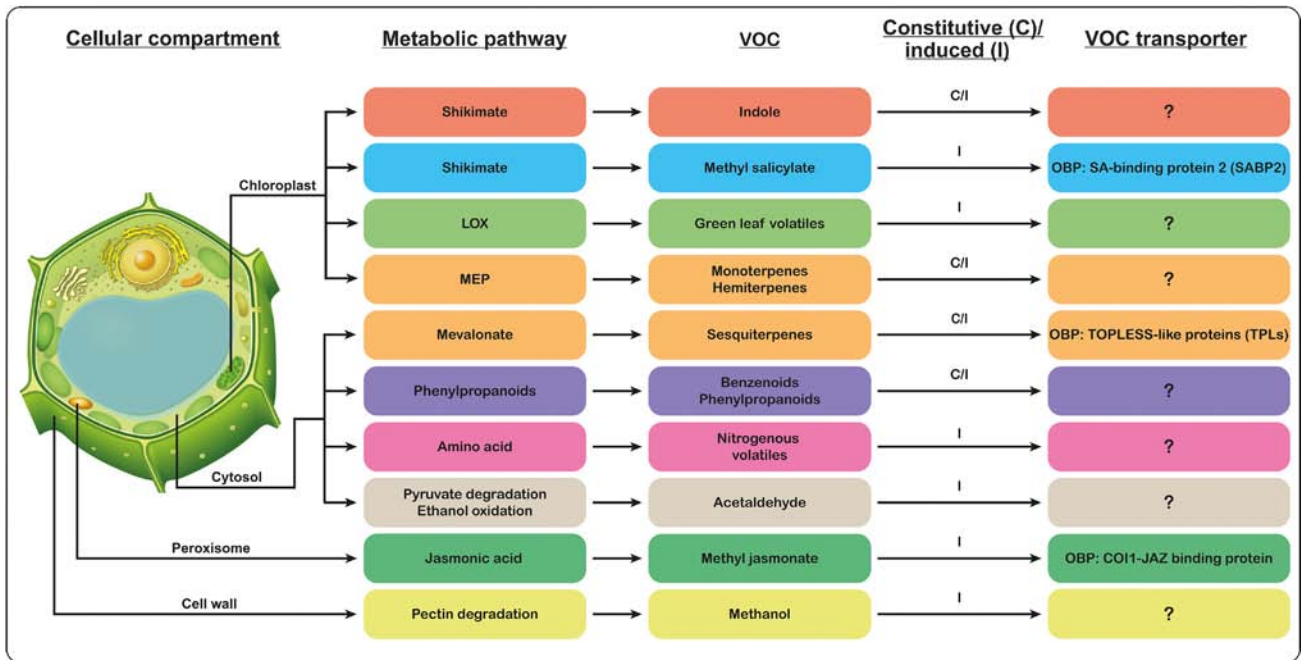


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Figure 2. Three levels of volatile organic compound (VOC)-driven interactions between VOC-emitting and VOC-receiving plants. Constitutive VOCs (VOCs are represented by red dots in all panels) may drive clear allelobiotic interactions, including attraction [12] or repellence [13], portrayed in the upper panels. They may also, arguably, activate basal stress-tolerance mechanisms [59], perhaps by modulating the expression and activity of other stress-induced VOCs. Stress-induced VOCs, however, may more often be interpreted as info-chemicals bringing a message of alert to receiving plants (lower panel). This message may be delivered to conspecific (kin; left on the panel) or allospecific (strangers; right on the panel) plants [17], where it primes or elicits the activation of defensive responses helping those eavesdroppers resist or tolerate upcoming stresses. Plants that are not close enough to receive the VOC message do not activate defenses and are more exposed to stress-related damage.

not transfer the odorant inside the cell. Thus, this second hypothesis would require further work aimed at identifying ORs and the cells that express them. (iii) Plants use active transporters to facilitate the passage of VOCs across the plasma membrane. For example, the presence of an ABC protein involved in active transport of VOCs into plant cells has been described [30]. This mechanism would represent a totally novel way of receiving and transferring VOC information in plants.

