

REVIEW: PART OF A SPECIAL ISSUE ON PLANT IMMUNITY

## Terpenoids in plant and arbuscular mycorrhiza-reinforced defence against herbivorous insects

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• **Background** Plants, though sessile, employ various strategies to defend themselves against herbivorous insects and convey signals of an impending herbivore attack to other plant(s). Strategies include the production of volatiles that include terpenoids and the formation of symbiotic associations with fungi, such as arbuscular mycorrhiza (AM). This constitutes a two-pronged above-ground/below-ground attack–defence strategy against insect herbivores.

• **Scope** Terpenoids represent an important constituent of herbivore-induced plant volatiles that deter herbivores and/or attract their predators. Terpenoids serve as airborne signals that can induce defence responses in systemic undamaged parts of the plant and also prime defence responses in neighbouring plants. Colonization of roots by AM fungi is known to influence secondary metabolism in plants; this includes alteration of the concentration and composition of terpenoids, which can boost both direct and indirect plant defence against herbivorous insects. Enhanced nutrient uptake facilitated by AM, changes in plant morphology and physiology and increased transcription levels of certain genes involved in the terpenoid biosynthesis pathway result in alterations in plant terpenoid profiles. The common mycorrhizal networks of external hyphae have added a dimension to the two-pronged plant defence strategy. These act as conduits to transfer defence signals and terpenoids.

• **Conclusion** Improved understanding of the roles of terpenoids in plant and AM defences against herbivory and of interplant signalling in natural communities has significant implications for sustainable management of pests in agricultural ecosystems.

**Key words:** Terpenoids, herbivorous insects, indirect defence, induced defence, priming, arbuscular mycorrhiza, common mycorrhizal networks.

### INTRODUCTION

Terpenoids represent the largest and structurally the most diverse group of volatiles released by plants. Biologically, a wide array of terpenoids can enable plants to interact with other organisms, such as insects, pathogens and neighbouring plants (Kant *et al.*, 2004; Mercke *et al.*, 2004; Kappers *et al.*, 2005; Cheng *et al.*, 2007a, b). Terpenoids are emitted either constitutively or induced in response to biotic (Dudareva *et al.*, 2006, 2013; Unsicker *et al.*, 2009; Rasmann *et al.*, 2012) and abiotic (Gouinguéné and Turlings, 2002; Loreto and Schnitzler, 2010) stresses.

Attack by insects induces plants to emit a blend of volatile organic compounds (VOCs). Terpenoids are important members of the class of herbivore-induced plant volatiles (HIPVs) (Gershenson and Dudareva, 2007; Mumm *et al.*, 2008). Some terpenoids serve as repellents (Laothawornkitkul *et al.*, 2008; Unsicker *et al.*, 2009; Maffei, 2010), while others function in indirect plant defence by attracting arthropods that prey upon or parasitize herbivores (Kessler and Baldwin, 2001; Rasmann *et al.*, 2005; Schnee *et al.*, 2006). Additionally, terpenoids are produced in response to oviposition and are involved in the attraction of egg-parasitizing insects (Conti *et al.*, 2008; Büchel *et al.*, 2011; Tholl *et al.*, 2011; Hilker and Fatouros, 2015).

In addition to their roles in direct and indirect defences, plant terpenoids, along with other HIPVs, such as green leaf volatiles

(GLVs), serve as airborne signals that can be perceived by undamaged systemic parts of the same plant (Frost *et al.*, 2007; Heil and Silva Bueno, 2007) and by neighbours (Karban *et al.*, 2000). In response to perceived volatile signals, plants express defence genes and synthesize secondary metabolites (Shulaev *et al.*, 1997; Arimura *et al.*, 2000b; Sugimoto *et al.*, 2014) or prime their defences against pests (Engelberth *et al.*, 2004; Heil and Kost, 2006; Ton *et al.*, 2006). Although primed plants do not show any trait of resistance, they become prepared to respond more rapidly and more intensely when attacked (Conrath *et al.*, 2006; Heil and Ton, 2008).

The synthesis of terpenoids can be altered by numerous biotic and abiotic factors (Owen and Peñuelas, 2005; Peñuelas and Munné-Bosch, 2005; Brunetti *et al.*, 2013). Among such influencing factors is the formation of arbuscular mycorrhiza (AM), defined as a symbiotic association of plant roots with soil fungi belonging to the phylum Glomeromycota. Arbuscular mycorrhizal fungi are heterokaryotic, obligate symbionts that confer on plants multifarious benefits, like improved access to nutrients and water and enhanced resistance to biotic and abiotic stresses (Finlay, 2008; Smith and Read, 2008; Miransari, 2010; Ruiz-Lozano *et al.*, 2012; Evelin *et al.*, 2013). In return for such colossal benefits, the fungus obtains carbon from the plants (Smith and Gianinazzi-Pearson, 1988; Smith and Read, 2008). Arbuscular mycorrhiza interconnects plants by means of

an extensive subterranean hyphal network. This network is specialized for nutrient (primarily phosphate) and water uptake (Miller *et al.*, 1995). The bidirectional exchange of nutrients between the symbionts takes place at highly branched intracellular structures called arbuscules, which are formed in the inner cortex of the plant root by the mycobiont (Harrison, 2005; Parniske, 2008). This interaction plays a crucial role in plant ecosystem functioning, as more than 80 % of the terrestrial plant species rely on AM fungi for their mineral nutrition (Smith and Read, 2008).

