

FOCUSED REVIEW

Volatile terpenes – mediators of plant-to-plant communication

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Received 10 April 2021; accepted 3 August 2021.

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SUMMARY

Plants interact with other organisms employing volatile organic compounds (VOCs). The largest group of plant-released VOCs are terpenes, comprised of isoprene, monoterpenes, and sesquiterpenes. Mono- and sesquiterpenes are well-known communication compounds in plant–insect interactions, whereas the smallest, most commonly emitted terpene, isoprene, is rather assigned a function in combating abiotic stresses. Recently, it has become evident that different volatile terpenes also act as plant-to-plant signaling cues. Upon being perceived, specific volatile terpenes can sensitize distinct signaling pathways in receiver plant cells, which in turn trigger plant innate immune responses. This vastly extends the range of action of volatile terpenes, which not only protect plants from various biotic and abiotic stresses, but also convey information about environmental constraints within and between plants. As a result, plant–insect and plant–pathogen interactions, which are believed to influence each other through phytohormone crosstalk, are likely equally sensitive to reciprocal regulation via volatile terpene cues. Here, we review the current knowledge of terpenes as volatile semiochemicals and discuss why and how volatile terpenes make good signaling cues. We discuss how volatile terpenes may be perceived by plants, what are possible downstream signaling events in receiver plants, and how responses to different terpene cues might interact to orchestrate the net plant response to multiple stresses. Finally, we discuss how the signal can be further transmitted to the community level leading to a mutually beneficial community-scale response or distinct signaling with near kin.

Keywords: interaction, isoprene, monoterpenes, plant communication, sesquiterpenes, signaling, terpenes, VOCs, volatile organic compounds.

INTRODUCTION

Plants are known to detect their neighbors by various cues, such as ratios of red:far red light or ethylene in the air (Binder, 2020; Devlin, 2016). However, to not only detect, but also identify the neighbor, more detailed information is needed. Such information can be transmitted by volatile organic compounds (VOCs) both above- and belowground. Plants release a high diversity of various VOCs such as terpenes, fatty acid derivatives, amino acid derivatives, and phenylpropanoid/benzenoid compounds. Volatile terpenes are the most diverse group of VOCs comprising the C5 compound isoprene, C10 monoterpenes, C15 sesquiterpenes, and also C11 and C16 homoterpenes and some C20 diterpenes

(Rosenkranz and Schnitzler, 2016). Terpenes can protect plants from various abiotic and biotic stresses (Loreto and Schnitzler, 2010; Unsicker et al., 2009). Moreover, they are important communication and interaction signals between plants and other organisms, including insects, fungi, and bacteria (Huang et al., 2003; Huang et al., 2012; Nieuwenhuizen et al., 2009; Schulz-Bohm et al., 2017). Different environmental constraints, such as herbivore feeding style (Simon et al., 2015), pathogen infection (Delaney et al., 2015), or below-ground microbial communities (Kong et al., 2021), can induce very specific emission patterns from plants.

During recent years, it has become clear that terpenes can also function as plant semiochemicals. Specific sesquiterpenes, for example, were shown to alter the growth and

BOX 1. SUMMARY

- Volatile terpenes can act as plant-to-plant signaling cues.
- The high structural diversity of terpenes and species- and organ-specific emission patterns bear a great potential to confer distinct signals.
- Volatile terpenes can influence plant innate immunity by modulating salicylic acid and jasmonic acid signaling.
- Volatile terpenes can sensitize complex signaling pathways in plant cells that enhance plant fitness, for example by fine-tuning plant stress tolerance through modulating phytohormone crosstalk.
- Volatile terpenes act as self-propagating signals that can potentially optimize plant performance at the community level.

BOX 2. OPEN QUESTIONS

- How are volatile terpene cues perceived by plant cells and what are possible receptors of volatile terpene cues?
- How important is the combination of compounds in a plant VOC blend to confer and perceive a correct, intraspecific message?
- What is the ecological benefit for an individual organism to emit defense cues that protect neighboring, non-kin individuals from incurring stress?
- How does terpene-mediated plant-to-plant communication function in mixed communities?
- How common is the self-propagation of distinct volatile terpenes in different plant species?

defense status of neighboring plants (Algarra Alarcon et al., 2015; Gfeller et al., 2019; Pazouki et al., 2016; Yoshioka et al., 2019). Functions as signaling cues were also revealed for monoterpenes and even for the smallest terpene compound, isoprene (Frank et al., 2021; Riedlmeier et al., 2017; Wenig et al., 2019). Mono- and sesquiterpenes are especially interesting mediators of plant-to-plant signaling for several potential reasons. These include a high species specificity of the emission patterns and the inducible, trigger-dependent release of mono- and sesquiterpenes. In contrast to more complex terpenes, isoprene emission is not known to be triggered by biotic stressors. They depend on the abiotic environment, such as light and temperature (Behnke et al., 2007; Loreto and Schnitzler, 2010). Even so, also isoprene has been shown to effectively induce resistance against pathogens (Frank et al., 2021), change plant growth rates (Loivamaki et al., 2007; Terry et al., 1995; Zuo et al., 2019), alter plant

redox status (Loreto and Velikova, 2001; Miloradovic van Doorn et al., 2020), and adjust receiver plants' internal signaling mechanisms (Frank et al., 2021; Zuo et al., 2019). Together, these results imply that isoprene is a bioactive molecule with multiple talents. The various different functions of isoprene and other terpenes might be easier to explain if they are considered as rapid, aerial within-plant signaling cues (Baldwin 2006; Frank et al., 2021). In fact, VOC-based plant-to-plant communication might in general have evolved to enhance the signaling speed within a plant rather than between plants. Especially for bigger trees, the air phase seems an attractive alternative to phloem-based transport and could help to convey information from one part of the tree to another. Such evolutionary origin of plant-to-plant signaling is supported by the finding that volatile-mediated signaling functions better between genetically related plants than between different species (Kalske et al., 2019; Karban et al., 2013).

The ability to perceive a signal is essential for effective communication. Recent studies revealed that terpenes can alter distinct internal signaling routes leading to terpene-specific responses in receiver plants. Such responses include phytohormone-associated defense responses against pathogens, such as induced systemic resistance (ISR) as well as systemic acquired resistance (SAR) or SAR-like immune reactions (Frank et al., 2021; Riedlmeier et al., 2017; Wenig et al., 2019). ISR is associated with jasmonic acid (JA) signaling and protects plants against necrotrophic pathogen attack as well as herbivore feeding (reviewed in Vlot et al., 2021). While ISR is also under the modulatory influence of salicylic acid (SA), the latter phytohormone primarily promotes SAR and associated defense responses to biotrophic pathogens (Vlot et al., 2009, 2021). As a result, plant–insect and plant–pathogen interactions might influence each other's outcomes through phytohormone crosstalk and associated, possibly regulatory, volatile terpene cues. In addition, terpenes are shown to alter the plant redox status even if the mechanisms are still unknown (Loreto et al., 2001; Loreto and Velikova, 2001; Miloradovic van Doorn et al., 2020; Riedlmeier et al., 2017; Vanzo et al., 2016). Together, different adjustments of plant internal signaling via terpenes can contribute to altered plant performance that may prepare plants to survive in changing environments (Frank et al., 2021; Riedlmeier et al., 2017; Wenig et al., 2019). Eventually, an intact receiver plant may also begin to release specific terpenes to the atmosphere, thus transmitting the information further in a plant community (Wenig et al., 2019).

