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FOCUSED REVIEW

The role of volatiles in plant communication

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SUMMARY

Volatiles mediate the interaction of plants with pollinators, herbivores and their natural enemies, other plants and micro-organisms. With increasing knowledge about these interactions the underlying mechanisms turn out to be increasingly complex. The mechanisms of biosynthesis and perception of volatiles are slowly being uncovered. The increasing scientific knowledge can be used to design and apply volatile-based agricultural strategies.

Keywords: terpenoids, phenylpropanoids, volatiles, plant–insect/microbe/plant interactions, pollination, biosynthesis, regulation, agriculture.

INTRODUCTION/BACKGROUND

Through volatile organic compounds (VOCs), plants are in constant dialogue with the organisms in their environment. This communication is of great importance as it allows plants and the organisms they interact with to tune their growth, development, defence, propagation and life cycle to achieve maximal fitness. Plants themselves but also the organisms in their environment produce VOCs, which belong to various chemical classes, such as the terpenoids, the benzenoids and phenylpropanoids, fatty acid-derived molecules including the green leaf volatiles (GLVs) and minor classes such as nitriles, (ald)oximes and sulfides (Figure 1). Here we review the recent literature on volatile communication between plants and other organisms as well as the biosynthesis, transport, perception in the receiver organisms, and potential importance for agriculture of these VOCs.

ANALYSIS AND INFORMATION CONTENT OF VOCs

Volatile organic compounds mediate the interaction between plants and mutualists, pests and pathogenic antagonists and, although not addressed much yet and experimentally challenging, also multi-trophic interactions. Semiochemicals that function in these interactions can be produced constitutively or in response to outside interactions and stimuli, and this occurs above as well as below

ground (Massalha *et al.*, 2017). Although there are indications that above- and below-ground semiochemical responses are integrated (Danner *et al.*, 2015; Van Dam *et al.*, 2018), details on what drives this remain to be elucidated. Although semiochemicals can travel long distances, plant–plant and plant–microbe communication usually take place at relatively short distances, while plant volatiles with a role in plant–insect interaction are perceived at distances of several hundred metres. The resulting extreme dilution, and the large variation in chemical structures and properties of the VOCs pose a challenge to the analysis of the volatiles and their precursors (Fu *et al.*, 2017). Another major challenge is to interpret VOC information content, especially across larger spatial scales in which the volatile blend carrying the information becomes increasingly complex through environmental effects (including noise) and community dynamics in an ecosystem (Aartsma *et al.*, 2017; Kessler and Kalske, 2018). Comparison of volatile profiles is complicated due to their complexity, but also because the presence/absence and quantity of compounds are not independent measures in case of a shared biosynthetic origin. An interesting approach to deal with this is a so-called biosynthetically informed pairwise distance measure, calculating compound similarity based on the proportion of shared biosynthetic enzymes (Junker, 2018). In the

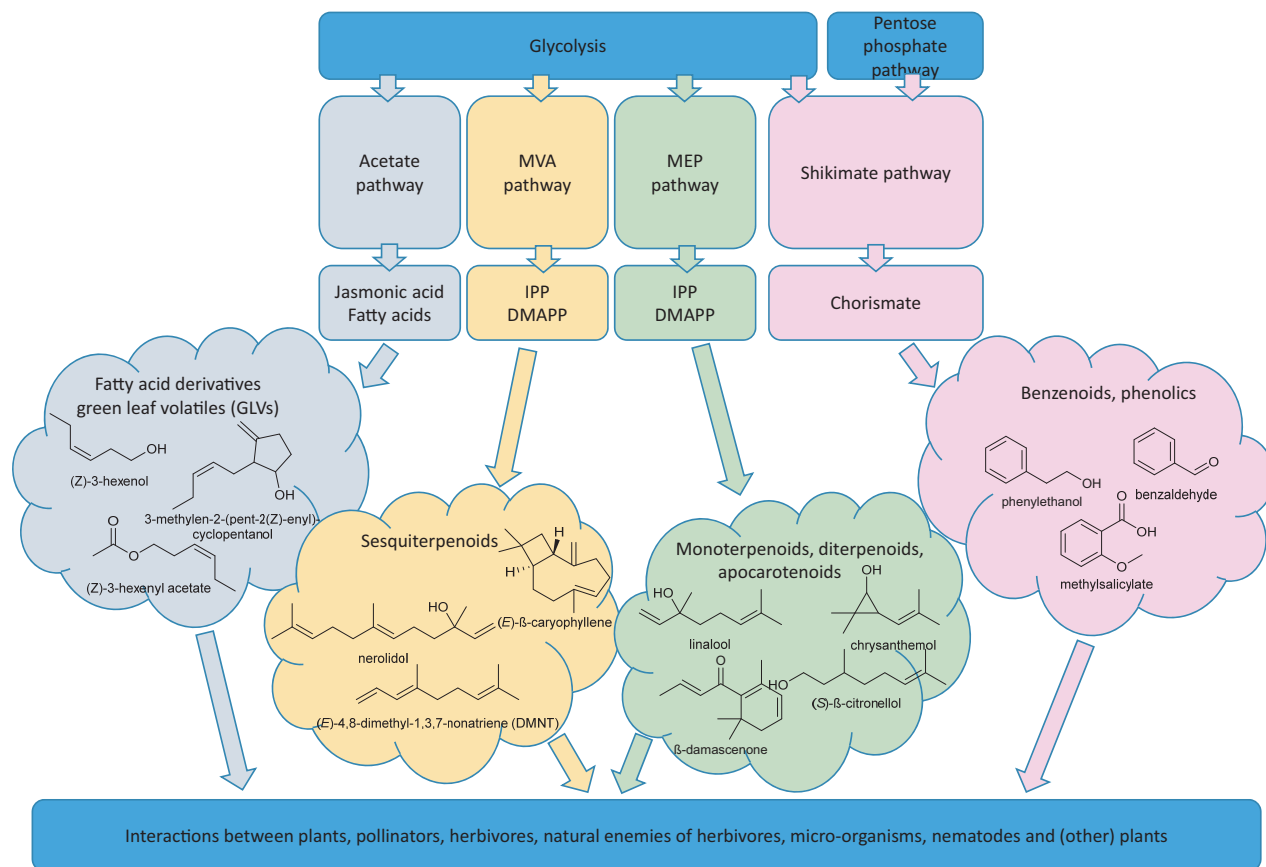


Figure 1. Biosynthetic pathways of the major volatile compound classes and selected examples of volatiles from these classes that are discussed in this review. Fatty acid-derived VOCs (including GLVs and methyljasmonate) are produced from C18 fatty acids, produced through the acetate pathway that gets its substrate, acetyl-coA, from glycolysis (Fu *et al.*, 2017). Acetyl-coA from glycolysis is also the substrate for the cytosolic mevalonic acid (MVA) pathway, while pyruvate from glycolysis is the substrate for the plastidic methylerythritol phosphate (MEP) pathway (Beyraghdar Kashkooli *et al.*, 2018; Pichersky and Raguso, 2018). The benzenoids and phenylpropanoids are produced through the shikimate pathway that gets its substrates from glycolysis and the pentose phosphate pathway (Widhalm *et al.*, 2015; Santos-Sánchez *et al.*, 2019).

coming years we will see a strong progress in the interpretation of the effect of volatile blends on biological processes. This development will be fuelled by the development of new high-throughput behavioural bioassays in combination with high-throughput VOC analyses and increasing sensitivity of GC-MS. Upcoming tools such as network analysis, large-scale data integration, and machine learning are going to provide a breakthrough in the interpretation of the biological meaning of the complex VOC blends (Cuperlovic-Culf, 2018).