The formation of AM changes the physiology and ecology of the plant. Arbuscular mycorrhiza potentially strengthens both direct and indirect plant defence systems (Pozo and Azcón-Aguilar, 2007; Jung *et al.*, 2012; Borowicz, 2013) by altering the secondary metabolism of the plant (Hohnjec *et al.*, 2005; Walker *et al.*, 2012). Formation of AM has been demonstrated to change the concentration and composition of terpenoids (Copetta *et al.*, 2006; Khaosaad *et al.*, 2006; Kapoor *et al.*, 2007; Rapparini *et al.*, 2008). This alters the plant's attractiveness and also the insect's behaviour (Schausberger *et al.*, 2012; Babikova *et al.*, 2014a; Shrivastava *et al.*, 2015). Cascading effects on higher trophic levels have also been reported (Gange *et al.*, 2003), as have indirect effect on predators and parasitoids of herbivores (Gange *et al.*, 2003; Guerrieri *et al.*, 2004; Laird and Addicott, 2007). Consequently, increased knowledge of the mechanisms that influence production of terpenoids in AM plants will make important contributions to the biocontrol and integrated management of pests.

In this review, readers are first introduced to the terpenoids that contribute to HIPVs, and their synthesis in the plant cell. The review emphasizes the role of terpenoids in plant defence against herbivorous insects (Fig. 1) and discusses their probable role in airborne signalling within the plant and to nearby plants. It then focuses on the significance of terpenoids in AM-mediated reinforcement of direct and indirect defences against herbivory (Fig. 2), further discussing various mechanisms underlying changes in the concentration and composition of terpenoids in mycorrhizal plants. Finally, it outlines the prospects for bioengineered terpenoid-producing plants and AM symbiosis in the sustainable management of pests in agricultural systems.

## TERPENOIDS IN HIPVS

Terpenoids are one of the important constituents of volatiles that are released by plants in response to herbivore attack (Gershenzon and Dudareva, 2007; Mumm *et al.*, 2008). They are low molecular weight compounds derived from the basic five-carbon building blocks of isopentenyl diphosphate (IPP). The key players among the terpenoid volatiles that significantly contribute to HIPVs are monoterpenes (C<sub>10</sub>), sesquiterpenes (C<sub>15</sub>) and homoterpenes such as 4,8-dimethylnona-1,3,7-triene (DMNT) and 4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT) (Leitner *et al.*, 2005; Arimura *et al.*, 2008; Mithöfer and Boland, 2012). Isoprene (2-methyl-1,3-butadiene), although not produced by many plants, has also been demonstrated to play an important role in defence against insect herbivory (Laothawornkitkul *et al.*, 2008).

There are two pathways for the production of terpenoids: the cytoplasmic mevalonate (MVA) pathway and the plastidial

2-C-methyl-D-erythritol 4-phosphate (MEP) pathway (Aharoni *et al.*, 2005; Rodríguez-Concepcion, 2006; Cheng *et al.*, 2007a). Both pathways generate universal precursors for terpenoid synthesis from IPP and its isomer dimethylallyl diphosphate (DMAPP). While monoterpenes are synthesized via the MEP pathway, sesquiterpenes are produced by the MVA pathway. In contrast to the conventional allocation, which suggests the MVA and MEP pathways are strictly independent, there is emerging evidence that the two pathways cross-talk by allowing IPP to shuttle between different compartments (Piel *et al.*, 1998; Bick and Lange, 2003; Bartram *et al.*, 2006; Rodríguez-Concepcion, 2006). However, it has been found that ~80 % of the IPP derived from the MEP pathway contributes to sesquiterpene biosynthesis following herbivory (Bartram *et al.*, 2006; Arimura *et al.*, 2008).

Condensation of C<sub>5</sub> units gives rise to all-*trans* or all-*cis* prenyl diphosphate precursors that are converted by the terpene synthase (TPS) enzymes of different subfamilies into acyclic, mono-, bi- or tricyclic monoterpenes, sesquiterpenes or semivolatile diterpenes (Chen *et al.*, 2011). Terpene synthases are generally multiproduct enzymes, and thus even a single TPS can significantly enhance the diversity of terpenoids (Gershenzon, 1994; Tholl, 2006; Arimura *et al.*, 2008). The primary terpene skeletons may be further modified through secondary enzymatic reactions, such as dehydrogenations, hydroxylations, methylations and acylations (Dudareva *et al.*, 2006).

Some terpenoids, such as  $\beta$ -ionone, are produced not directly from IPP, but instead from tetraterpenes such as carotenoids, by carotenoid cleavage dioxygenases (Dudareva *et al.*, 2013). Homoterpenes such as DMNT and TMTT are synthesized by oxidative degradation of the sesquiterpene (3S)-(*E*)-nerolidol and the diterpene geranyl linalool by cytochrome P450 enzymes (Arimura *et al.*, 2009; Maffei, 2010).

## TERPENOIDS IN DEFENCE AGAINST HERBIVORY

### *Direct interaction*

Terpenoids can serve as repellents and reduce larval feeding and oviposition by herbivores (De Boer *et al.*, 2004; Laothawornkitkul *et al.*, 2008; Unsicker *et al.*, 2009; Maffei, 2010). For example, linalool (a monoterpene) and (*E*)- $\beta$ -farnesene (a sesquiterpene) produced by plants repel herbivores and aphids, respectively (Aharoni *et al.*, 2003; Unsicker *et al.*, 2009; Maffei, 2010). Although the exact mechanisms by which terpenoids affect insect pests are not known, probable processes include the inhibition of ATP synthase, alkylation of nucleophiles and interference with moulting (Langenheim, 1994). Terpenoids such as  $\alpha$ -pinene and  $\beta$ -pinene have been shown to disturb the nervous system in insects by inhibition of acetylcholinesterase (Yeom *et al.*, 2012).