In this review we discuss the potential of individual terpene compounds, as well as of terpenes in VOC blends, as intra- and interspecific information transmitters. We review the current knowledge on terpenes as effective plant signaling cues, focusing on (i) how these cues may be perceived by plants, (ii) how the performance of receiver

plants is adjusted, and (iii) how terpenes may function as a tool to induce rapid community-level responses.

POTENTIAL SPECIFICITY OF TERPENE CUES

Terpenes possess a high structural diversity

In general, two pathways, the 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway in plastids and the mevalonate (MVA) pathway in the cytosol, are responsible for forming the initial C5 building blocks of terpenes, isopentenyl diphosphate and dimethylallyl diphosphate (DMADP) (Chizzola, 2013; Davis and Croteau, 2000). These building blocks can be converted by prenyltransferases to further, longer-chained molecules, including geranyl diphosphate (GDP) and farnesyl diphosphate (FDP), that serve as mono- and sesquiterpene precursors, respectively. Terpene synthesis rates are mainly controlled by the availability of the precursors and the activity of the terpene synthases/cyclases (TPSs) (Ghirardo et al., 2014; Karunanithi and Zerbe, 2019). In general, isoprene (ISPS), monoterpene (MTS), and sesquiterpene (SQTS) synthases catalyze the formation of a range of different terpene skeletons from DMADP, GDP, and FDP, respectively (Davis and Croteau, 2000). The different TPSs exhibit a high diversity that may have emerged under selection pressure from mutations and other changes in the genetic code (Alicandri et al., 2020; Tholl and Lee, 2011). Moreover, one TPS can be responsible for the synthesis of various terpenes, which additionally enhances the potential number of terpene chemical structures in a plant emission blend (Tholl et al., 2005). Depending on various modification steps, different acyclic and cyclic terpene scaffolds are obtained (examples of common terpene scaffolds are given in Figure 1). The formation of different mono- and bicyclic monoterpenes, such as limonene, α -terpinene, pinene, or camphene, requires, among others, pyrophosphorylation and cyclization steps. Various further monoterpenes can be obtained by hydroxylation, peroxidation, methylation, acylation, or glycosylation steps (Böttger et al., 2018; Degenhardt et al., 2009; Mahmoud and Croteau, 2002). Similarly, initially formed sesquiterpene skeletons can be further modified to enhance the diversity of volatile molecules. For example, formation of (*E,E*)-germacradienyl or (*E,E*)-humulyl cations depends initially on the different cyclization positions on the farnesyl cation carbon skeleton. Through a series of further reactions β -selinene or (*E*)- β -caryophyllene can be synthesized. Alternatively, farnesyl cation isomerization can yield a nerolidyl cation, from which different sesquiterpenes, such as (–)-sesquithujene and (+)- δ -cadinene, can be obtained depending on the position of carbon skeleton cyclization. Some unique sesquiterpenes, such as the 5-epi-aristolochene from tobacco (*Nicotiana tabacum*), are results of a series of different reactions with a vast number of in-between products that may as well be volatile (Böttger et al., 2018; Chizzola, 2013;

Degenhardt et al., 2009). Sesquiterpene alcohols and diterpenes, moreover, can function as precursors of the homoterpenes 4,8-dimethylnona-1,3,7-triene (DMNT) and 4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT), which are formed by oxidative degradation from (*E*)-nerolidol and (*E,E*)-geranyl linalool, respectively. Also, Arabidopsis roots were shown to biosynthesize DMNT by the degradation of the C30 triterpene diol arabidiol (Sohrabi et al., 2015). DMNT and TMTT are especially bioactive terpene compounds with various roles in tritrophic signaling (Kappers et al., 2005; Vuorinen et al., 2004). The vast majority of terpene modifications and oxidations are performed by cytochrome P450 monooxygenases (P450). Through the activity of cytochromes P450 or other enzymes, including dehydrogenases, methyltransferases, acyltransferases, and glycosyltransferases, terpenes can undergo modifications that enhance the structural diversity and enable further reactions and tailoring of the molecule structures (Bathe and Tissier, 2019; Boachon, Burdloff, et al., 2019; Zhou and Pichersky, 2020). In sum, the vast array of different TPSs, as well as further enzyme-driven terpene modifications, may lead to enormous chemical diversity and associated options to fine-tune messages that are spread throughout plant populations.

Ratio-, species-, and organ-specific terpene cues

Development of an ability to eavesdrop the signaling cues of others may provide an evolutionary advantage to some species. In that context it has been suggested that different species could exploit a language that can be understood only by the closest kin (Kalske et al., 2019; Karban et al., 2013). Compared to more common volatile compounds, such as wound response-related green leaf volatiles (GLVs) (ul Hassan et al., 2015), the diverse isomers of terpenes bear a great potential to transmit distinct information to the neighborhood. Recently, over 100 different plant species were classified based on their terpenomes (Vivaldo et al., 2017). The classification was possible especially due to distinct, species-specific terpene and sulfur compounds that were detected in the emission patterns. The species specificity is based not only on the chemical structures, but also on the blends and ratios in which different molecules are emitted. VOC blends are known to play important roles in plant-to-insect interactions (Junker et al., 2018; Proffit et al., 2020) and they may also be used in plant-to-plant signaling (Bouwmeester et al., 2019; Erb, 2018; Kikuta et al., 2011). According to the results of Kikuta et al. (2011), all the compounds in an emission blend consisting of a sesquiterpene and GLVs are important to trigger the induction of pyrethrin in *Pyrethrum daisy* (*Tanacetum cineraiifolium*) receiver plants. Separating the VOC mixture into its individual components abolished the signaling effect (Kikuta et al., 2011). Simpraga et al. (2016)