A third option is that plant sensing of VOCs is not mediated by protein transporters and receptors as in other organisms. When reaching a receiving plant, VOCs may act in a more direct way; for example, by changing the physical and chemical properties of cell membranes or by scavenging reactive oxygen species (ROS) that are formed in stressed leaves. There is solid experimental evidence in favor of these two mechanisms. Most VOCs are lipophilic, and by dissolving in cellular membranes they may change the membrane permeability to ions [31]. Some cations, such as Ca^{2+} and K^+ , are able to trigger changes of membrane potentials, in turn activating defensive



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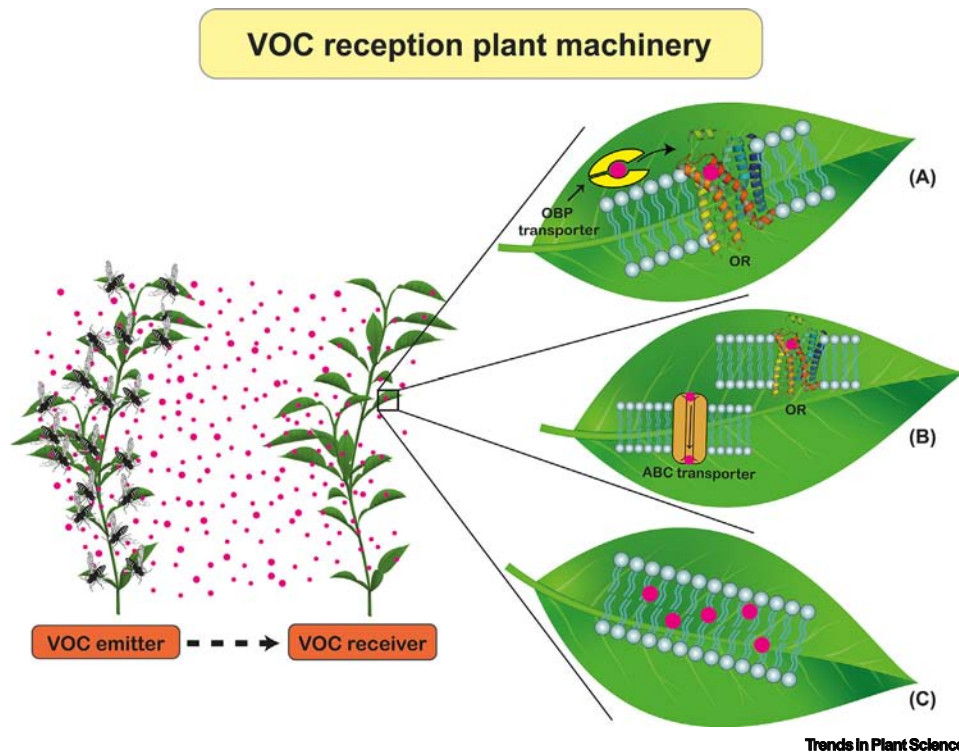
Figure 3. Classes of volatile organic compounds (VOCs) produced by different biosynthetic pathways in emitting plants and current knowledge about the existence of a VOC reception system for them. VOCs are categorized by the cellular compartment from which they are emitted (synthesis may require the cooperation of different organelles), by the metabolic pathway involved in their synthesis, and by their constitutive (C) or induced (I) nature. The emission of many constitutive VOCs can be further induced by stresses, and this is also noted when more significant in nature (C/I). VOC transporters have been rarely found in plants so far. Odorant-binding proteins (OBPs) of methyl salicylate (MeSA) and methyl jasmonate (MeJA) have been described [23–25] and a putative cytosolic OBP for sesquiterpenes has also been found [28]. For all other VOC classes, the possibility that VOCs are bound and transported by specific OBPs needs to be tested (represented by ?). Preliminary *in silico* experiments show that monoterpenes might be bound by the same OBPs binding MeSA and MeJA, whereas the constitutive and abundant hemiterpene isoprene is not bound by known OBPs [45].

metabolisms and physiological changes. In the case of isoprene, the most common and abundant constitutive VOC emitted in the atmosphere, high solubility in the membrane phospholipid bilayer has again been invoked to explain the maintenance of the conformation and elasticity of the chloroplast membranes under stress [32]. Isoprene and monoterpenes also have an antioxidant effect, probably due to a direct scavenging of ROS and reactive nitrogen species in the leaf mesophyll [33,34]. Even in this second case, the presence of volatile isoprenoids alters the overall plant metabolism and the response of plants to stress, which explains the large reprogramming of the transcriptome [35], proteome [36], lipidome [37], and metabolome [38] in isoprenoid-emitting plants. Whether this also occurs in neighboring plants that sense isoprenoids remains to be seen. Recent experimental results indicate that isoprene and β -caryophyllene sensed by arabidopsis plants that eavesdrop emissions of infected neighbors are able to induce resistance to the pathogen. It is suggested that isoprene and β -caryophyllene may act by strengthening SA and JA signaling, respectively, through upregulation of the two pathways [27].