### *Indirect above-ground interactions*

Terpenoids emitted as a result of herbivore attack have an important role in a plant's indirect defences, attracting predators or parasites of herbivores and facilitating location of the attacked plants (Heil, 2008). For example, infestation of lima bean leaves by spider mites (*Tetranychus urticae*) triggers the

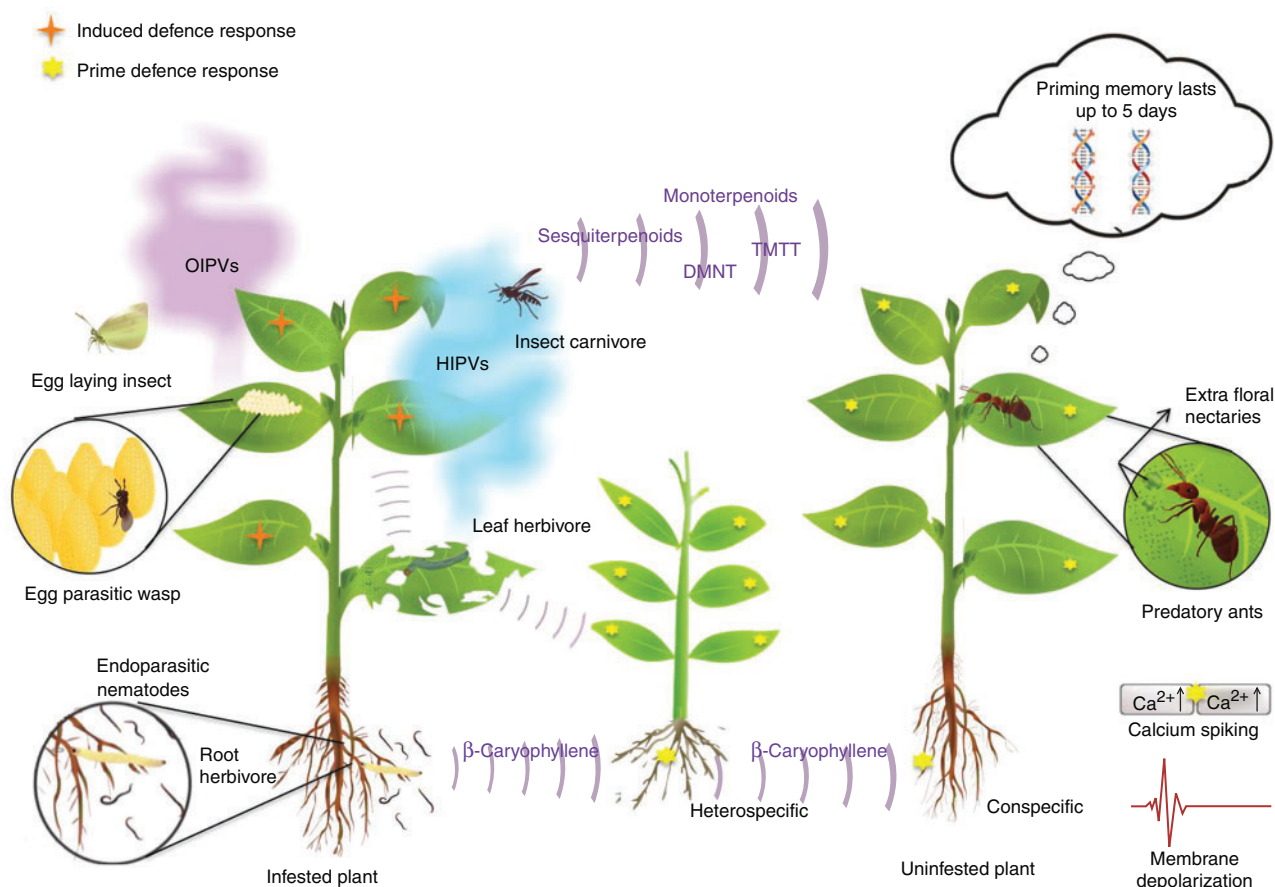


FIG. 1. Overview of terpenoids in plant defence against herbivorous insects. Volatile terpenoids that belong to the HIPVs (herbivore-induced plant volatiles) and OIPVs (oviposition-induced plant volatiles) are released in response to herbivore attack and oviposition, respectively. Terpenoids induce defence responses in the systemic parts of the same plant. These volatiles attract insect carnivores that feed on the herbivores, thereby inducing indirect defence in plants, and prime neighbouring conspecific and heterospecific plants. The perception of terpenoids by neighbouring plants results in influx of calcium ions and membrane depolarization. Epigenetic regulation of this priming response is reported to evoke the priming memory for up to 5 d. Terpenoids also affect tritrophic interactions in soil.

*de novo* production of terpenoids such as (*E*)- $\beta$ -ocimene, linalool, DMNT and TMTT (Dicke *et al.*, 1990, 1999; De Boer *et al.*, 2004; Shimoda *et al.*, 2005), which lure the predacious mites (*Phytoseiulus persimilis*) that prey on spider mites (Takabayashi and Dicke, 1996). The volatiles from spider mite-infested lima beans, treated with fosmidomycin (an inhibitor of the MEP pathway) were less attractive to the predatory mites than those from infested control plants, indicating the significance of terpenoids in indirect defence (Mumm *et al.*, 2008).