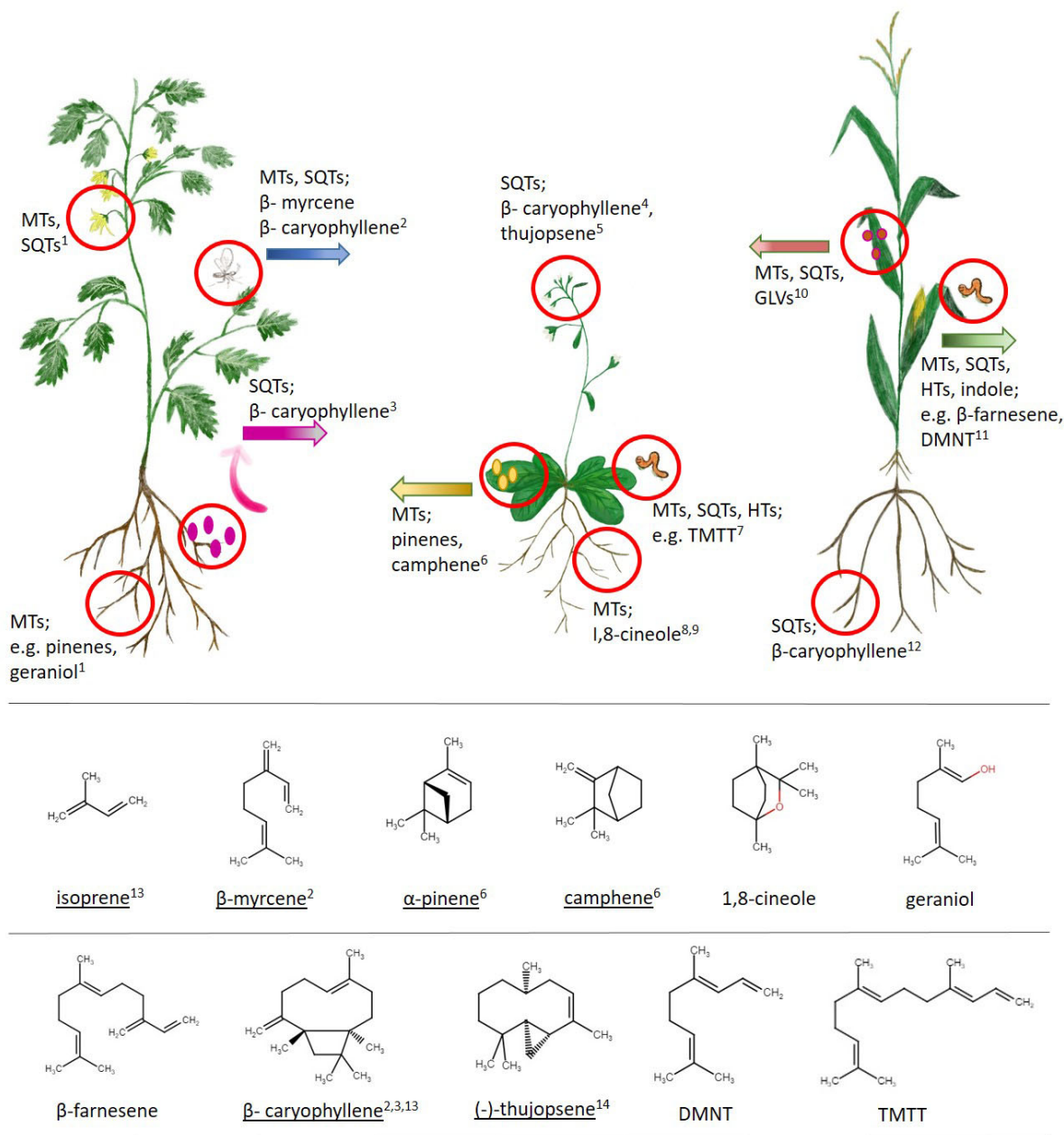


Figure 1. Plant organ- and species-specific, biotic stress-induced emission patterns of the model species tomato, Arabidopsis, and maize. For each organ and plant species some prominent terpene(s) and oxygenated terpenes with potential ecological functions are named. The arrows highlight the volatile patterns for which ecological roles in plant-to-plant communication have been reported. The respective chemical structures are shown in the lower panels. In addition to terpenoid compounds that are included in the upper panel, also the structure of the smallest terpene, isoprene, is shown. The names of terpenes which are known to elicit responses in receiver plants are underlined. MTs, monoterpenes; SQTs, sesquiterpenes; HTs, homoterpenes; GLVs, green leaf volatiles; DMNT, (3E)-4,8-dimethyl-1,3,7-nonatriene; TMTT, 4,8,12-trimethyltrideca-1,3,7,11-tetraene. The numbers refer to the following publications: 1 (Zhou and Pichersky, 2020); 2 (Zhang et al., 2019); 3 (Kong et al., 2021); 4 (Huang et al., 2012); 5 (Tholl et al., 2005); 6 (Riedlmeier et al., 2017); 7 (Loivamaki et al., 2008); 8 (Chen et al., 2004); 9 (Steeghs et al., 2004); 10 (Delaney et al., 2015); 11 (Ramadan et al., 2011); 12 (Rassmann et al., 2005); 13 (Frank et al., 2021); 14 (Ditengou et al., 2015). Marvin was used to draw the chemical structures (Marvin JS by ChemAxon Ltd; <http://www.chemaxon.com>).

suggested that terpenes may fill the interspecific plant language with a high variety of ‘words’ and ‘word combinations’, which enable plants to send and receive distinct, targeted information. Such private communication

channels might also help to restrict the signaling cues only to genetically closely related neighbors.

Several studies have shown that *TPS* and *ISPS* genes are expressed in specific plant tissues or even in specific

cell types (Chen et al., 2003, 2004; Cinege et al., 2009; Huang et al., 2012; Miloradovic van Doorn et al., 2020; Zhou and Pichersky, 2020). This suggests a highly optimized employment of distinct terpenes. In support of this hypothesis, distinct emission patterns have been measured from leaves, flowers, and belowground parts of *Arabidopsis thaliana* (Blanch et al., 2015; Chen et al., 2003, 2004; Huang et al., 2012; Steeghs et al., 2004) and tomato (*Solanum lycopersicum*) (Zhou and Pichersky) (Figure 1). For example, 1,8-cineole TPS is expressed in very distinct *Arabidopsis* root cells (Chen et al., 2004) that release low amounts of 1,8-cineole (Steeghs et al., 2004). *Arabidopsis* flowers, on the other hand, emit various terpenes, the main compound being β -caryophyllene (Huang et al., 2012; Tholl et al., 2005). Also tomato leaves emit, in addition to several other sesqui- and monoterpenes, β -caryophyllene, whereas the tomato root emission pattern consist mainly of monoterpenes (Kong et al., 2021; Zhang et al., 2019; Zhou and Pichersky, 2020). In tomato, the emission pattern was shown, moreover, to depend on the developmental stage of the flower and leaves (Zhou and Pichersky, 2020). Recently, the cytochrome P450 enzyme CYP706A3 was shown to oxidate a series of terpene molecules in *Arabidopsis* flowers. The resulting oxidation products altered the flower microbiomes, suggesting a role of these compounds in the interaction of the floral tissue with its associated microbes (Boachon, Burdloff, et al., 2019). Sesquiterpenes, such as germacrene D, are also involved in protection and development of petunia (*Petunia hybrida*) flowers. Tube-specific TPS1 products were shown to accumulate in the closed flower buds, thereby potentially protecting the developing stigma from pests and pathogens (Boachon, Lynch, et al., 2019). Evolutionarily thinking, it might be worthwhile to specifically invest in the defense responses of flowers as reproductive organs. Such organ-specific terpene emissions may help plants to balance the costs and benefits that are associated with terpene release.