THE ROLE OF VOCs IN POLLINATION

One of the major functions of floral volatiles is the attraction of pollinators, either through triggering innate behavioural responses or by providing a stimulus that can be associated with the presence of rewards (Schiestl and Johnson, 2013; Haverkamp *et al.*, 2016a). Pollinator attraction is often surprisingly specific, which can be beneficial as specificity increases the efficiency of pollen transfer between conspecific stigmas. Specificity in pollination can

be achieved with floral filters (Raguso, 2008), for example through specialized morphology that prevents access to rewards for most animals, or signals that are only detectable or of interest to few potential pollen vectors. Among signals, colour is rarely highly specific, because most animals have limited abilities to discriminate subtle colour nuances. Therefore, floral scent is typically more important in encoding highly specific signals, because of its chemical complexity, and the high number of different olfactory neurons usually used by insects to detect it (Haverkamp *et al.*, 2018). The chemical complexity in floral scent entails interactions between neurons detecting individual chemical components, together producing the sensation of a bouquet, which is different from the sum of the individual components (Strutz *et al.*, 2014; Schiestl, 2015). An example for this is scent compounds that modify the attractive function of other molecules, as was shown, for example, in scent bouquets of orchids attracting fragrance-gathering male euglossine bees (Milet-Pinheiro *et al.*, 2018). Floral scent is mostly detected by insects with neurons located

on the antennae, but recently olfactory neurons on the tip of the proboscis have also been characterized (Haverkamp *et al.*, 2016b).

Some of the most specific chemical signals are those that mimic non-floral items of interest to potential pollinators, such as oviposition substrates or mating partners (Johnson and Schiestl, 2016). Such signals are usually not attractive or not even detectable to 'normal' floral visitors that visit flowers for nectar and/or pollen, and therefore filter out a large number of potential visitors. Even more so, scent bouquets emitted by mimetic flowers are sometimes more specific than the volatiles emitted by the model they mimic. One curious example comes from the flowers of *Rafflesia cantleyi* (Wee *et al.*, 2018) that emit a smell mimicking rotten meat and attracting flies that normally oviposit in such substrates, as pollinators. In the field, where this *Rafflesia* species flowers, rotting meat was found to attract nine species of flies, whereas only five species were found on *Rafflesia* flowers, and of those, only a single species, the blowfly *Chrysomy chani*, comprised 97% of all flower visitors and was the only species carrying pollen. On traps with rotting meat, *C. chani* represented only 25% of all flies caught, suggesting that floral volatiles of *Rafflesia cantleyi* effectively filter the available carrion-fly pollinator community (Van der Niet *et al.*, 2011). The two main compounds of *Rafflesia's* floral bouquet are dimethyl disulfide (DMDS) and dimethyl trisulfide (DMTS), products of bacterial breakdown of methionine and cysteine in meat, that are typically found in the floral emission of floral carrion mimics (Martin *et al.*, 2017; Du Plessis *et al.*, 2018; Wee *et al.*, 2018). Many species of blowflies are attracted to these volatiles, but *Rafflesia* flowers also produce terpenoids, benzenoids and fatty acid derivatives, which may have a modulating function leading to higher specificity of the whole bouquet.

A similar case has recently been recorded in *Ceropegia mixta*, which is mostly pollinated by the house fly *Musca domestica* (Du Plessis *et al.*, 2018). *M. domestica* is usually not strongly associated with carrion but also oviposits in dung, suggesting that *C. mixta* uses mixed carrion/faeces mimicry (Jürgens *et al.*, 2013). The floral scent of this plant is also dominated by DMDS and DMTS, in combination with a complex blend of other compounds. A fascinating twist is the fact that even though vision models suggest that for flies the colour of the flowers is indistinguishable from the background, bioassays suggest that there is a visual component of attraction. Whereas odour alone was sufficient to attract flies, combined olfactory and visual signals attracted more flies. This finding is paralleled by data from the *Rafflesia* system, in which floral scent alone was insufficient to trigger landing behaviour of the pollinators in wind tunnel bioassays, suggesting visual signals are needed to guide insects to carrion flowers (Du Plessis *et al.*, 2018).

A well known, and highly specific example of floral mimicry is sexual mimicry, in which flowers imitate mating signals and are pollinated by sexually aroused male insects during a mating attempt (Johnson and Schiestl, 2016). This type of pollination system is most commonly found among Australian orchids, in which a minimum of 11 genera are (at least partly) pollinated in this way. In some of these groups, exciting progress has been made in recent years in terms of identifying the pollinator-attracting floral scent compounds (i.e. the mimicry of the sex pheromone), and several unusual compounds have been identified. For example, (methylthio)phenols, up to now only known as natural products produced by bacteria, were identified as pollinator-attracting signals in the orchid genus *Caladenia* (Bohman *et al.*, 2018b). *Caladenia crebra* produces four types of (methylthio)phenols, and a 10:1 blend of two of these compounds attracts and releases copulation attempts in its legitimate pollinator, a thynnine wasp. Interestingly, a 1:1 blend of the same compounds attracts another, as yet undescribed, thynnine wasp (*Campylothynnus* sp. A), which is the pollinator of *Caladenia attingens* subsp. *attingens*, demonstrating the importance of specific ratios of active volatiles for the specificity of pollinator attraction in sexual mimicry.

In another paper, Bohman and colleagues show a different mechanism of specificity, in which pollinators of sexual mimics strongly discriminate between structural isomers of active volatiles (Bohman *et al.*, 2018a). This was shown to be the case for *Caladenia plicata*, which employs two unusual and biosynthetically unrelated volatiles as pollinator attractants, (*S*)- β -citronellol and 2-hydroxy-6-methylacetophenone. When (*S*)- β -citronellol was replaced by its enantiomer (*R*)- β -citronellol or 2-hydroxy-6-methylacetophenone by one of its regio-isomers in bioassays with synthetic volatiles, the volatile blend lost almost all of its attractiveness (Figure 2a). In a generalist pollinator searching for food on flowers, namely honey bees, a different result was found, as worker bees only poorly discriminated between isomers of different volatiles, even when they were paired with aversive stimuli like bitter taste (Aguar *et al.*, 2018). A fascinating aspect of specific floral signals is the potential of generalist predators to eavesdrop on such signals to optimize prey catching. On a Balearic island, for example, lizards use carcasses, but also the carrion-mimicking flowers of *Helicodorus muscivorus*, as a lurking site to catch flies (Perez-Cembranos *et al.*, 2018). A very similar example, but without involving mimetic flowers, is represented by crab spiders that wait for their prey at flowers (Knauer *et al.*, 2018). Both lizards and crab spiders are attracted by floral scent, which makes sense because a 'sit and wait' predator is likely to be more successful when using the same signals as its prey to identify potential hunting sites. Both lizards and crab spiders eat or repel pollinators and therefore have a negative effect on

the pollination success of the plant. In both cases, however, there is also a positive effect on plant fitness, as lizards act as fruit dispersers of *Helicodorus* and crab spiders also feed on florivores. This potential fitness increase counterbalances selection on plants to avoid eavesdropping predators and are likely to stabilize these associations. Another, often highly specific and scent-driven, pollination system is nursery pollination, in which pollinators oviposit into flowers and the pollinators' larvae consume floral tissue of developing seeds. Jackfruit (*Artocarpus heterophyllus*) is a monoecious crop pollinated by gall midges that visit male and female inflorescences, but oviposit only into male, fungus-infected inflorescences (Gardner *et al.*, 2018). Male inflorescences are typically infested by a fungus after blooming. Female inflorescences are deceptive to pollinators as they do not provide reward, even though they produce more volatiles than the male flowers. Floral scent of both male and female inflorescences is dominated by three methyl esters that release responses in the midges' olfactory neurons and also occur in the fruits. Highly specific, unusual scent compounds – such as (*E,E*)- α -farnesene-2(3),9(10)-diepoxyde and 3-methylen-2-(pent-2(*Z*)-enyl)-cyclopentanol – were found in three *Carludovicoideae* plant species with nursery pollination (Teichert *et al.*, 2018) (Figure 2b). The floral staminoids of these plant species produce scent and elevated temperature to attract flower weevils that oviposit into the staminoids. In summary, highly specific associations between flowers and insects are typically mediated by chemical signals, that act as floral filters together with visual signals, floral morphology and specific types of reward.