The high chemical diversity within HIPV mixtures complicates identification of the compound(s) actually responsible for signalling herbivore enemies. However, it has been demonstrated by investigation of individual compounds that terpenoids such as the homoterpene TMTT can attract predatory mites (De Boer *et al.*, 2004). Genetic engineering for enhanced expression of genes encoding enzymes for the formation of terpenoids has ascertained the role of individual compounds in tritrophic interactions. Transgenic *Arabidopsis thaliana* overexpressing strawberry nerolidol synthase, a TPS, attracted more predatory *P. persimilis* mites (Kappers *et al.*, 2005). Similarly, overexpression of a corn TPS gene (*TPS10*) in *A. thaliana* augmented the attractiveness of these transgenic plants to the parasitic wasp *Cotesia marginiventris* (Schnee *et al.*,

2006). Interestingly, changes in HIPV blends emitted at different times can impact the interactions among a plant, its herbivores and their parasitoids, and stimulate different preferences for herbivores and their parasitoids (Mathur *et al.*, 2013; Pashalidou *et al.*, 2015). The generalist *Spodoptera littoralis* preferred undamaged *Brassica juncea* plants, whereas its parasitoid (*C. marginiventris*) preferred 48-h damaged plants (Mathur *et al.*, 2013). In *Brassica nigra*, parasitoid wasps (*Cotesia glomerata*) were attracted to plants infested with eggs just before and shortly after larval hatching of *Pieris brassicae* (Pashalidou *et al.*, 2015). The authors have correlated this preference to temporal changes in the blend of HIPVs (terpenoids).

#### Response to oviposition

Plants may respond to herbivore egg deposition and activate defences before actual feeding injury is initiated, which might be a successful tactic to reduce impending herbivory (Hilker *et al.*, 2002; Mumm and Hilker, 2006; Pashalidou *et al.*, 2015). Analogous to HIPVs, plant volatiles induced specifically by insect oviposition are termed oviposition-induced plant volatiles (OIPVs) (Hilker and Fatouros, 2015). Terpenoids are important

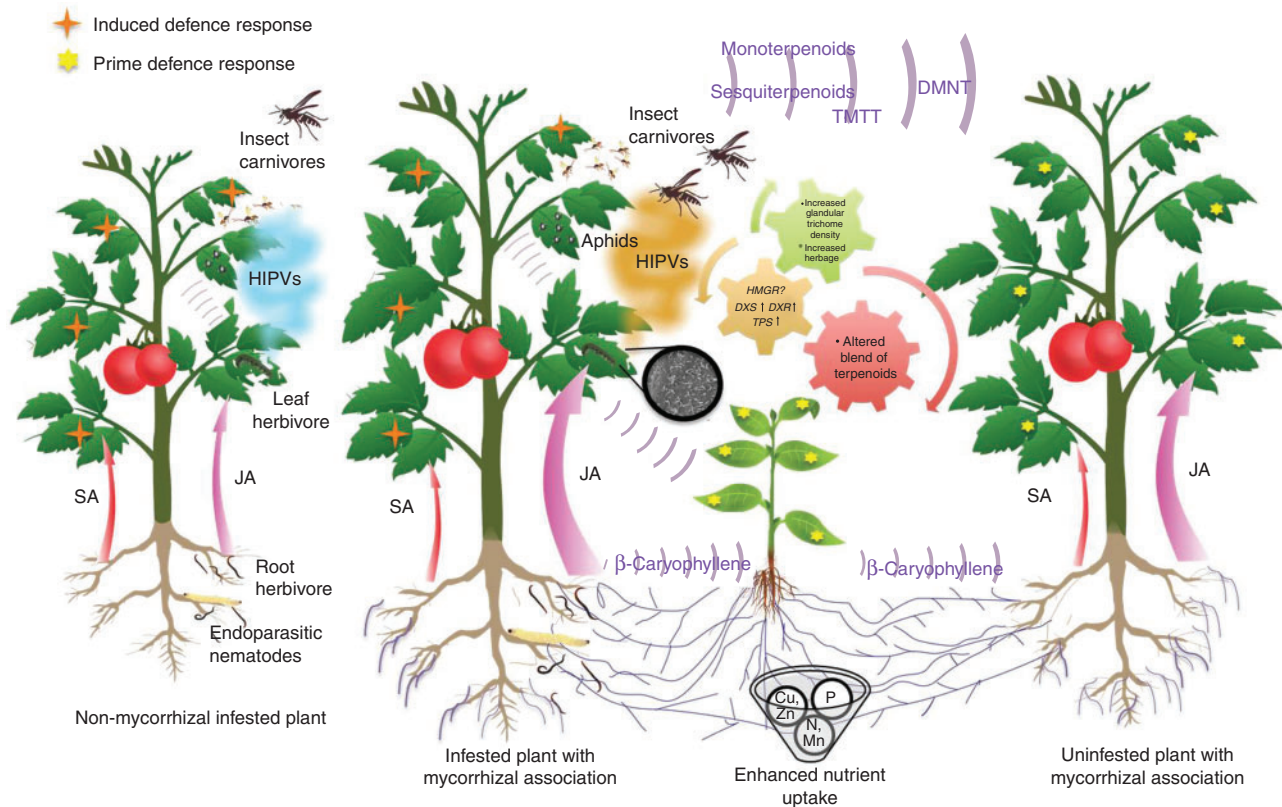


Fig. 2. Overview of arbuscular mycorrhiza (AM)-reinforced defence against herbivorous insects. Plants colonized by AM fungi are more tolerant by virtue of superior growth and nutrient uptake. Formation of AM may result in increased glandular trichome density, availability of substrates, induction of MEP (higher expression of *DXS* and *DXR*) and MVA (higher expression of *HMGR*) pathways, and induction of terpene synthases (TPSs). These factors in various combinations result in changes in the terpenoid profile in mycorrhizal (M) plants, inducing both direct and indirect defence responses against herbivore attack in the plant. Mycorrhizal colonization results in amplification of a wound signal, leading to priming of neighbouring plants. Common mycelial networks (CMNs) serve as signalling conduits between interconnected plants under herbivore attack. JA, jasmonic acid; SA, salicylic acid.