Some studies suggest that terpenes may also be perceived by specific organs or at least different terpene isoforms can alter the receiver plant performance in a distinct, organ-specific manner. *Arabidopsis*, for example, shows distinct responses to different sesquiterpene isoforms (Ditengou et al., 2015; Frank et al., 2021). Exposure of *Arabidopsis* leaves to β -caryophyllene leads to induced resistance against a leaf pathogen, whereas (–)-thujopsene exposure does not (Frank et al., 2021). In contrast, external (–)-thujopsene alters root architecture and induces accumulation of reactive oxygen species in roots, whereas β -caryophyllene exposure does not appear to induce such changes (Ditengou et al., 2015). Interestingly, whereas *Arabidopsis* releases both of these sesquiterpenes from flowers (Boachon, Burdloff, et al., 2019), it is not known to release either of them from leaves or roots, at least not

constitutively (Huang et al., 2012; Loivamaki et al., 2008; Steeghs et al., 2004). Whether *Arabidopsis* leaves can detect β -caryophyllene concentrations emitted by flowers, and if such detection could have evolutionary benefits, remains to be elucidated. The receiver leaves, exposed to flower-released β -caryophyllene, might induce JA signaling and a related resistance reaction (Frank et al., 2021) for a short period to ensure successful reproduction (Figure 2).

Depending on the plant species, different sesquiterpene isoforms may have distinct functions that are associated with specific plant organs. For the sesquiterpene β -caryophyllene, ecological functions were revealed in *Arabidopsis* flowers and the aboveground organs of tomato (Figure 1) (Huang et al., 2012; Kong et al., 2021; Zhang et al., 2019); however, it has been shown to diffuse relevant distances also in soil environments (Hiltbold and Turlings, 2008). Indeed, β -caryophyllene appears to play a role in belowground interactions of several plant species (Gfeller et al., 2019; Huang et al., 2019; Rasmann et al., 2005). Recently, β -caryophyllene was shown to function as a belowground plant-to-plant cue, adjusting the germination, growth, and defense of sympatric neighboring plants of *Centaurea stoebe* (Gfeller et al., 2019; Huang et al., 2019). *Centaurea stoebe* releases β -caryophyllene from roots in a constitutive manner, suggesting continuous profit of the emission for the sender and/or the community.

Terpene emission is triggered by various environmental factors

Volatile compounds can be released from plants constitutively or in an induced manner. Constitutively released compounds are mostly released from storage organs such as resin ducts (Loreto and Schnitzler, 2010) and are crucial for example in defense of many conifers (Kopaczky et al., 2020). To convey correct information about actual, changing environmental constraints, however, trigger-specific volatile patterns are necessary. Terpene emission can be induced in plants by various abiotic and biotic stresses in processes that are relatively well characterized compared to those underlying the perception of potential signaling cues. Various triggers, including herbivore feeding, egg deposition, pathogen attack, altered microbiome, or different abiotic stresses, have been shown to induce specific VOC emission patterns (Ament et al., 2004; Arimura et al., 2000; Baldwin and Schultz, 1983; Büchel et al., 2011; Delaney et al., 2015; Kong et al., 2021; Pazouki et al., 2016). In the release of at least some VOCs from plant tissues, ATP-binding cassette transporters can be involved (Adebesin et al., 2017; Liao et al., 2021). Interestingly, more common compounds, such as GLVs, are often released rapidly after the leaf tissue is disturbed, whereas the emission of more specific terpene blends is induced later (Erb et al., 2015;

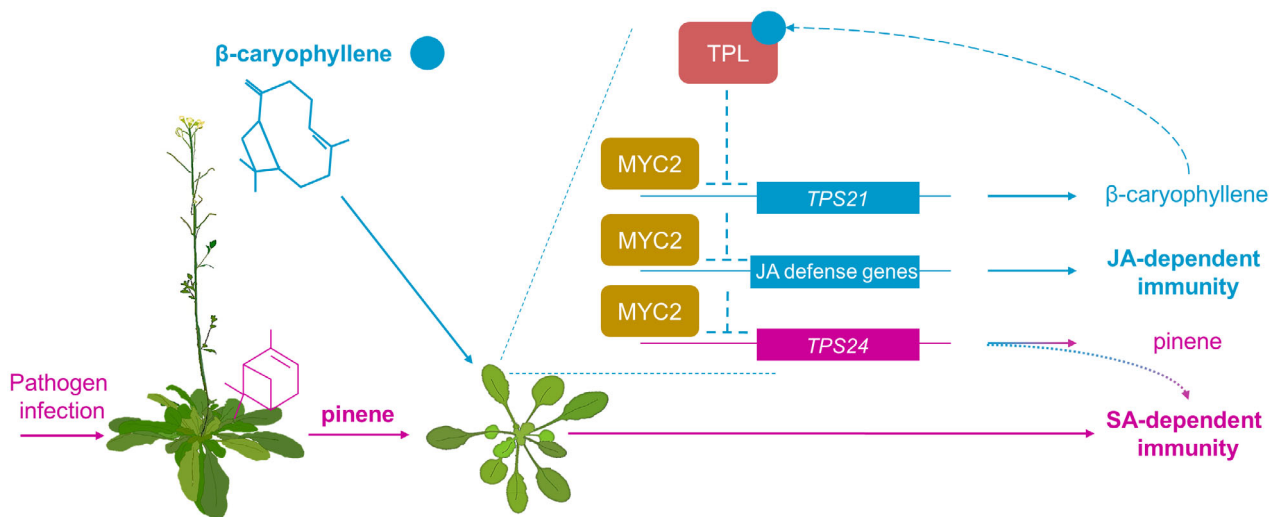


Figure 2. Terpenes in plant–pathogen interactions.

Pathogens which trigger a salicylic acid (SA)-associated immune response induce emissions of monoterpenes, including pinene. These monoterpenes are recognized as defense cues in the systemic tissues of the same and neighboring *Arabidopsis thaliana* plants, resulting in the propagation of SA-dependent defense responses. *Arabidopsis* flowers emit β-caryophyllene. This compound is recognized as a defense cue in plants. Direct interaction of β-caryophyllene with TOPLESS-like (TPL) transcription factors might release TPL-mediated inhibition of MYC2-dependent transcriptional regulation of *TPS21* (encoding β-caryophyllene synthase), JA-associated defense genes, and *TPS24*, a monoterpene synthase that contributes to the propagation of interplant SA defense cues.

Simpraga et al., 2016). It can be speculated that GLVs that are released also after mechanical damage function as initial, more general signaling cues, whereas later released volatile terpenes could activate more specific plant responses (please see further discussion below under ‘Do plants whisper to avoid eavesdropping?’).