THE ROLE OF VOCs IN THE INTERACTION OF PLANTS WITH HERBIVOROUS INSECTS

The unique constitutive volatile blend produced by plants is used by mutualists such as pollinators, but also by antagonist such as herbivorous insects who use volatiles to identify and home-in on a host. The host blend consists of major and minor constituents, but the most abundant compounds do not automatically determine the response to the blend as a whole (McCormick *et al.*, 2012). The olfactory system of insect antennae can discriminate patterns and use this to determine biological relevance, that is host suitability or unsuitability. This odour-mediated behaviour appears to be innate in insects (Hatano *et al.*, 2015). Within a plant community, the chemical diversity in constitutive volatiles between individuals can be large enough to drive herbivore preference-behaviour (Clancy *et al.*, 2018).

Herbivore-induced plant volatiles (HIPVs) are blends of volatiles – mostly GLVs, terpenes and aromatic compounds – that a plant produces in response to herbivory (McCormick *et al.*, 2012). HIPVs are released after tissue disruption; however, albeit at low levels, some are also emitted

constitutively into the plants headspace (Holopainen and Gershenzon, 2010). HIPVs serve as signals to attract natural enemies of herbivores such as parasitoids and predators (Aartsma *et al.*, 2017; Gasmi *et al.*, 2018; Turlings and Erb, 2018). Cockchafer larvae feeding on roots of *Populus* spp. induced the emission of a number of monoterpenes including 1,8-cineole, which had an inhibitory effect on *Phytophthora cactorum* (Lackus *et al.*, 2018) (Figure 2c). Turlings and Erb (2018) question the common notion that HIPVs are signals produced to attract the pest enemy or as 'cry for help', as there is no evidence for directed evolution or a fitness benefit (Turlings and Erb, 2018). The signal itself that is produced in direct response to the attacker is associated with prey so accurately that parasitoids and predators have evolved to rely on the volatile cues to such an extent that they, for example, have even lost vision.

THE ROLE OF VOCs IN THE INTERACTION OF PLANTS WITH MICRO-ORGANISMS

Not only plants produce volatiles in response to interspecies interaction, but also micro-organisms associated with plants are a source of volatile (and non-volatile) compounds that can alter plant physiological and metabolic responses (Piechulla *et al.*, 2017; Wenke *et al.*, 2019). *Bacillus*, *Pseudomonas*, *Arthrobacter*, *Fusarium* and *Alternaria* rhizobacteria, for example, can stimulate root growth through the production of volatiles such as 3-hydroxy-2-butanone (acetoin), 2,3-butanediol and 2-pentylfuran (Fincheira and Quiroz, 2018) (Figure 2d). Others can induce resistance and tolerance in plants such as acetoin, dimethyl disulfide, 3-pentanol and 6-pentyl- α -pyrone (Fincheira and Quiroz, 2018) (Figure 2d). This shows that plants do not only produce volatiles, but also perceive them, and respond to them with altered growth or defence signalling (Schenkel *et al.*, 2018). This is further discussed below under 'Molecular mechanisms underlying VOC perception'. Microbe-induced plant volatiles can inhibit microbial growth and act as local bacteriostatic agents (Sharifi *et al.*, 2018) as discussed for 1,8-cineole and *P. cactorum* above (Lackus *et al.*, 2018). Indoles and green leaf volatiles (GLVs) can affect membrane integrity of bacteria on the plant surface and interfere with bacterial quorum sensing, thereby deregulating bacterial virulence (Joshi *et al.*, 2016). In response to pathogen attack, plants do not only activate their own defence response, but the infection can also induce volatile emission into the headspace that can lead to an immune response in neighbouring plants (Riedlmeier *et al.*, 2017) (Figure 2e). However, when multiple volatile signals have to be integrated, the immune (or defence) response can also be reduced. Hormonal cross-talk has a role in balancing trade-offs, which can also result in the suppression of volatile emission (Martinez-Medina *et al.*, 2017; Erb, 2018). Therefore, plants can produce specific volatiles upon microbial interactions but, in turn, microbes