The idea that VOCs are perceived by plants without any specific reception system is seductive and not fully convincing at the same time. On the one hand, it supports the notion that plants lack the olfactory system of animals whose stereospecificity explains the need for OBPs and ORs. On the other hand, the wealth of emitted VOCs (with more than 1700 different VOCs emitted [1], many in both enantiomeric forms [39]) seems to be better explained by a superior level of organization of VOC perception by plants [6].

Key figure

Hypothesized plant volatile organic compound (VOC) reception machineries



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Figure 4. Three different plant VOC reception machineries are hypothesized. VOCs emitted by the plant after stress induction (a pest attack is represented in the left-hand plant) can be perceived by the receiving (right-hand) plant, and by its magnified leaves, as follows. (A) Through the presence of a reception system similar to that present in vertebrate organisms (Figure 1), which includes the presence of odorant-binding proteins (OBPs) as odor transporters and the presence of olfactory receptors (ORs) that receive the VOCs, transduce the chemical signal, and generate the response of the plant (top leaf). (B) By binding of VOCs directly to the ORs, which again induces a change in OR conformation and generates a plant response through the transduction of a chemical signal. Alternatively, VOCs may be bound and transported into the cell through protein active systems (e.g., the ABC transporter, suggested by [30]) (middle leaf, with both potential mechanisms depicted). (C) By binding VOCs directly onto the cell membrane. This may change physical and chemical properties altering the membrane's permeability to ions, which in turn modifies membrane potentials. As for the previous cases, these changes may also trigger a defensive response and the activation of secondary metabolism (bottom leaf).

A framework for early steps of VOC perception in plants

Based on the available information, we may hypothesize that plants possess more than one way of sensing exogenous VOCs, which ultimately effectively induce metabolic changes and reprogram gene synthesis and regulation (Figure 4). However, is there a pattern that can help to streamline how VOCs are perceived by plants?

OBP transporters may be available for all VOCs that are induced by stresses (Figure 3); that is, beside the three cases mentioned in the preceding text, isoprenoids formed by the MEP and MVA pathways (monoterpenes and sesquiterpenes other than β -caryophyllene), GLVs formed

by the LOX pathway and the consequent breakdown of lipids in the membranes (C_6 alcohols, aldehydes, and acids, but note that GLV may undergo glycosylation before perception [40]), and VOCs formed by the degradation of cell-wall pectins (methanol). Other induced VOCs seem to directly prime the activation of defenses (e.g., mitogen-activated kinases and WRKY TFs in the case of indole [41]) without being specifically bound by OBPs and/or ORs. Further research should investigate whether more plant OBPs are present or whether OBPs that are known to bind MeJA, MeSA, or β -caryophyllene are also able to bind other odorant molecules; that is, are not specific for a single VOC. This is the case with vertebrate and insect OBPs where several odors can be bound by the same OBP but with different association/dissociation constant values [42]. Future research should also highlight whether plant OBPs are VOC transporters (*sensu* those found in animals) or act as true ORs. In the first case, the chemical structures acting as ORs also await discovery.

While induced VOCs may or may not bind OBPs, it may be hypothesized that OBPs are never able to bind VOCs that are 'constitutively' emitted by plants. Herbivory and abiotic stresses often enhance levels of constitutive compounds rather (or besides) inducing the emission of new VOCs [43,44]. While enhancing constitutive VOC emissions may help plants to self-defend against stressors, the same compounds may not be involved in plant–plant communication (but see, e.g., [15]) or may not need OBPs to be recognized by neighboring plants. We have preliminary evidence that the main constitutive VOC (isoprene) does not fit well on the binding sites of known or putative plant OBPs, where other induced VOCs are likely to dock [45]. Moreover, the continuous and generally large biosynthesis of isoprene and other constitutive VOCs [9] may saturate the OBP binding sites and may not be efficiently released by the protein at the delivery site. Finally, it is unclear what message can be carried by VOCs that are continuously emitted without being elicited by alien factors. The ecological value for a receiving plant of being continuously informed or primed by emitters is unclear, unless these VOCs co-regulate other defensive pathways [35] or serve as a background on which other (active) VOCs can be better perceived. For example, the human nose, which can perceive more than 1 trillion different odors, becomes 'habituated' and tends to ignore continuous VOC stimulation, rather processing sudden variations of the sensed VOC blend [46]. Animals are likely to respond differentially to different blends comprising the same molecules in different ratios, which indicates that there may be more than a simple turning on and off by individual chemicals. Insects are also believed to perceive blends rather than single VOCs [47,48]. Is this also true for plants [49]?