HOW PLANTS ‘SENSE’

Direct employment of atmospheric terpenes for plants’ own defense

Herbivorous insects and parasitoids recognize plant VOCs by olfactory proteins such as odorant-binding proteins, odorant-degrading enzymes, and odorant receptors (Leal, 2013). Although plants do not possess similar ‘olfactory nerves’, they can still detect different VOCs, including terpenes. There have been several attempts to explain how plants may employ volatile compound cues in the atmosphere. Maybe the simplest means is the so-called passive associational resistance hypothesis. According to this hypothesis, plants employ atmospheric terpenes and their antibiotic properties for their own defense. The receiver plants can adsorb beneficial terpenes or terpene oxidation products and either store them in epidermal cells or release them slowly to the environment (Camacho-Coronel et al., 2020; Mofikoya et al., 2017, 2020). This phenomenon was observed in birch (*Betula*) (Himanen et al., 2010), broccoli (*Brassica oleracea* var. *italica*) (Li and Blande, 2015), and cabbage (*Brassica oleracea* var. *capitata*) (Mofikoya et al., 2017). Employing artificial imitation wax layers of *Palo brea* trees, Camacho-Coronel and colleagues proved that, in

principle, such mechanisms can exist. The wax layers sequestered and released 18 types of terpene compounds, thereby effectively inhibiting the germination of *Colletotrichum lindemuthianum* conidia (Camacho-Coronel et al., 2020). This ‘passive associational resistance’ strategy seems to be low-cost compared with the *de novo* synthesis of terpenes in plants. Storing various kinds of beneficial terpenes in the epidermal cells might help plants to rapidly respond to changes in a dynamic environment and, moreover, increase the diversity of various VOCs in the blend of an individual plant. It remains, however, unclear to which extent stress tolerance can be increased by simply sequestering terpenes that are released by neighbors. It is certainly not the only means of plants to convey and respond to information in the air. Based on many recent publications it has become evident that plants have additional means of perceiving volatile terpenes and, upon perception, make distinct adjustments in their internal signaling pathways.

Potential mechanisms of terpene perception

It has so far remained largely unsolved how plants perceive terpenes and integrate the received information into their metabolism. There are several hypotheses of potential mechanisms, which are based on the knowledge of how plants may perceive other volatile compounds. For example, the phytohormones SA and JA are well known to switch between their volatile, methylated and bioactive, non-methylated forms. While methyl salicylate (MeSA) can act as an airborne defense cue in plant-to-plant communication (Shulaev et al., 1997), the methyl group is believed to inactivate the respective within-plant signal (Park et al.,

2007). Thus, MeSA is hydrolyzed in receiving tissues to promote SA immune reactions (Park et al., 2007; Park et al., 2009). Similarly, methyl jasmonate (MeJA), which is believed to contribute to plant-to-plant communication modulating plant-insect interactions (Baldwin et al., 2006), upon its arrival in the receiver plant, is presumably converted to JA by MeJA esterase (Tamogami et al., 2008; Wu et al., 2008). Also other VOCs, including terpenes, may be taken up by plants and further converted to VOC derivatives, metabolic products which might serve as additional defense chemicals (Matsui, 2016; Schmelz et al., 2014). The sesquiterpene alcohol nerolidol, for example, was shown to be modified after uptake in tea plants (*Camellia sinensis* (L.) O. Kuntze). Under cold stress, tea releases nerolidol, which primes cold tolerance in receiver plants by regulating cold stress-related C-repeat binding factors (Zhao, Wang, et al., 2020). The exogenous nerolidol was glycosylated in receiver plants by UDP-glycosyltransferases to nerolidol glucoside. The glycosylation significantly increased the solubility of the sesquiterpene and, moreover, altered the plant redox balance (Zhao, Zhang, et al., 2020). Similarly, the monoterpene 1,8-cineole emitted by eucalyptus (*Eucalyptus globulus*) trees was shown to be taken up by grapevine (*Vitis vinifera*) plants, where it was eventually glycosylated (Capone et al., 2012; Pardo-Garcia et al., 2015).

Terpenes may also potentially serve as volatile precursors of essential phytohormones. Exposure to the volatile *ent*-kaurene, which is a tetracyclic diterpene precursor for gibberellic acid (GA) biosynthesis (Yamaguchi, 2008), was shown to rescue the dwarf phenotype of *ent*-kaurene- and GA-deficient *ga1-3* and *ga2-1* mutant Arabidopsis receiver plants (Otsuka et al., 2004). This finding suggests that plants may be able to take up exogenous terpenes and use them as substrates for the production of distinct plant hormones. The sesquiterpenes δ -cadinene and β -macrocarpene, for example, might have similar properties. These compounds are associated with the biosynthesis of the antimicrobial non-volatile hemigossypol and a zealexin, respectively (Mafu et al., 2018; Wang et al., 2003). Such terpene derivatives might act to delicately adjust plant metabolism in response to environmental and/or developmental cues.

In addition to the potential absorbance of terpenes and different hypotheses of converted, bioactive terpene derivatives, a perception of terpenes by potential receptor(s) can be postulated. So far, a VOC receptor has been described only for one compound, ethylene (reviewed recently by Binder, 2020). Recently, however, Nagashima and colleagues used β -caryophyllene derivative-linked beads, and observed a direct interaction between β -caryophyllene and TOPLESS-like (TPL) transcription factors from tobacco (Nagashima et al., 2019). Since TPLs act as transcriptional co-repressors in a variety of signaling pathways (Hao et al., 2014), a TPL-dependent recognition of β -caryophyllene might directly

regulate the associated gene expression profiles (Figure 2). Strikingly, TPLs regulate auxin and JA signaling (Li et al., 2019; Perez and Goossens, 2013), and might thus act as receptor-like intermediates regulating β -caryophyllene-induced developmental and defense-associated responses (Nagashima et al., 2019).

At present it still remains to be elucidated if plants possess various different mechanisms to perceive terpenes. In the future, it will be of great interest to tackle questions as to which mechanisms are needed to sort between distinct terpene cues and how the various signals are integrated to a specific response in receiver plants. In light of recent evidence on, e.g., metabolized VOCs (Zhao, Wang, et al., 2020; Zhao, Zhang, et al., 2020), transcription factor binding (Nagashima et al., 2019), and passive associational resistance (Camacho-Coronel et al., 2020), it seems plausible that plants may employ a range of different response mechanisms. Even the same compound might provide the receiver plant benefits by various means, such as by enhancing passive associational resistance and by adjusting plant internal signaling.

TERPENES ACT AS SIGNALING MOLECULES

Terpenes alter plant metabolism and internal signaling

Increasing evidence suggests that airborne terpenes are recognized as immune cues in systemic tissues of the same or neighboring plants (Frank et al., 2021; Riedlmeier et al., 2017; Zuo et al., 2019). Downstream responses to these cues include the induction of phytohormone signaling pathways and of defense-related gene expression. First hints of such communication are based on studies with seedlings of poplar (*Populus* \times *euroamericana*) and sugar maple (*Acer saccharum*) almost 40 years ago (Baldwin and Schultz, 1983). In these experiments, undamaged receiver seedlings exposed to VOCs from sender plants accumulated phenolic compounds in the leaves. Similar responses were also observed in cotton (*Gossypium hirsutum*) when exposed to the monoterpene myrcene (Zeringue, 1987), a major volatile from the essential oil of cotton glanded flower buds. Later, several studies showed that intact receiver plants can change their metabolism when exposed to specific terpene compounds. The major terpenes (*E*)- β -ocimene, DMNT, and TMTT, released from *Tetranychus urticae*-infested lima bean (*Phaseolus lunatus*) leaves (Arimura et al., 2000), led in receiver beans to enhanced transcript accumulation of *PATHOGENESIS-RELATED-1* (*PR-1*), *PR-2* (encoding β -1,3-glucanase), and *PR-3* (encoding chitinase), as well as of *PHENYLALANINE AMMONIA LYASE* (*PAL*), indicating the activation of SA-associated defense pathways. Very recently, it was shown that terpenes may even be a tool to inform conspecifics about available beneficial soil microbiota. In tomato receiver plants, SA accumulates in root exudates after exposure of the plants to

β -caryophyllene emitted by their neighbors (Kong et al., 2021). Exposure to β -caryophyllene has also been shown to alter plant performance in other studies (Frank et al., 2021). Recently, exposure of *Arabidopsis* to β -caryophyllene was shown to enhance plant resistance against pathogenic *Pseudomonas syringae* (Frank et al., 2021). Because β -caryophyllene-induced resistance was lost in mutants with defects in the biosynthesis of JA-isoleucine (JA-Ile), the bioactive form of JA in defense (Fonseca et al., 2009), the data suggest a possible connection between β -caryophyllene and ISR.