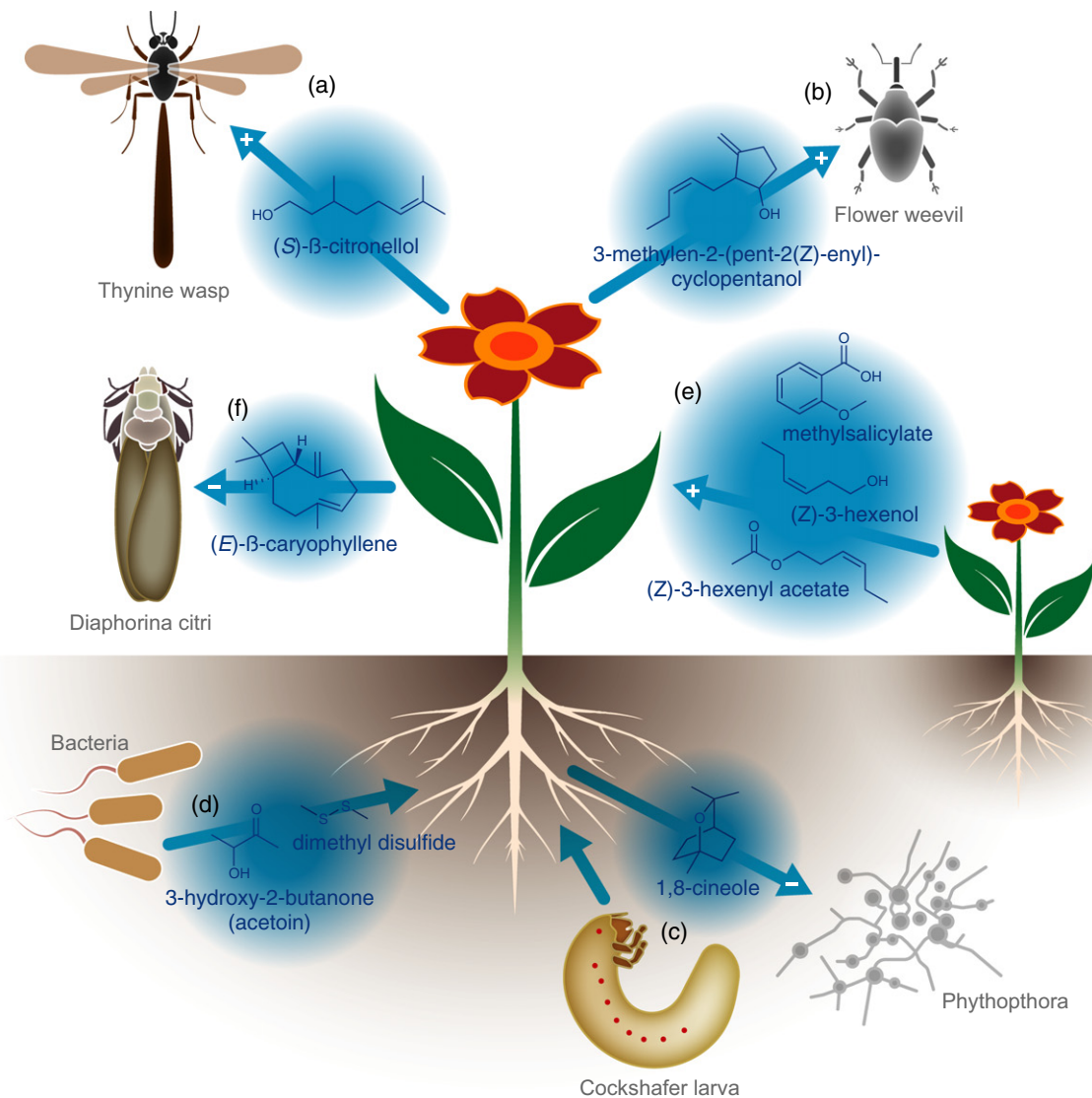


Figure 2. Communication between plants and other organisms. (a) Flowers of *Caladenia plicata* emit (S)-β-citronellol as attractant of pollinator thynnine wasps (Bohman *et al.*, 2018a). (b) *Carludovicoideae* plant species emit the unusual 3-methylen-2-(pent-2(Z)-enyl)-cyclopentanol to attract flower weevils (Teichert *et al.*, 2018). (c) Cockchafer larvae feeding on roots of *Populus* spp. induce the emission of monoterpenes such as 1,8-cineole, which has an inhibitory effect on *Phytophthora cactorum* (Lackus *et al.*, 2018). (d) Rhizobacteria can stimulate root growth and induce resistance through the production of volatiles such as 3-hydroxy-2-butanone (acetoin) and dimethyl disulfide, respectively (Fincheira and Quiroz, 2018). (e) Upon infection and/or herbivory, plants emit for example (Z)-3-hexenol, (Z)-3-hexenyl acetate and methyl salicylate. Receiver plants show remarkably specific responses to these volatiles (Park *et al.*, 2007; Sugimoto *et al.*, 2014; Cofer *et al.*, 2018b; Erb, 2018; Hu *et al.*, 2018b). (f) (E)-β-caryophyllene repels HLB transmitting *Diaphorina citri*. Naturally (E)-β-caryophyllene emitting plant species such as guava, the use of (E)-β-caryophyllene dispensers and metabolic engineering of (E)-β-caryophyllene production can potentially be used to protect citrus trees against HLB (Mafrá-Neto *et al.*, 2013; Alquézar *et al.*, 2017).

have been shown to be able to suppress VOC biosynthesis through the use of effectors (Sharifi *et al.*, 2018). Microbes, in combination with their host plant, can also mediate tri-trophic interactions (Shikano *et al.*, 2017). For example, viruses that depend on a (mobile) vector, may alter plant volatile biosynthesis in order to recruit the vector insect. The 2b protein of cucumber mosaic virus manipulates aphid behaviour by modifying the host volatile profile (Tungadi *et al.*, 2017; Wu *et al.*, 2017). Even further complicating the story, herbivorous insects carry facultative

endosymbionts that can attenuate the production of predator-attracting volatiles emitted by the plant under attack (Frago *et al.*, 2017). The role of micro-organisms in the volatile communication of plants also extends to flower volatiles. Microbes can colonize the nectar and change the volatile blend of a flower, which may alter floral visitation and hence plant reproduction (Vannette and Fukami, 2016; Rering *et al.*, 2018). In conclusion, the dialogue between plants and microbes is complex and deciphering the info-chemical exchange between plants and beneficial as well

as pathogenic microbes remains of unaltered interest for application in (crop)plant production, as further discussed below.

THE ROLE OF VOCs IN PLANT–PLANT INTERACTION

An intriguing function of volatiles is their signaling role in and between plants, a phenomenon first described already more than 35 years ago (Baldwin and Schultz, 1983; Rhoades, 1983). When attacked by herbivorous arthropods, plants often emit a different blend of volatiles, both qualitatively and quantitatively and this blend of volatiles can initiate responses in systemic leaves and neighbouring plants. As such, plants are also indicated as having a certain dialect or chemotype (Karban *et al.*, 2014a, 2016). Many studies have shown that this volatile blend can activate or prime defence responses, for reviews see for example Heil and Karban (2010) and Ameye *et al.* (2018). A recent meta-analysis showed that adjacent plants exposed to volatiles from damaged neighbours become more resistant to herbivores (Karban *et al.*, 2014b). However, tomato plants infested by whiteflies (*Bemisia tabaci*) produce a volatile blend that makes neighbouring plants more susceptible to whiteflies (Zhang *et al.*, 2019). Whether this is an adaptive response, as it might make the plants more resistant to the viruses transmitted by the whiteflies, remains to be seen, but it indicates that not all HIPV blends result in more resistance to herbivores in the neighbours.

MOLECULAR MECHANISMS UNDERLYING VOC PERCEPTION

An intriguing function of volatiles is their signaling role in and between plants, and particularly how plants can perceive these signals (Cofer *et al.*, 2018b; Erb, 2018). For examples of this, authors normally refer to the gaseous hormone ethylene and its receptor (Schaller and Bleecker, 1995) and suggest that other volatiles may also be detected by receptors in plants. However, receptors for other volatiles have remained elusive so far. Still, plants show an often surprisingly specific response to different volatiles. Therefore perhaps one has to look at alternative scenarios of which one example is the perception of CO₂ by plants in guard cells. These cells in Arabidopsis have an S-type anion channel, SLOW ANION CHANNEL1 (SLAC1) that has bicarbonate-interaction sites (Yamamoto *et al.*, 2016; Zhang *et al.*, 2018a). It is conceivable that other ion channels have interaction sites for particular volatiles as well that can change their activity just as CO₂/HCO₃[−] can change SLAC1 activity and stomatal movement. Indeed, the first response to volatiles that can be measured in plants is a change in plasma membrane potential and cytosolic calcium flux (Zebelo *et al.*, 2012). Very recently, the transcriptional co-repressor TOPLESS-like (TPL) protein was identified to bind volatile sesquiterpenes, that is caryophyllene analogues (Nagashima *et al.*, 2018). TPL

proteins are known to regulate various hormonal responses such as those induced by jasmonic acid (Pauwels *et al.*, 2010). This suggests that nuclear proteins can be involved in volatile sensing, and opens up an interesting field of research while at the same time raising the question how these volatiles are transported to establish a relatively high concentration in the nucleus.

Also enzymes have been demonstrated to play a role in transport and perception of volatiles within or between plants. The most well known intracellular signalling volatile is methylsalicylate (MeSA) that is transported via the phloem from a tobacco (*Nicotiana tabacum*) leaf infected with tobacco mosaic virus (TMV) to a non-infected, systemic leaf to induce resistance (Park *et al.*, 2007). Accumulation of high levels of salicylic acid (SA) in TMV-infected leaves results in the production of MeSA and the inhibition of a MeSA esterase in the local leaf (Figure 2e). In the systemic leaf, SA levels are low and the transported MeSA is converted to SA by the esterase resulting in SA production and resistance. In plant–plant communication it has recently become clear that in receiver tomato plants, the GLV (*Z*)-3-hexenol can be glycosylated to (*Z*)-3-hexenylvicinanoside, which induces defence responses (Sugimoto *et al.*, 2014) (Figure 2e). Intriguingly this particular glycosylation seems very plant species specific, as it does not occur in Arabidopsis, even though the latter also glycosylates many different volatile alcohols – GLVs, phenylpropanoids, terpenes – upon exposure (Sugimoto *et al.*, 2015).