Concluding remarks: is VOC listening a good strategy for sustainable agriculture and plant protection?

Understanding how plants react to information sent by neighbors in the form of VOCs has promising applications in 'bioinspired' strategies to optimize plant cultivation while the reducing need and execution of agricultural practices [50]. For example, if induced VOCs are early indicators of drought stress, and this is phenotyped with current advanced high-throughput technologies, timely irrigation may avoid loss of production and optimize water and carbon resources (e.g., avoiding wasteful redistribution of carbon into secondary metabolites). If VOC perception allows natural reinforcement of the defense barriers of receiving plants, this can enable a step change in the use of biologically based approaches for integrated pest management and the enrichment in plants of metabolites of interest for their nutritional and pharmacological value.

The biological control of insects both in the field and in greenhouses using herbivore-induced plant VOCs is a well-established application [51]. In many other cases, however, (and particularly when addressing plant–plant interactions) the use of VOCs in agriculture has not been as successful as promised [6,11]. The VOC effect may be limited to plants living very near to an

Outstanding questions

How do plants perceive VOCs that are sent by neighboring plants?

Is there a difference for eavesdropping receivers between the sensing of induced VOCs and of VOCs that are constitutively and lifelong emitted by plants?

How do sensed VOCs activate the transduction signal leading to metabolic changes and eliciting natural defenses?

Are the few OBPs so far retrieved in plants able to bind nonspecifically to plant VOCs and how do they release the VOCs for the transduction pathways to start?

Can VOCs be exploited to implement sustainable practices of plant protection or is plant–plant communication via VOCs limited (e.g., by air-composition diversity) in the real world?

emitter and that receive a clear and strong message. Herbivory-induced changes of the blend of emitted VOCs may be sensed by all neighboring conspecifics or only by neighbor plants of the same genotype of VOC emitters [52]. The impacts of VOCs as signaling molecules that elicit plant defenses or attract beneficial microorganisms has often been seen belowground, where VOC movements may be restrained by soil compactness, and VOCs are associated with other stress-induced compounds that may also have a signaling role, such as oxylipins [53]. Aboveground VOCs are also more sensed by plants growing in restricted environments (laboratories or greenhouse) than in open fields [11]. In the air, VOCs may travel long distances [54], but they mix and react with many other atmospheric components and are lost [54] or transformed into secondary compounds that may not be active for plant–plant interactions [55].

VOCs may also be sensed differently by domesticated and wild plants. It could be expected that the VOC alert signal is less sensed in domesticated plants that are less exposed to stress and more protected by pesticides and where breeding might have selected against carbon loss in the form of VOCs, but there are good examples that domesticated plants are both better and worse listeners than their wild relatives in nature (reviewed in [56]).

By improving our knowledge of VOC perception by plants (see [Outstanding questions](#)), these and many other factors that may change VOCs' efficacy as signaling molecules may be better addressed. Even with our limited current knowledge, applications of VOCs for sustainable plant protection are moving from simple 'push–pull' practices for the management of pests [57] to more sophisticated and ambitious trials, including the use of VOC-induced damage associated molecular patterns (DAMPs) for plant vaccination against diseases [58]. Future progress may even be aimed at 'teaching' plants to listen to the voices of their crying friends; for example, by using technologies such as 'directed evolution' to further improve the properties of OBPs as VOC transporters or by using artificial-intelligence algorithms to reproduce the best conditions for receiving VOC signals and activating plant defenses after VOC listening. The exploitation of VOCs may contribute to fostering a transition toward sustainable agriculture, making biological control the successor of synthetic chemistry pesticides, with obvious ecological and environmental benefits and positive implications for food safety and health.

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Declaration of interests

No interests are declared.

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