Strikingly, also isoprene, the smallest terpene that was previously mainly suggested to improve plant tolerance against abiotic stresses (Loreto and Schnitzler, 2010), has meanwhile been shown to adjust plant signaling. Several studies indicate that isoprene might have a more general function in modulating plant performance of isoprene-producing plants and also of (neighboring) plants receiving isoprene cues (Behnke et al., 2010; Frank et al., 2021; Loivamaki et al., 2007, 2008; Loreto and Velikova, 2001; Terry et al., 1995; Velikova and Loreto, 2005; Zuo et al., 2019). At present, it remains unclear what are the molecular mechanisms behind this role of isoprene. Previously, isoprene was suggested to function by altering the plant redox and S-nitrosylation status (Behnke et al., 2010; Vanzo et al., 2016). While direct antioxidative effects of isoprene are weak, it might be able to indirectly regulate more effective antioxidants, for example by activating expression of transcription factors. (Harvey and Sharkey, 2016; Monson et al., 2021). Furthermore, no consensus exists on whether exogenously applied isoprene triggers similar responses in receiver plants as those that are detected in isoprene-producing sender plants. When the natural non-isoprene emitters *Arabidopsis* and tobacco (*N. tabacum*) were transformed to constitutively emit isoprene, several plant growth-related parameters as well as JA-associated defense gene expression were modulated (Zuo et al., 2019). Exposure of *Arabidopsis* to synthetic isoprene or naturally isoprene-emitting poplar plants enhanced the resistance of the plants to *P. syringae* in a JA-independent manner (Frank et al., 2021). Here, the induced resistance response in the receiver plants in these plant-to-plant communication experiments depended on functional SAR components, including the SA receptor NPR1 (Ding et al., 2018; Frank et al., 2021). Together, these studies reveal that isoprene is able to modulate plant internal signaling and priming, even if the response may be complex and dependent on various environmental and/or plant physiological factors. Monson et al. (2021) suggested that the hydrophobic nature of isoprene may allow it to access signaling components in the hydrophobic domains of membrane lipids and to influence signaling pathways across membranes. Such ability may set a stage for rapid, almost simultaneous adjustment of different signaling pathways

within a plant. Whatever the mechanisms behind isoprene function are, it seems to have a global ability to modulate plant performance.

Complex adjustments of phytohormone levels upon perceiving terpenes

In light of the above, it is of interest to note that SA and JA defenses are generally believed to act mutually antagonistically (Pieterse et al., 2012). This antagonism is modulated by different parameters, including further interactions with other phytohormone pathways (Burger and Chory, 2019). These include the GA pathway, which promotes growth and inhibits JA defenses, and is upregulated in transgenic, isoprene-emitting *Arabidopsis* plants (Burger and Chory, 2019; Zuo et al., 2019). Since GA in this manner compromises the inhibitory effect of JA on SA, it is conceivable that subtle nudges in one or the other direction drive plant responses to isoprene towards either JA or SA defenses. Similarly, monoterpenes appear to propagate SA- and SAR-associated immunity between plants (Riedlmeier et al., 2017). The induction of SA-associated immune responses in *Arabidopsis*, tobacco, and tomato leads to the emission of volatile mono- and/or sesquiterpenes (Huang et al., 2003; Riedlmeier et al., 2017; Zhang et al., 2019). In *Arabidopsis*, subsequent recognition of monoterpene cues in systemic tissues of the same or other plants leads to the induction of SA-dependent defense against *P. syringae* (Figure 2) (Frank et al., 2021; Wenig et al., 2019). In contrast to monoterpene-associated SAR in *Arabidopsis*, which does not appear to be subject to SA–JA antagonism (Frank et al., 2021; Wittek et al., 2015), the terpene-containing emissions of tomato plants undergoing white fly infestation prime SA defenses in neighboring plants (Zhang et al., 2019). In this case, SA–JA antagonism inhibits JA defenses, making neighboring plants more attractive to white flies. Similarly, accumulation of the monoterpene α -limonene in orange (*Citrus × sinensis*) peels modulates the balance between SA and JA, with α -limonene biosynthesis being positively correlated with pathogen-induced priming of SA defenses and reduced α -limonene levels being associated with JA immunity (Rodriguez et al., 2014).

While monoterpenes thus appear to exert protective effects through regulating SA defenses, the sesquiterpene β -caryophyllene appears to be strongly correlated with JA immunity. JA signaling is essential for plant defense against necrotrophic pathogens and insect herbivory (Pieterse et al., 2012), and triggers the emission of volatiles which function as defense cues in plant-to-plant communication (Baldwin et al., 2006; Bouwmeester et al., 2019). These volatiles include β -caryophyllene (e.g., Capra et al., 2015; Cheng et al., 2007; Huber et al., 2005), whose biosynthesis is enhanced in *Arabidopsis* upon the activation of MYC2, a transcription factor which is central to the JA

signaling response (Hong et al., 2012). When applied to the headspace of Arabidopsis plants, β -caryophyllene, in turn, elicits ISR-like, JA-dependent immunity against *P. syringae* (Frank et al., 2021). Similarly, β -caryophyllene emissions from the roots of *C. stoebe* might modify plant–herbivore interactions on the roots of neighboring *Taraxacum officinale* plants (Huang et al., 2019). Recent evidence further suggests that β -caryophyllene emissions from the leaves of tomato plants trigger responses in neighboring plants, which lead to strongly enhanced SA levels in the root exudates of these receiver plants (Kong et al., 2021). It thus seems conceivable that – similarly to monoterpenes – the sesquiterpene β -caryophyllene modulates phytohormone crosstalk in plants. Such crosstalk might be facilitated further by monoterpenes and MeSA, whose emissions are induced downstream of MeJA treatment or JA-associated defense responses in Arabidopsis and tomato (Figure 2) (Ament et al., 2004; Kegge et al., 2013).