Plants show remarkably specific responses to different volatiles (Cofer *et al.*, 2018b; Erb, 2018). Recent findings show that dual-volatile exposed plants respond differently than plants exposed to single volatiles. Maize (*Zea mays*) plants respond with stronger defences to exposure with both indole and the GLV (*Z*)-3-hexenyl acetate than to the single volatiles (Hu *et al.*, 2018b) (Figure 2e). This adds another layer of complexity and might explain some of the very specific responses that have been observed. For instance, plant–plant communication in the shrub *Baccharis salicifolia* is specific for a particular aphid species: induced resistance in neighbours is only obtained against the same aphid (Moreira *et al.*, 2018). This specificity can be assigned to the different volatile blends induced by the different aphids. Similarly, as in maize, a blend of synthetic volatiles mimicked this response better than the individual compounds. This seems to indicate that plants have multiple mechanisms to detect volatiles as already suggested by Cofer *et al.* (2018b).

Many new aspects of responses to volatiles and volatile signal transduction in plants are being discovered. GLVs, for example, can protect maize seedlings against cold stress (Cofer *et al.*, 2018a) and particular GLVs can induce stomatal closure thereby enhancing resistance against *Pseudomonas syringae* pv. *tomato* infection (López-Gresa

et al., 2018). This GLV-induced priming comes at a cost for the plants as it reduced growth rates (Engelberth and Engelberth, 2019). Other interesting findings are that touch-induced volatiles can synchronize defences in neighbouring plants (Markovic et al., 2018) and that goldenrod (*Solidago altissima*) responds to (*E,S*)-conophthorin, a volatile produced by a specialist herbivore, the goldenrod gall fly (*Eurosta solidaginis*) (Helms et al., 2017). This brings another dimension to the field of plant–herbivore interactions. Regarding signalling, an advanced publication (Ye et al., 2018) indicates a role for mitogen-activated kinases and WRKY transcription factors in indole-mediated priming, similar to what has been shown for GLV signaling in *Arabidopsis* (Ameye et al., 2018), perhaps pointing to signalling commonalities. Finally, one very intriguing aspect is the response of plants to microbial volatiles (Ryu et al., 2003; Sharifi and Ryu, 2018). With, for instance, clear growth responses to specific volatiles as read out, genetic screens to identify potential receptors and signal transduction cascades should be more feasible than with volatiles in plant–plant communication (Scala et al., 2017).

VOC BIOSYNTHESIS

Intriguingly, the VOCs that mediate the communication of plants and other organisms belong to a range of different compound classes such as fatty acid-derived molecules (including GLVs), terpenoids, benzenoids, and phenylpropanoids, and minor classes such as nitriles, (ald)oximes and sulfides. Fatty acid-derived VOCs (including GLVs) are produced from the C18 unsaturated fatty acids, linoleic and linolenic acid. These are produced through the acetate pathway that gets its substrate, acetyl-coA, from glycolysis (Fu et al., 2017) (Figure 1). Through a series of oxidation and reduction steps and acetylation these fatty acids are converted to aldehydes, alcohols and acetates, such as (*Z*)-3-hexenol and (*Z*)-3-hexenyl acetate (Figure 1). Methyl jasmonate biosynthetically originates from linolenic acid through multiple enzymatic steps (Li et al., 2005). Methyl jasmonate is formed through methylation of jasmonic acid by jasmonic acid carboxyl methyltransferase (Cheong and Choi, 2003).

Acetyl-CoA from glycolysis is also the substrate for the cytosolic mevalonic acid (MVA) pathway, while pyruvate from glycolysis is the substrate for the plastidic methylerythritol phosphate (MEP) pathway (Beyraghdar Kashkooli et al., 2018; Pichersky and Raguso, 2018). These two pathways both produce the isoprenoid precursors, isopentenyl diphosphate (IDP) and its isomer, methylallyl diphosphate (DMADP). IDP and DMADP are condensed by prenyl transferases, such as geranyl diphosphate (GDP) synthase, farnesyl diphosphate (FDP) synthase, and geranylgeranyl diphosphate (GGDP) synthase to produce GDP (C10), FDP (C15), and GGDP (C20), respectively. FDP from the MVA pathway is the precursor for cytosolic sesquiterpenoid

biosynthesis catalyzed mainly by sesquiterpene synthases, cytochrome P450s, alcohol dehydrogenases and reductases. GDP from the MEP pathway is the precursor for plastidic monoterpenoid and carotenoid formation. Monoterpenoid formation is mostly catalyzed by monoterpene synthases, cytochrome P450s, alcohol dehydrogenases and reductases (Beyraghdar Kashkooli et al., 2018; Pichersky and Raguso, 2018). GGDP is the precursor for carotenoid formation through a series of enzymatic steps, involving a.o. phytoene synthase and phytoene desaturase. Carotenoids such as β -carotene are precursors for the production of volatile apocarotenoids through oxidative cleavage, catalyzed by carotenoid cleavage dioxygenases (Liang et al., 2018) (Figure 1).

The benzenoids and phenylpropanoids are derived from the shikimate pathway, which starts with the condensation of phosphoenolpyruvic acid from glycolysis, and D-erythrose-4-phosphate, from the pentose phosphate cycle (Widhalm et al., 2015; Santos-Sánchez et al., 2019) (Figure 1). Then six more enzymatic steps result in the formation of the key branch-point compound, chorismic acid, the final product of the shikimate pathway and the common precursor for all (volatile) phenolics. The volatile phenolics are represented by benzenoids (C6–C1), such as benzaldehyde, methyl salicylate and benzyl benzoate, which are formed from cinnamic acid; C6–C2 compounds such as 2-phenylethanol and phenyl acetaldehyde which are produced from phenylalanine; and C6–C3 compounds such as eugenol, methyl eugenol, and chavicol which are produced from 4-coumaroyl-CoA (Widhalm et al., 2015) (Figure 1).

The (ald)oximes are amino acid-derived metabolites and include volatiles, such as 2- and 3-methylbutyraldoxime. The volatiles are herbivory-induced or flower volatile blend constituents. See (Sørensen et al., 2018) for a recent review. In addition to these canonical VOC biosynthetic pathways occasionally unexpected biosynthetic solutions appear in the literature, showing how immensely intricate volatile biosynthesis has evolved (Sun et al., 2016). The enzyme responsible for geraniol biosynthesis in rose, for example, turned out not to be a monoterpene synthase but a Nudix hydrolase (a diphosphohydrolase) (Magnard et al., 2015). More function-based overviews of volatile biosynthesis are given in papers on the role of volatiles in plant–herbivore interaction including the perception by plants of herbivory and downstream signalling (Stahl et al., 2018), the role of volatiles in plant–microbe interaction (Sharifi et al., 2018) and on flower volatile biosynthesis (Ramya et al., 2017; Wong et al., 2017). Ryu and co-workers review the induction of volatiles by microorganisms and the effects that these volatiles have on plants, showing that microbes are true manipulators of their plant host (Sharifi et al., 2018).

With regard to progress in our understanding of the biosynthesis of herbivory-induced volatiles, Liu et al.

(2018a) identified two cytochrome P450s, GhCYP82L1 and GhCYP82L2, that can both catalyze the formation of the C-11-homoterpene (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and the C-16-homoterpene (*E,E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT) from nerolidol and geranylinalool, respectively (Liu *et al.*, 2018a). These cytochrome P450s are highly homologous to AtCYP82G1 that is responsible for TMTT production from geranylinalool in *Arabidopsis* (Lee *et al.*, 2010). The absence of specificity for either nerolidol or geranylinalool in the cotton P450s contrasts with maize in which two P450s, ZmCYP92C5 and ZmCYP92C6, are specific for either DMNT or TMTT production, respectively (Richter *et al.*, 2016).