members of the class of OIPVs (Conti *et al.*, 2008; Tholl *et al.*, 2011). The OIPV-specific terpenoids attract egg parasitoids (Wegener and Schulz, 2002; Mumm and Hilker, 2005; Büchel *et al.*, 2011). Intriguingly, the attractiveness of egg-laden foliage to the egg parasitoid has been related to an increase in transcription levels of sesquiterpene synthase (Köpke *et al.*, 2010; Beyaert *et al.*, 2012). Oviposition on *Pinus sylvestris* needles by the sawfly *Diprion pini* induced both local and systemic emission of terpenoid volatiles (Hilker *et al.*, 2002; Mumm and Hilker, 2006). This response was specific to oviposition, and could not be induced by artificial wounding (Hilker and Fatouros, 2015). However, volatile cues to attract egg parasitoids have not yet been identified.

#### Response to below-ground infestation

Below-ground VOC patterns are generally distinct from volatiles released from above-ground plant tissues (Peñuelas *et al.*, 2014). Terpenes are the most prominent VOCs emitted from below-ground tissues (Rasmann *et al.*, 2005; Ali *et al.*, 2011; Palma *et al.*, 2012; Peñuelas *et al.*, 2014), and among these sesquiterpenes are the compounds that show the greatest diffusion in the soil (Hiltpold and Turlings, 2008). Terpenoids have been shown to play a crucial role in the specificity of below-ground

tritrophic interactions (Rasmann and Turlings, 2008). The most well-studied example is the induction of (*E*)- $\beta$ -caryophyllene by maize roots infested by larvae of the leaf beetle *Diabrotica virgifera virgifera*, which attracted the entomopathogenic nematode *Heterorhabditis megidis* (Rasmann *et al.*, 2005). On the other hand, (*E*)- $\beta$ -caryophyllene also served as an attractant aiding *D. virgifera* larvae to identify a susceptible host (Robert *et al.*, 2012). One possible explanation for the contradictory observations in the above studies is that as maize roots only emit (*E*)- $\beta$ -caryophyllene (Hiltpold and Turlings, 2008), it can be presumed that the entomopathogenic nematode *H. megidis* has developed an adaptation to take cues from the (*E*)- $\beta$ -caryophyllene emitted by maize roots for efficient prey-searching.

#### Multiple herbivore infestations

In nature, plants are generally infested by two or more herbivore species, either concurrently or serially. However, most of the studies in this area have been conducted on single-herbivore attack under controlled conditions. Infestation by two or more insect species causes complex variations in volatile profile, and cannot be predicted on the basis of observations on single herbivores. When two or more herbivores co-infest, the effects may be negative or additive, or one type of herbivore takes priority. For

example, concurrent occurrence of herbivory above- as well as below-ground by *S. littoralis* and *D. virgifera*, respectively, negatively influenced tritrophic signalling due to decreased (*E*)- $\beta$ -caryophyllene production by maize roots (Rasmann and Turlings, 2007). This may be explained by reduced availability of a C source required for the synthesis of the terpenoid precursors. On the other hand, HIPVs emitted by lima beans and pepper plants infested by two herbivore species attracted more predatory mites and predatory mirid bugs, respectively, compared with volatiles emitted by plants infested by either herbivore separately (Dicke et al., 2009). Furthermore, most studies are performed under highly controlled conditions, which impedes application of the results in natural environments. Thus, a major challenge is the development of experimental designs that consider the ecological reality of infestations.

#### AIRBORNE SIGNALLING TO NEIGHBOURING PLANTS AND SYSTEMIC PARTS OF THE SAME PLANT

The airborne volatile signals from herbivore-damaged plants (emitters) enable nearby conspecific and heterospecific undamaged plants (receivers) to foresee the impending arrival of herbivores and tailor their defence accordingly (Baldwin and Schultz, 1983; Arimura et al., 2000a; Engelberth et al., 2004; Karban et al., 2006; Heil and Silva Bueno, 2007; Ramadan et al., 2011). Herbivore-induced plant volatiles serve as external signals for within-plant communication, and elicit a defence response in systemic parts of the affected plant (Karbon et al., 2006; Frost et al., 2007; Heil and Silva Bueno, 2007; Park et al., 2007; Das et al., 2013). Damaged leaves immediately release VOCs and communicate more quickly with leaves located nearby that are not directly connected by vasculature (Heil and Ton, 2008). Plants may react to the signals connected with the presence of herbivores by upregulating defence genes (Arimura et al., 2000b), leading to increased production of defence-related metabolites such as phytohormones, proteinase inhibitors, terpenoids and/or extrafloral nectar (Tschamtko et al., 2001; Engelberth et al., 2004; Kost and Heil, 2006; Frost et al., 2008a; Blande et al., 2010). These changes are ultimately translated into reduced herbivory and improved fitness of receiver (Karbon and Maron, 2002; Kost and Heil, 2006; Muroi et al., 2011). The responses include a combination of priming and induced defences, according to the allocation cost of different classes of defence, with plants priming more expensive responses and inducing less costly metabolites, such as extrafloral nectar or HIPVs, to attract natural enemies of the herbivore (Kost and Heil, 2006; Frost et al., 2008b). Participation of volatiles in interplant below-ground interactions is not well elucidated (Schenkel et al., 2015; Delory et al., 2016). Whether VOCs emitted by roots in the rhizosphere can diffuse into the phyllosphere and convey signals to prime above-ground parts of the same plant is also not effectively documented (Erb et al., 2008).