In Arabidopsis flowers, the expression of the β -caryophyllene synthase TPS21 and associated β -caryophyllene emissions are regulated by MYC2 integrating signals from the GA and JA signaling pathways (Hong et al., 2012). A regulatory role of MYC2 in the expression of TPS21 was confirmed in the ornamental plant *Freesia hybrida* (Yang et al., 2020). In these plants, MYC2 physically interacts with another transcription factor, MYB21, which promotes the expression of TPS21 and, independently of MYC2, also of the linalool synthase gene TPS14. Also, MYB21 was previously shown to be involved in regulating terpene emission in developing Arabidopsis flowers. *myb21* mutant Arabidopsis showed drastically reduced TPS21 and TPS11 expression as well as reduced β -caryophyllene and thujopsene emission from flowers (Reeves et al., 2012). Strikingly, MYC2 might further enhance the expression of the monoterpene synthase gene TPS24 (Hong et al., 2012), which in our hands promotes plant-to-plant propagation of SAR (Wenig et al., 2019). As introduced above, β -caryophyllene, upon interacting with TPLs, might relieve TPL-driven repression of MYC2-containing transcription factor complexes (Nagashima et al., 2019), driving downstream gene expression and a positive feedback loop promoting its own biosynthesis and that of SAR-associated monoterpenes (Figure 2). This strongly suggests a modulatory role of β -caryophyllene and/or JA signaling in SA-associated SAR-like immune responses to volatile monoterpene cues.

Taken together, accumulating evidence suggests an intimate relationship between different terpenes and phytohormone signaling pathways. As previously proposed (Erb, 2018), terpenes and other VOCs might mitigate plant responses to their environment by fine-tuning phytohormone crosstalk. As discussed above, ratio-dependent reactions have been observed, which might influence the balance between SA and JA signaling. If

we add the fact that terpenes and other VOCs appear in plant volatile mixtures, the chemical variability of such mixtures might well provide these interactions with a high sensitivity to integrate signals from different environmental cues, while optimizing plant fitness in the face of combinatorial stresses.

TRANSMITTING INFORMATION THROUGH THE AIR

Do plants whisper to avoid eavesdropping?

Several studies have shown concentration specificity in plant responses to volatile terpene cues. Concentrations that are too low do not trigger a response in receiver plants, but also concentrations which are too high can be ineffective (Frank et al., 2021; Riedlmeier et al., 2017). Concentration specificity of a cue can have ecological advantages when the aim is to communicate, e.g., only with conspecifics or within a plant. Terpene-mediated within-plant signaling might be a rapid alternative for the phloem-based internal signaling to distribute information on the whole plant level. More ‘quiet’ VOC cues, in that case, may help to reduce eavesdropping by neighboring plants. From a Darwinian perspective, volatile signals might indeed be most appropriately considered at the scale of individual plants (Baldwin et al., 2006; Monson et al., 2020), or for neighbors of the same species. In natural populations of plants there is a high likelihood that neighbors are genetically related and therefore that they share genetic contributions to fitness that are carried forward to future generations. In mixed communities, however, volatile signals may concomitantly favor the fitness of different, eventually competing species (Figure 3). Interspecific interactions may have led to the evolution of VOC patterns that favor effective within-plant signaling, but limit the transfer of signals to neighbors. Here, concentration dependency might have several benefits for the emitter if terpenes should act as semiochemical signals within a species, but be muted as a function of distance such that a competing species cannot eavesdrop on the message. Selection in neighbors, on the other hand, may have favored mechanisms that enhance sensitivity to low-concentration messages. Neighbors may thus have ‘learned to listen’ to especially low terpene concentrations. Volatile cues from sender plants may, however, also have opposite effects, reducing the fitness of the neighbors (Huang et al., 2019; Zhang et al., 2019). Turning the sympatric *T. officinale* plants more sensitive against herbivores (Huang et al., 2019) might directly benefit the sender, at least in the short term. Long-term benefits and effects on the community level remain, however, to be elucidated.

Until now, it has remained elusive why and how a ‘too high’ concentration of VOCs could be ignored physiologically. A similar phenomenon is observed in plant responses to non-volatile SAR signaling cues (Witteck et al.,

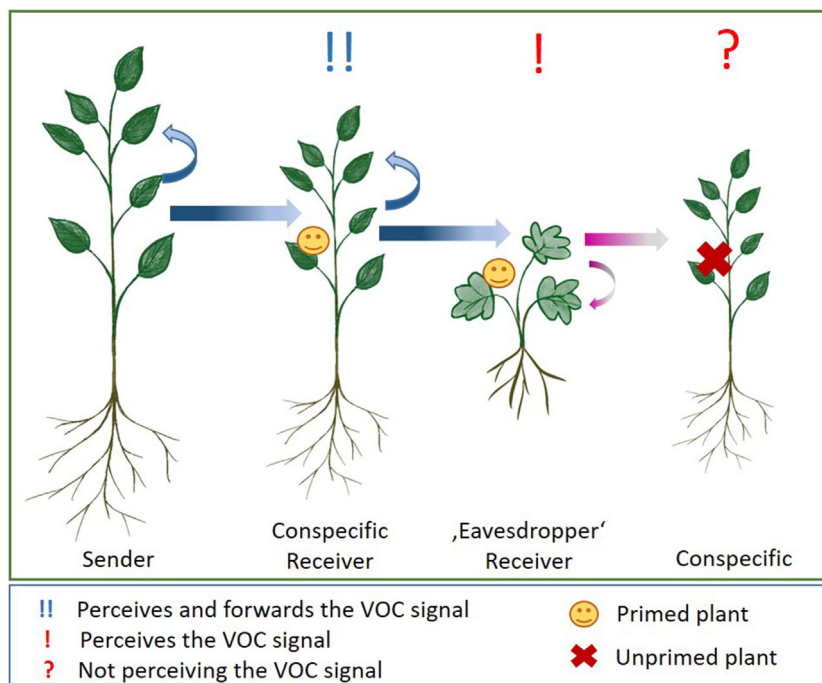


Figure 3. Hypothetical schema of potential plant-to-plant signaling events in a heterogenic plant community.

2014), and thus might represent a general principle, which applies to plant responses to SAR and related phytohormone signals. If we argue that terpenes and other VOCs influence plant responses to stress by fine-tuning phytohormone responses, any peculiarities of the associated phytohormone response would automatically apply to the plant response to the upstream volatile cue. During SAR, SA levels are increased, which is causatively associated with the establishment of the SAR-associated enhanced disease resistance state (Vlot et al., 2009, 2021). However, SA signaling and SAR promote feedback inhibition on themselves, inhibiting programmed cell death and stunted growth phenotypes, which are often associated with a prolonged elevation of SA defenses (Breitenbach et al., 2014; Yoshimoto et al., 2009). Feedback inhibition might be a homeostatic mechanism that has evolved to prevent unnecessary use of resources after the inducing pathogen attack has been fended off. Perhaps, ‘too high’ monoterpene concentrations drive SA levels and/or SAR up beyond a level at which feedback inhibition dampens the response (Frank et al., 2021; Riedlmeier et al., 2017). Similar mechanisms might act downstream of isoprene and/or β -caryophyllene recognition (Frank et al., 2021). In order to optimize dose–response curves, it will be of interest to further study these and other mechanisms underlying the markedly concentration-dependent responses of plants to terpenes and other VOCs.