With regard to progress in our understanding of the biosynthesis of flower volatiles, Wong *et al.* describe a study into the biosynthetic origin of the putatively fatty acid-derived, UV-B induced, chiloglottones, 2,5-dialkylcyclohexan-1,3-diones, that are employed by Australian sexually deceptive orchids of the genus *Chiloglottis* to attract male wasp pollinators (Wong *et al.*, 2018). Using transcriptomics data, they identified upregulation of fatty acid biosynthesis and β -oxidation in flowers and flower parts producing chiloglottones. Using an inhibitor of fatty acid biosynthesis, they demonstrated that this pathway is indeed involved in the production of the precursor of these chiloglottones.

Zhou and colleagues used stable isotope-labelled phenylalanine and acetophenone, and the isolation and characterization of a short chain dehydrogenase, to show that the acetophenone is the preferred substrate for phenylethanol production in tea flowers (Zhou *et al.*, 2018). This provides a fourth biosynthetic route to phenylethanol in plants (Sun *et al.*, 2016). In a follow-up study they show that two different SDRs are responsible for the production of the two stereoisomers of phenylethanol that are present in the emitted volatiles of tea flowers (Zhou *et al.*, 2019) (Figure 1). In rose, a eugenol synthase was identified and characterized, and shown to be highly similar to other eugenol synthases from for example *Clarkia brewerii*, *Ocimum basilicum* and *Petunia hybrida* (Yan *et al.*, 2018). Although the core β -oxidative pathway leading to benzoic acid has been elucidated (Qualley *et al.*, 2012), Adebessin and colleagues recently added another player, a peroxisomal thioesterase, PhTE1, that plays an auxiliary role in *Petunia hybrida* flowers (Adebessin *et al.*, 2018). With its capability to hydrolyze aromatic acyl-CoA esters, the authors concluded that PhTE1 exerts control on the flux between β -oxidation in the peroxisomes and phenylpropanoid biosynthesis in the cytosol.

For the identification of genes involved in volatile biosynthesis several different strategies are being used. An example of a genomics approach is the work by Kumar *et al.* (2018) who mined the genome sequence of *Ocimum sanctum* for terpene synthases (Kumar *et al.*, 2018). They

identified 47 putative terpene synthases. To get a better insight in their involvement in the biosynthesis of the *O. sanctum* terpenoids additional analyses will be necessary, such as transcriptomics preferably in combination with chemical analysis (and followed by functional characterization through heterologous expression). Transcriptome analysis through RNA sequencing is increasingly being used to identify genes involved in volatile biosynthesis. Fan *et al.* (2018), Huang *et al.* (2018) and Tian *et al.* (2018) used RNA-seq to try to pinpoint genes that are involved in flower volatile biosynthesis in *Polianthes tuberosa*, *Freesia hybrida* and wintersweet, respectively, that emit benzenoids and terpenoids, mostly terpenoids and terpenoids and benzenoids, respectively (Fan *et al.*, 2018; Huang *et al.*, 2018; Tian *et al.*, 2018). All three base their selection of gene candidates on homology and expression patterns. Although in these studies chemical analysis was also carried out, these data were not used to the maximum to further narrow down and/or support their candidate genes and the studies therefore remain rather descriptive. A more advanced network (co-expression) analysis with RNA-seq and GC-MS results is very powerful in identifying promising candidate genes and will therefore shorten the gene discovery process substantially (He *et al.*, 2018). A next step in this process will be the use of metabolomics as exemplified for strawberry (Haugeneder *et al.*, 2018), which will allow correlation analysis also with non-volatile precursors and/or further functionalized non-volatile downstream products.

With these advanced approaches, the discovery process of biosynthetic genes will further speed up. The elucidation of biosynthetic pathways of VOCs – in combination with the possibility to genetically knock out or knock in the production of specific volatiles through (transient) transformation in combination with behavioural assays – will remain an important tool in elucidating the exact role of individual VOCs in the communication of plants with other organisms.

REGULATION OF VOC BIOSYNTHESIS

Perhaps even more than for the biosynthetic genes, we are just scratching the surface in which our understanding of the regulation of VOC production is concerned. VOC production in flowers and upon herbivory, for example, is tightly controlled and regulated, developmentally in the case of flower volatiles, biochemically in the case of herbivores. Plants recognize herbivory from damage by herbivore associated molecular patterns (HAMPS), present in the oral secretions of the herbivore, or damaged associated molecular patterns (DAMPS), endogenous plant signals (Duran-Flores and Heil, 2016). This leads to the production of the defence-regulating hormones, predominantly jasmonoyl isoleucine (JA-Ile), and the induction of volatile production, with other hormones also playing a

role, while herbivores try to produce effector proteins to counteract this induction (Vos *et al.*, 2013; Kant *et al.*, 2015; Villarroel *et al.*, 2016).

In flowers, volatile production transcription factors of especially the MYB family have been demonstrated to regulate biosynthesis, especially of the benzenoids/phenylpropanoids, as reviewed by Ramya *et al.* (2017). The importance of MYB TFs in regulating flower scent is supported by the discovery of a MYB TF, LhODO1, in lily which seems to regulate volatile benzenoid/phenylpropanoid production (Yoshida *et al.*, 2018). LhODO1 showed a diurnal rhythm in tune with the expression of shikimate pathway and PAL genes. LhODO1 expression was high in the strongly scented oriental hybrids and very low in wild lilies. Although the role of the bHLH (basic helix–loop–helix) transcription factors in regulating plant-specialized metabolism has become quite clear (Goossens *et al.*, 2017), recent papers also point to their role in regulating volatile sesquiterpene production in *Arabidopsis* (Hong *et al.*, 2012) and in volatile mono- and sesquiterpene biosynthesis in the type VI glandular trichomes of tomato (Xu *et al.*, 2018). By using stable transformation in maize and transient activation assays in citrus, a role for AP2/ERF transcription factors in regulating a terpene synthase was illustrated (Li *et al.*, 2015, 2017). Similarly, in kiwi NAC transcription factors were shown to bind to the promoter of terpene synthase 1 (Nieuwenhuizen *et al.*, 2015). To allow for the identification of TFs that regulate terpene biosynthesis in the traditional Chinese medicinal plant *Amomum villosum*, He *et al.* (2018) used a combination of RNA sequencing and volatile analysis after induction by methyl jasmonate (MeJA) (He *et al.*, 2018). Network analysis revealed correlations between putative terpene synthase Unigenes, terpene abundance and candidate WRKY TFs. Further analyses will be needed to prove that these WRKYs indeed regulate terpene biosynthesis.

On top of regulation by classical TFs, specialized metabolite biosynthesis is likely to involve transcriptional and post-transcriptional silencing, that is regulation via endogenous small non-coding RNAs (sRNAs). Although a substantial number of sRNAs has been computationally predicted to target genes in specialized metabolic pathways, very few have so far been experimentally validated (Kortbeek *et al.*, 2018). microRNAs (miRNAs), although quantitatively by far a minor type amongst the total of small RNAs encountered, have been studied most extensively. In relation to specialized metabolites, there appears to be a pivotal role for miRNA156b (Schwab *et al.*, 2005; Gou *et al.*, 2011; Yu *et al.*, 2015). Yu *et al.* (2015) showed that miR156b targets an SPL9-type transcription factor that directly binds the promoter of TPS21, thereby affecting (*E*)- β -caryophyllene biosynthesis in *Arabidopsis* (Figure 1). With that finding and the insight in the role of the conserved miR156 in developmental processes, the authors

revealed a link between development and volatile biosynthesis, a link that was confirmed by Singh and Sharma (2017) studying the role of miR156b in cucurmin biosynthesis and rhizome development (Singh and Sharma, 2017).