#### ROLE OF TERPENOIDS IN AIRBORNE SIGNALLING

An important step in understanding the mechanistic foundations of airborne priming is the elucidation of the actual messengers.

Green-leaf volatiles and terpenoids are two important components of HIPVs. Green-leaf volatiles, which are aldehydes, alcohols and esters resulting from lipoxygenase cleavage of fatty acids, account for the distinctive odour of damaged leaves (Paré and Tumlinson, 1999). Although evidence for GLVs as priming signals has been observed in several plant species (Frag and Paré, 2002; Ruther and Fürstenau, 2005; Ruther and Kleier, 2005; Kost and Heil, 2006; Sugimoto et al., 2014), reports on terpenoids have been variable. The role of volatile terpenes in plant–plant interactions was initially reported in lima bean, where terpenoids such as  $\beta$ -ocimene, DMNT, TMTT and linalool, released upon feeding of *T. urticae*, induced the expression of defence genes encoding lipoxygenase (synthesis of jasmonic acid) and the pathogenesis-related protein PR-2 ( $\beta$ -1,3-glucanase) (Arimura et al., 2000b). In maize, however, terpenoids were not associated with priming defence responses in the receiver plants (Ruther and Fürstenau, 2005).

Early events in the perception of volatile signals comprise an alteration of the plasma membrane potential ( $V_m$ ) and an increase in cytosolic calcium ( $[Ca^{2+}]_{cyt}$ ) (Zebelo et al., 2012). It was observed that GLVs such as (*E*)-2-hexenal, (*Z*)-3-hexenal and (*Z*)-3-hexenyl acetate induced stronger  $V_m$  depolarization and a greater increase in cytosolic calcium flux compared with terpenoids such as  $\alpha$ -pinene and  $\beta$ -caryophyllene. These terpenoids induced a significant  $V_m$  depolarization with respect to controls, but did not exert any significant effect on  $[Ca^{2+}]_{cyt}$  homeostasis (Zebelo et al., 2012). Moreover,  $V_m$  depolarization was found to increase with increasing GLV concentration. Green-leaf volatiles are immediately released after damage and their release ceases within a few minutes of damage (Arimura et al., 2009), while the release of monoterpenes typically starts 24 h after attack (Dudareva et al., 2006; Pichersky et al., 2006). The emission of terpenoids is often systemic and extended (Paré and Tumlinson, 1999). These observations indicate that GLVs are better candidates than terpenoids for conveying airborne signals of herbivore attack. Further studies are required to identify the messengers (volatiles) involved in transmitting signals within and to nearby plants. The complementary approach of using plant mutants deficient in various components of HIPVs (GLVs or terpenoids) has enabled the role of individual compounds in plant–plant signalling to be deciphered (Baldwin et al., 2006). However, using this technique, Paschold et al. (2006) observed that neither GLVs nor terpenoids prime the expression of defence genes in *Nicotiana attenuata*. The role of various HIPVs as volatile priming signals has continued to be uncertain because in most studies healthy plants were treated with synthetic volatiles, a procedure that does not satisfactorily mimic the exact timing and concentrations of HIPV emissions in nature. Furthermore, genetic manipulation of plants for enhanced synthesis of HIPVs may result in several undesirable effects (Erb et al., 2015). As individual volatile compounds do not participate in plant–insect interactions in isolation, another key issue for exploration is the interactive effects of different VOCs in these interactions. Furthermore, techniques based on the limit of detection of terpenoids do not take into consideration the sensitivity of perception by biological systems (insects), and hence do not necessarily provide biologically useful information.

After herbivore departure, plants likely cease to release HIPVs that attract parasitoids (Puente et al., 2008). If emission

were to continue, signals would deliver unreliable information to parasitoids, which would then be incapable of tracking their hosts. Receiver plants are not aware of how much later the herbivores will arrive, and therefore have no clues regarding how long the primed state should be maintained. However, very little is known about how receiver plants control the duration of the primed state, which is of importance in terms of the arrival time of herbivores. The molecular mechanisms involved in sustaining the primed state are also unresolved. Ali *et al.* (2013) demonstrated that the priming effect of HIPVs on resistance against herbivores is memorized and stored by plants through epigenetic regulation of DNA, with plants able to evoke this memory when attacked by herbivores. Treatment with HIPV was shown to result in demethylation of cytosine sites in the promoter region of a herbivore-responsive gene for Bowman-Birk-type trypsin inhibitor (*Tl*). Further experiments are required to substantiate understanding of the epigenetic control of airborne signalling between plants.

#### ARBUSCULAR MYCORRHIZA AND HERBIVOROUS INSECT RESISTANCE

Arbuscular mycorrhizal fungi are reported to affect the performance of herbivores (Gange and West, 1994; Vicari *et al.*, 2002; Pozo and Azcón-Aguilar, 2007; Gehring and Bennett, 2009; Borowicz, 2013). Arbuscular mycorrhiza symbioses adversely affect root-feeding insects, while their effects on leaf-feeding insects are variable (Pozo and Azcón-Aguilar, 2007; Gehring and Bennett, 2009; Borowicz, 2013). The extent of protection also changes with the feeding style of the attacking herbivore. Arbuscular mycorrhiza symbiosis seems to benefit phloem-sucking insects (aphids) (Gange *et al.*, 1999; Koricheva *et al.*, 2009), while effects on chewing and leaf-mining insects are largely adverse (Gange and West, 1994; Vicari *et al.*, 2002; Hoffmann *et al.*, 2009); counter-examples, however, also exist (Babikova *et al.*, 2014b; Shrivastava *et al.*, 2015). This considerable variation can be ascribed to some extent to the species (plant, fungus and herbivore) involved in the tripartite interactions (Bennett and Bever, 2007; Gange, 2007; Leitner *et al.*, 2010; Pineda *et al.*, 2010). Akin to the complexity of plant–herbivore–natural enemy tripartite interactions, AM also affects predators and parasitoids of herbivores (Gange *et al.*, 2003; Guerrieri *et al.*, 2004; Laird and Addicott, 2007).