The intensity of volatile emissions may also depend on the community context. Kigathi and colleagues revealed that plants growing together with their kin have

considerably lower emission rates. Also, plants in communities show lower emission rates upon herbivory than plants grown alone (Kigathi et al., 2013). The emission rates decreased in the community independently of whether the plants could perceive each other aboveground or belowground (Kigathi et al., 2013). According to these results, plants may be able to reduce the costs (i.e., the amount of carbon released to the atmosphere) in a community compared to individual plants. In a community the emission rate could be kept lower for several ecological reasons, such as (i) to avoid more fit plants to become primed, (ii) to avoid specialist herbivores to find the community, or (iii) to restrict communication to the individual plant and related kin, excluding competitors.

In addition to concentration, also a certain accumulation, i.e., a dose of volatile exposure, may be necessary to induce a specific response in the receiver plant (Giron-Calva et al., 2012). A dose-dependent trigger might help the plants to verify that the situation is acute and demands action. Alternatively, in the case of a rather feeble trigger a certain number of incidents can be needed to activate a response in the receivers (Markovic et al., 2019). Markovic et al. (2019) revealed not only that VOC production of senders depends on the level/duration of a trigger, but also that the defense-related gene expression in receivers mirrored this level. The duration of VOC exposure might aid the receiver plants to verify the correctness of the message: An ability to ignore less persistent cues and respond only to actual ones could provide evolutionary benefits. The specific response to a certain number of incidences

might be additionally fine-tuned by qualitatively different volatile molecules that are detected one by one. At least the sender plants are able to release different VOCs in a specific rhythm upon a trigger. This is nicely shown for maize (*Zea mays*) plants, which induce GLV, indole, and terpene emission one after another upon herbivore feeding (Erb et al., 2015). Such rhythm of VOC cues may be important in perceiving the signal, too. It might aid plants to respond only to 'correct' signals and facilitate the communication even in VOC-rich, mixed communities.

Interruption of the 'call'

The lifetime of terpenes in the atmosphere varies, which is directly connected to the effective concentration of a signaling cue. As terpenes can react with various air pollutants (Claeys et al., 2004; Joutsensaari et al., 2005), the potential signaling distance of VOCs has elicited quite some discussion in the past (Baldwin et al., 2006; Li and Blande, 2015; Mofikoya et al., 2017; Simpraga et al., 2016). Especially in highly polluted areas, degradation of the original bioactive compounds may affect the ability of VOCs to convey information transfer. Terpene-mediated plant-insect interaction has been shown to be altered in high ozone concentrations (Mofikoya et al., 2020), the reaction products potentially being repellent instead of attractive for insects (Li and Blande, 2015; Mofikoya et al., 2020). Similarly, Blande and colleagues revealed that lima bean plant-to-plant signaling, i.e., VOC-mediated induction of extrafloral nectar production in neighboring plants, was disturbed in an ozone-rich atmosphere. As a consequence, the effective distance of lima bean communication was shorter in the ozone-rich as compared to the ambient atmosphere (Blande et al., 2010). Also, the VOC-mediated priming between infested and uninfested cabbage (*Brassica oleracea*) plants was impaired under elevated ozone concentrations in the field (Giron-Calva et al., 2017). To tackle this problem, receivers might adapt and learn to perceive VOC reaction products (Mofikoya et al., 2020; Simpraga et al., 2016). Especially in polluted atmospheres, reaction products, such as oxygenated terpenes, might theoretically function as signals.

VOC-mediated plant-to-plant information exchange may also be challenged by the biotic environment. Microorganisms can assimilate, degrade, or transform volatile compounds, which can thereby lose or change their bioactivity. Microbes can use VOCs as their own sole carbon source, thus quenching the signals by simply 'feeding' on them. For example, several isoprene-degrading microbial species have been identified on the leaves of isoprene-emitting plants (Crombie et al., 2018; McGenity et al., 2018). Also, mono- and sesquiterpenes are converted to various products by microorganisms (Marmulla and Harder, 2014). Additionally, microbes themselves emit a high diversity of terpenes and other VOCs (Lemfack et al., 2018) that have

chemical structures that are largely similar to those of plant-released VOCs. Thus, plants and microbes can potentially speak the same language, which should not be forgotten when considering chemical ecology in more complex communities. The fraction of microbial VOCs in the VOC blends detected from plant leaves or roots has so far remained largely unexplored. It will be of high interest to study the relative importance of microbial VOCs in plant-derived volatile blends, as well as their ecological importance.

OUTLOOK: SIGNALING IN NATURAL COMMUNITIES

In nature, plants grow in communities with multiple different species rather than in monocultures. Still, most of the studies on VOC-mediated plant-to-plant interactions have so far been performed in laboratories using two-species setups and/or axenic cultures. Recent results on VOC blends in mixed communities (Kigathi et al., 2019) and the ability of plants to forward a received signaling cue (Wenig et al., 2019) suggest that neighbors matter (Figures 2 and 3). Plants may use terpenes to synchronize and optimize responses to environmental changes at the community level. Together, these recent results imply that plants can employ VOCs to inform neighbors about environmental challenges, but also about potential chances/advantages in their proximity (Kalske et al., 2019; Kigathi et al., 2019; Kong et al., 2021; Markovic et al., 2019). VOCs, such as isoprene and several monoterpenes and sesquiterpenes, appear to sensitize complex signaling pathways in plant cells that, in turn, trigger cellular responses to enhance plant fitness. The apparent connections between different terpenes and phytohormone signaling cascades allow for fine-tuning of net plant responses to multiple stresses through phytohormone crosstalk. Such responses can not only regulate plant stress tolerance, but also modulate development and growth, thus flexibly driving plant health and yield. Plant-to-plant propagation of such responses within communities might reduce the 'costs' of maintaining, e.g., a high stress tolerance level for each individual. Regarding agriculture and food production, VOC application has been suggested as a potential new tool to induce plant immunity and stress tolerance in a more natural manner (recently reviewed by Brill et al., 2019). Such use might be especially promising when integrated with plant-to-plant propagation of priming (Vlot et al., 2021). Sentinel plants that respond to feeble environmental triggers by specific VOC blends could be used as senders to prepare the main cultivars for improved tolerance of environmental changes. Volatile signals can also serve as a mechanism to collectively change the behavior of a plant community, eventually leading to more powerful actions. In natural communities the signaling cues can be highly beneficial over generations if direct kin are prepared to face environmental changes and ensure reproduction.

The advantages or repercussions of interspecific communication within mixed communities, however, remain to be elucidated. It might be of interest to study if members of highly mixed communities, for example, benefit from a higher diversity of volatile cues emitted by various species to maintain a high, or rapidly adjustable stress tolerance level in the face of a changing climate.

ACKNOWLEDGMENTS

We apologize to those colleagues whose work could not be cited due to space restrictions. Research on volatile-mediated poplar interactions in the lab of MR is funded by the DFG (grant number RO5311/4-1). YC is funded by a fellowship from the Chinese Scholarship Council. Research on the role of terpenes in plant innate immunity in the lab of ACV is funded by the DFG as part of SFB924. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTERESTS

The authors declare no conflict of interest.

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