Co-transcription, another intriguing form of regulation – through alternative splicing – is described by Liu *et al.* (2018b) in tea (Liu *et al.*, 2018b). The authors found that *CsLIS/NES* is transcribed into two splicing forms: *CsLIS/NES-1* and *CsLIS/NES-2* with the latter lacking a 305 bp-fragment at the N-terminus and is why the encoded protein is targeted to the cytosol, while *CsLIS/NES-1* is targeted to the plastids. Upon expression in *E. coli*, both splice forms produce nerolidol and linalool from FDP and GDP, respectively (Figure 1). Expression in tobacco and silencing in tea leaves suggested that *CsLIS/NES-1* *in vivo* acts as linalool synthase and *CsLIS/NES-2* as a nerolidol synthase, although the experimental evidence for the latter is not very strong, possibly due to conjugation of the produced nerolidol (Houshyani *et al.*, 2013). Intriguingly, only one of the two splice forms, *CsLIS/NES-1*, was induced by MeJA (Liu *et al.*, 2018b). It would be interesting to see if this matches with the induction of linalool but not nerolidol (or the derived DMNT) upon JA application.

Volatile formation in plants is also effected by abiotic factors. Abscisic acid (ABA) seems to play a role in this regulation. Upon application of exogenous ABA to tomato the level of volatile compounds such as 1-penten-3-one, β -damascenone and benzaldehyde increased just as the expression of genes possibly involved in the biosynthesis of these volatiles, such as a lipoxygenase, alcohol dehydrogenase, carotenoid cleavage dioxygenase and a hydroperoxide lyase (Wu *et al.*, 2018) (Figure 1). Promoter analysis showed that *cis*-acting elements involved in ABA responsiveness (ABREs) exist in some of these genes. In a very different study, a similar phenomenon was demonstrated. Drought increased the level of ABA in *Salvia dolomitica* and increased the production of sesquiterpenes and the expression of FDP synthase that produces the substrate for sesquiterpene biosynthesis (Caser *et al.*, 2019). In a study on the influence of salt on volatile emission from tomato leaves, however, the results are less clear (Zhang *et al.*, 2018b). The production of some volatiles is altered, as is the expression of some genes involved in volatile biosynthesis, but the relationship between the two is unclear. Clearly, we are making ample progress in identifying the transcription factors regulating VOC biosynthetic pathways. The networks in which these TFs operate remain to be elucidated as well as the role of sRNAs and epigenetic regulation, especially in the developmental regulation of floral volatile biosynthesis.

EMISSION OF VOCs

Work on transport of volatiles intensified some 5 years ago when it was realized that volatiles, just as other lipophilic

secondary metabolites, are likely to need active transport to be emitted by plants (Widhalm *et al.*, 2015). Although there are still many caveats in our knowledge on transport (Tissier *et al.*, 2017), there is also progress with the identification of the role of ABC transporters and LTP proteins as important players (Wang *et al.*, 2016; Adebessin *et al.*, 2017). Direct proof for the involvement of an ABC transporter in volatile emission in *Petunia hybrida* came from the silencing of *PhABCG1*, which resulted in a decrease in volatile emission (Adebessin *et al.*, 2017). For the further unravelling of transport, particularly transcriptomics studies will be instrumental (Tissier *et al.*, 2017). Intriguingly, in such a transcriptomics study in *Petunia axillaris*, an ABC transporter, PaABCG1, was reported with high homology to PhABCG1 (Amano *et al.*, 2018). The authors did not carry out any functional characterization but discussed the fact that these types of ABCG transporters are mostly involved in transport of suberin and cuticle components. This also holds to some extent for the lipid transfer proteins for which Van der Krol and co-workers show evidence that they also play a role – in concert with an ABC transporter for transport across the cell membrane – in transport of volatile and non-volatile sesquiterpenoids across the cell wall (Wang *et al.*, 2016). To what extent ABC transporters and LTPs play a role in the secretion of volatiles from the glandular cells of a trichome to the extracellular cavity remains to be investigated. A recent, elegant, opinion paper describes various scenarios on how this can be achieved (Tissier *et al.*, 2017), but little information is known about this. This also holds true for how these volatiles are retained in the extracellular cavity as emission is often limited. Clearly, several questions remain and further studies are indeed needed to completely resolve the mystery of volatile transport and storage in plants (Tissier *et al.*, 2017).

AGRICULTURAL IMPORTANCE OF VOCs

The multitude of biological effects of VOCs makes them an attractive target to try to improve agriculture but the complexity of these interactions also make the application a large challenge (Beck *et al.*, 2018). Beck and co-authors review a number of possible applications in agricultural of our knowledge about volatiles. This includes the identification and subsequent application in the field of microbes that enhance flower volatile attractiveness to pollinators (Beck *et al.*, 2018). Also they discussed the importance of taking the microbiome, in a broader sense, into account when studying the role of volatiles in plant–organism communication and its possible application in agriculture.

One of the applications that is being pursued for quite some time already is insect-pest control. During the domestication of crops and production on a large scale, the emphasis of breeders historically was not on herbivore protection, but rather on optimizing traits such as yield

and productivity. To compensate for this, (synthetic) pesticides were employed to allow food production on the massive scale needed. These synthetic compounds were often inspired by plant-specialized metabolites but were chemically optimized for effectivity and stability. However, the use of synthetic chemicals for protection of our food is increasingly debated and the use of certain, very commonly used products such as neonicotinoids, have been severely restricted in the EU [regulations (EU) 2018/783–784–7885]. As an alternative to the use of synthetic pesticides, scientists and companies have turned to the introduction of insect resistance through genetic modification (Gutensohn *et al.*, 2014; Sun *et al.*, 2017; Douglas, 2018) and the employment of so-called biopesticides (Pavela, 2016). A plethora of natural specialized metabolites is described in the literature for their potential in replacing chemicals. There are, however, only a handful of examples of such endogenously produced metabolites validated *in planta*, let alone in a field situation (Isman and Grieneisen, 2014; Kortbeek *et al.*, 2018).

Arthropod pests will almost always evolve resistance to insecticides, which on average takes only 60–78 generations (Brevik *et al.*, 2018). Different approaches, or layers of defence will therefore have to be combined to move towards a more sustainable solution. The use of semiochemicals and volatile signalling between plants and pest organism can be a part of such an integrated, more holistic and ecological, pest management approach (Beck *et al.*, 2018). An intriguing example of the integration of semiochemicals in agriculture is the control of stemborers through a ‘push–pull’ strategy (Pickett and Khan, 2016). Here, cereals were offered protection from the stemborer moth, *Busseola fusca*, by the intercropped *Desmodium* spp. that provide ‘the push’ through producing volatiles that repel the moth. ‘The pull’ comes from (*E*)- β -caryophyllene emitted by Napier grass that attracts the moth and moreover produces a viscous substance that kills the larvae of the stemborer (Khan *et al.*, 2007). A variation on the push–pull system described above is a semiochemical-based pest management strategy that targets insect behaviour by using pheromones in a lure application (Mafra-Neto *et al.*, 2013). The authors developed a matrix that provide a steady release of a variety of volatile compounds including attractants such as sex pheromones in combination with insecticides, but also repellents. The system is targeted to disrupt mating, repel or attract-and-kill insects. The authors provide successful examples of the latter for serious crop-pest species such as the fall armyworm (*Spodoptera fugiperda*) and the tomato pest, *Tuta absoluta*, both of which are lured to formula-treated host plants by insect-specific pheromones where they are killed by the insecticide. A formulation that releases verbenone, a repellent of the pine bark beetle *Dendroctonus ponderosae*, was shown to effectively keep the tree free of this

bark beetle (Mafra-Neto *et al.*, 2013). The same holds for dimethyl disulfide, a repellent of the Asian citrus psyllid (*Diaphorina citri*) that transmits the Greening disease Huanglongbing (HLB), which severely threatens citrus production around the world (Mafra-Neto *et al.*, 2013). As described above, the ubiquitous volatile terpene (*E*)- β -caryophyllene repels a number of agriculturally important pests, including psyllids (Zhang *et al.*, 2017). Intercropping (with the (*E*)- β -caryophyllene emitting guave) or possibly the application of (*E*)- β -caryophyllene dispensers may provide solutions for this enormous agricultural problem (Mafra-Neto *et al.*, 2013; Alquézar *et al.*, 2017) (Figure 2f).