Participating AM fungi may induce resistance to neighbouring plants, via hyphal networks functioning as plant–plant underground communication systems (Song *et al.*, 2010; Babikova *et al.*, 2013). Common mycorrhizal network serve as conduits facilitating the transfer of defence signals and also terpenoids between neighbouring plants under herbivore attack (Song *et al.*, 2014).

#### ROLE OF TERPENOIDS IN AM-REINFORCED RESISTANCE AGAINST HERBIVOROUS INSECTS

The significance of below-ground interactions between plant and AM fungi for assessing VOC emission rates and their consequent ecological role in the deployment of indirect defences by plants has been emphasized (Rapparini *et al.*, 2008). The

indirect effect of AM on herbivore defence has been correlated to changes in the blend of terpenoids that alter plant attractiveness and insect behaviour (Babikova *et al.*, 2014a). In *Phaseolus* challenged by spider mites, for example, AM symbiosis with *Funneliformis mosseae* increased the emission of  $\beta$ -ocimene and  $\beta$ -caryophyllene, resulting in increased attraction of predators of spider mites (Schausberger *et al.*, 2012). Similarly, Shrivastava *et al.* (2015) observed a greater defence response against beet armyworm (*Spodoptera exigua*) in AM than in non-mycorrhizal plants, partly attributable to the difference in levels and blends of terpenoids. Arbuscular mycorrhiza formation led to enhanced levels of monoterpenes and sesquiterpenes, including monoterpenes such as myrcene, which were not detected in non-mycorrhizal plants. Myrcene is a semiochemical utilized by insects for communication, e.g. to deter thrips (Broughton and Harrison, 2012) or to attract aphidophagous hoverflies in a terrestrial orchid (Stökl *et al.*, 2011).

#### EFFECTS OF ARBUSCULAR MYCORRHIZA ON TERPENOIDS

Arbuscular mycorrhiza symbiosis can affect a number of volatile organic compounds, including terpenes. Arbuscular mycorrhiza fungal colonization has been shown to enhance the production of triterpenoids (Akiyama and Hayashi, 2002), apocarotenoids (Klingner *et al.*, 1995; Fester *et al.*, 2002; Strack and Fester, 2006; Akiyama, 2007; Walter and Strack, 2011) and abscisic acid (Meixner *et al.*, 2005) in roots of various plants. Systemic effects of AM on the quantity and quality of terpenoids in above-ground parts of plants have also been mooted (Kapoor *et al.*, 2002a, b; Copetta *et al.*, 2006; Khaosaad *et al.*, 2006; Kapoor *et al.*, 2007; Zubek *et al.*, 2010; Weisany *et al.*, 2015; Rydlová *et al.*, 2016). These studies have so far been largely confined to the effects of AM on individual components of terpenoids or a suite of terpenoids (essential oil composition) that have pharmaceutical value. Arbuscular mycorrhiza may enhance the biosynthesis of an individual terpenoid either by increase in isoprene precursors through the induction of biosynthesis pathways and/or by induction of terpene synthase enzymes (Shrivastava *et al.*, 2015). Increases in the level of substrates by enhanced P uptake and increased photosynthetic efficiency have been described (Wright *et al.*, 1998a, b; Kapoor *et al.*, 2002a, b; Rasouli-Sadaghiani *et al.*, 2010). The role of P is perceptible in the synthesis of terpenoids both via the MVA pathway, which requires acetyl-CoA, ATP and NADPH, and via the MEP pathway, requiring glyceraldehyde phosphate and pyruvate, of which P is a constituent. Photosynthesis provides ATP and carbon substrate (glyceraldehyde-3-phosphate or pyruvate) for isoprene synthesis. Increased foliar biomass in AM plants results in greater photosynthetic capacity and thus increased production of total photosynthates required for terpenoid biosynthesis (Niinemets *et al.*, 2002; Cao *et al.*, 2008; Hofmeyer *et al.*, 2010). However, P nutrition alone fails to explain terpenoid accumulation in AM fungus-colonized plants (Copetta *et al.*, 2006; Khaosaad *et al.*, 2006; Rydlová *et al.*, 2016). This is not unanticipated, assuming that the biosynthesis of isoprene precursors is regulated by complex

mechanisms, some of them independent of P nutrition (Kirby and Keasling, 2009; Vranova et al., 2012; Kumari et al., 2013).

The enzyme 1-deoxy-D-xylulose 5-phosphate synthase (DXS) catalyses the rate-limiting step of the MEP pathway. Walter et al. (2000) first demonstrated fungal-induced upregulation of DXS and DXR (1-deoxy-D-xylulose 5-phosphate reductoisomerase) transcript levels in AM-colonized roots of various cereals. This was followed by a series of reports on the upregulation of DXS transcripts in mycorrhizal roots of various plants (Hans et al., 2004; Strack and Fester, 2006; Floß et al., 2008). Transcription of genes encoding DXS and DXR enzymes is upregulated by AM symbiosis and correlated with quantitative terpenoid concentration in leaves (Mandal et al., 2015a). This increase in transcription and terpenoid content has been ascribed to an increased concentration of the phytohormone jasmonic acid (Mandal et al., 2015a; Nair et al., 2015) and/or improved mineral nutrient availability (Mandal et al., 2015a), and may therefore be influenced by both nutritional and non-nutritional mechanisms (Mandal et al., 2013). Results obtained so far suggest that the AM fungal-mediated increase in concentrations of terpenoids is due to enhanced production of IPP/DMAPP derived from the MEP pathway (Mandal et al., 2015a). There were have been no reports of AM-mediated changes in the MVA pathway in the literature until recently, when Venkateshwaran et al. (2015) reported that mevalonic acid is crucial for the transduction of symbiotic signals produced by AM fungi to induce symbiotic gene expression in plants.

Arbuscular mycorrhiza influences the concentration of specific terpenoids and their derivatives in plants by upregulating the transcription of downstream genes of the dedicated biosynthesis pathway (Mandal et al., 2015a, b). Induction of TPS family genes *TPS31*, *TPS32* and *TPS33* in mycorrhizal tomato (Zouari et al., 2014) further suggests a probable mechanism underlying the change in terpenoid profile observed in AM plants.

Glandular trichomes are one of the most common secretory structures that produce and accumulate terpenoids in plants (Karban and Baldwin, 1997; Van Schie et al., 2007; Kang et al., 2010; Schilmiller et al., 2010). A direct relation between augmented concentration of terpenoids and glandular trichome density has been observed in a number of plants (Ringer et al., 2005; Bartram et al., 2006; Behnam et al., 2006; Muñoz-Bertomeu et al., 2006). Correspondingly, an increase in trichome density upon colonization by AM fungi has often been proposed to augment concentration of terpenoids (Copetta et al., 2006; Kapoor et al., 2007; Morone-Fortunato and Avato, 2008). It was demonstrated in *Artemisia annua* that AM enhances glandular trichomes by inducing the transcription of *TTG1* (transparent testa glabra 1), a transcription factor that acts at the top of the regulatory hierarchy of trichome development (Mandal et al., 2015a). However, continued studies are required to elucidate the mechanisms of enhanced production of glandular trichomes and further ascertain the role of phytohormones in AM plants.

## CONCLUSIONS AND FUTURE PROSPECTS

The volatile nature of terpenoids confers the ability to act as efficient signalling molecules. Potential deployment in pest management practices in agriculture depends upon the efficient

control of emission (augmenting or repressing) in plants (Vickers et al., 2014). Genetic manipulation of plants for terpenoid emission is a promising method to alter tritrophic interactions. In recent years, transgenic plants producing terpenoids have been used to repel herbivores (Aharoni et al., 2003), deter oviposition (McCallum et al., 2011) and attract predators (Bouwmeester et al., 2003; Kappers et al., 2005; Beale et al., 2006) and parasitoids (Schnee et al., 2006). The physiological cost of terpenoid production has been assumed to be minor, given their low molecular weight and the relatively low concentrations emitted (Dicke and Sabelis, 1990; Halitschke et al., 2000). On the other hand, a number of studies have demonstrated that constitutive transgenic production of terpenes can result in negative physiological effects on the plant (Aharoni et al., 2003; Robert et al., 2013). These effects may be manifested as stunted growth, reduced reproductive yield and also enhanced conspicuousness and attractiveness of plants to pests (Robert et al., 2013). Furthermore, constitutive emission of HIPVs by transgenic plants would render these emissions unreliable as cues for natural enemies that might waste hunting time in prey-free environments (Gish et al., 2015). Therefore, synchronized engineering strategies that consider herbivore-induced emissions are required to circumvent these cost effects. Further studies are required to evaluate the physiological and ecological costs of terpenoid manipulation in the field to determine the future of this approach for environmental pest management strategies (Robert et al., 2013).

Engineering of tritrophic interactions to successfully protect crop species requires consideration of a number of aspects (Bouwmeester et al., 2003; Degenhardt et al., 2003). For example, identification of an appropriate carnivore species for effective control of herbivore populations is required – one that is naturally present in the cultivation area and attracted by manipulating a known terpenoid (Vickers et al., 2014). Engineered emissions, however, should not attract other herbivores. The overall benefit of manipulated terpenoid emissions can be significantly enhanced by making the release inducible, by inserting a herbivore-inducible tissue-specific promoter with the terpene synthase gene (Degenhardt et al., 2009). Such controlled release would prevent the attraction of herbivores by healthy plants and would lead to recruitment of natural enemies only when the plant is attacked by herbivores (Robert et al., 2013). The lack of understanding of mechanisms by which plants recognize and respond to olfactory cues restricts the prospects for the utilization of terpenoids in crop plants. The highly simplified community structure of large-scale agricultural plantings is another challenge for the effective application of HIPVs, as natural enemy attraction may be ineffective in controlling pests in the core regions of large agricultural fields (Gish et al., 2015).

Alteration of the terpenoid profile in AM plants appears to be one of the important mechanisms for augmented defence against herbivorous insects. Different AM fungal species have variable effects on terpenoid blends (Kapoor et al., 2002b; Sailo and Bagyaraj, 2005; Arpana et al., 2008), and consequently likely differentially influence plant–herbivore and higher trophic level interactions. In this context, comparative studies using different AM fungal species are warranted, to enable differentiation of universal from species-specific responses, and also to identify those AM fungal species efficient

in defence against specific herbivores. As the efficiency of AM symbiosis may be limited by nutrient availability in agricultural fields, comprehensive studies are also required to evaluate the relevance of AM symbiosis to herbivore defence under different nutrient regimes.

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