Insect control can potentially also be pursued using metabolic engineering of volatiles (Paul *et al.*, 2016; Sun *et al.*, 2016; Abbas *et al.*, 2017; Tissier, 2018). In an attempt to change the resistance of chrysanthemum against aphids, Hu *et al.* (2018a) introduced chrysanthemol synthase that was isolated from pyrethrum and catalyzes the first committed step in pyrethrin biosynthesis, into chrysanthemum (Hu *et al.*, 2018a) (Figure 1). Interestingly, this did not only result in the emission of the, expected, volatile chrysanthemol but also in accumulation of a chrysanthemol glycoside. Both compounds were shown to protect the transgenic chrysanthemum against aphids due to their repellent and antifeedant activity, respectively. In an attempt to protect citrus against *D. citri*, the Arabidopsis (*E*)- β -caryophyllene synthase was overexpressed in Arabidopsis (Alquézar *et al.*, 2017). Transgenic plants with enhanced (*E*)- β -caryophyllene emission repelled *D. citri* suggesting that this strategy can potentially be used to protect citrus trees against HLB (Figure 2f).

Also the engineering of precursor pathways is an interesting tool to alter volatile production. Intriguing work of Dudareva and co-workers (Henry *et al.*, 2018) demonstrates an alternative role for the Nudix hydrolases that were previously shown to catalyze the first step in the formation of geraniol in rose (Magnard *et al.*, 2015). They make it likely that the Arabidopsis NUDIX1 and 3 are involved in the dephosphorylation of isopentenyl diphosphate (IPP) to isopentenyl phosphate (IP), which then serves as a substrate for isopentenyl phosphate kinase. Although not completely understood yet IPP dephosphorylation seems to be an important regulatory mechanism as *nudix* mutants produce more terpenes while *AtNUDIX1* overexpression in tobacco results in lower volatile terpenoid production. Counter-intuitively, however, when IP levels were increased by overexpression in tobacco of a bacterial phosphomevalonate decarboxylase (MPD), monoterpene and sesquiterpene production increased. Moreover, the authors then tested overexpression of Arabidopsis 3-hydroxy-3-methylglutaryl-coenzyme A reductase, *AtHMGR* – considered the rate-limiting step in the mevalonate pathway – with *MPD* in tobacco and found a considerable further increase in both monoterpene and sesquiterpene production. Overexpression of these two genes in combination with

the *Santalum album* santalene synthase resulted in almost 10-fold higher emission of α -santalene.

Zhang *et al.* (2018c) studied the effect of overexpression of two enzymes that catalyze an important, possibly rate-limiting, steps in the plastidic MEP pathway, 1-deoxy-d-xylulose-5-phosphate synthase (DXS) and 1-deoxy-d-xylulose-5-phosphate reductoisomerase (DXR) (Zhang *et al.*, 2018c). The encoding genes were isolated from *Lilium* ‘Siberia’ and heterologously overexpressed in tobacco of which the flowers produced more of the monoterpene, linalool (LiDXR overexpression line; as anticipated) but also of the sesquiterpene, caryophyllene (in both the LiDXR and LiDXS overexpression line), possibly as a result of increased IPP transport from the plastids to the cytosol as a result of the larger IPP pool produced in the transgenic lines (Figure 1).

In case the engineered volatiles needed to be stored in the plant rather than emitted, Delatte and colleagues invented an interesting engineering strategy in which oil bodies are heterologously introduced through transient expression of a diacylglycerol acyltransferase (*DGAT*), the transcription factor WRINKL1 and oleosin (*OLE1*) in *Nicotiana benthamiana* (Delatte *et al.*, 2018). This indeed resulted in the formation of oil bodies that were associated with the heterologous sesquiterpenes that were simultaneously produced through the transient expression of sesquiterpene synthases, together resulting in a 17-fold increased accumulation of volatile sesquiterpenes.

In conclusion, there are many promising scientific reports about the biological relevance of volatiles in the interaction of plants with other organisms. In these reports, the potential application of this knowledge in agriculture is usually mentioned. These possible applications include the use of volatiles in dispensers, or other matrices, the optimization of volatile production by plants through breeding or genetic modification and the application of selected microbes to change volatile emission by the plant. Particularly the use of natural enemies (that use volatile cues to find their prey), especially in greenhouses and the successful lure and kill strategies that employ attractive volatiles are examples that show that these approaches can work, despite the fact they have not really been optimized. The use of natural enemies for example has not, or hardly, been selected for despite the fact that scientists have shown there is genetic variation for HIPV induction in crops and that this results in difference in attractiveness of natural enemies (Kappers *et al.*, 2011). Further research should show whether more intricate applications and optimization of the existing ones are possible such that they can be used to achieve a more sustainable agriculture.

CONCLUSIONS/FUTURE DIRECTIONS

The field of VOC research is going through an exciting phase. We are seeing intriguing new developments such

as the role of micro-organisms in VOC communication, producing volatiles themselves (Lemfack *et al.*, 2017; Schenkel *et al.*, 2018), affecting the induction of HIPVs as endosymbionts of herbivorous insects (Frago *et al.*, 2017) or changing the flower VOC blend because they colonize nectar (Vannette and Fukami, 2016; Rering *et al.*, 2018). Also the elucidation of VOC transport, emission and accumulation and their perception in the receiver organism are hot topics in research and we are only just beginning to understand how specific volatiles and their blends convey information from one organism to the other and how flexible this process is. Advanced techniques such as genomics, transcriptomics and metabolomics will be associated with behavioural data using novel tools such as network analysis, large-scale data integration and machine learning approaches, facilitating the interpretation of the biological meaning of the complex VOC blends in various dimensions. With these advanced approaches, the discovery of biosynthetic genes will also further speed up, allowing – through genetic modification/metabolic engineering in combination with behavioural assays – to further underpin the role of individual VOCs in the communication of plants with other organisms. This also holds for the genes and regulatory mechanisms underlying the regulation of the – constitutive and induced – formation of VOCs and their transport and sequestration. Genetic screens using the response to specific VOCs will be used to identify receptors and signal transduction cascades (Scala *et al.*, 2017). With regard to the use of scientific knowledge on VOCs in agriculture, the use of natural enemies in greenhouses and lure and kill strategies are examples that already prove that the biological effect of VOCs can be employed in agriculture. A further deepening of our knowledge on the mechanisms underlying plant communication with beneficial as well as harmful organisms will surely provide the basis for more intricate applications in a more sustainable agriculture.

Box 1. Open questions

- How large is the role of the microbiome in determining the plant volatile blend?
- What is the underlying mechanism of (specificity in) the perception of volatiles by plants?
- What makes volatile communication between plants and other organisms an evolutionary stable strategy?

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors contributed equally to the writing and revising of the paper.

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