

Research review

Microbe-induced plant volatiles

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Summary

Plants emit a plethora of volatile organic compounds in response to biotic and abiotic stresses. These compounds act as infochemicals for ecological communication in the phytobiome. This study reviews the role of microbe-induced plant volatiles (MIPVs) in plant–microbe interactions. MIPVs are affected by the taxonomic position of the microbe, the identity of the plant and the type of interaction. Plants also emit exclusive blends of volatiles in response to nonhost and host interactions, as well as to beneficial microbes and necrotrophic/biotrophic pathogens. These MIPVs directly inhibit pathogen growth and indirectly promote resistance/susceptibility to subsequent plant pathogen attack. Viruses and phloem-limiting bacteria modify plant volatiles to attract insect vectors. Susceptible plants can respond to MIPVs from resistant plants and become resistant. Recent advances in our understanding of the molecular mechanisms of MIPV synthesis in plants and how plant pathogen effectors manipulate their biosynthesis are discussed. This knowledge will help broaden our understanding of plant–microbe interactions and should facilitate the development of new emerging techniques for sustainable plant disease management.

Introduction

Plants belong to an ecological network and are under attack from insect pests and microbial pathogens from a vast array of taxonomic groups. Plants must have rapid and precise ways to recognize their attackers and launch a proper response. Upon direct contact, plants recognize their invaders through their molecular characteristics, such as herbivore-associated molecular patterns (HAMPs), pathogen-associated molecular patterns (PAMPs) and danger-associated molecular patterns (DAMPs) (Barrett & Heil, 2012). Plants detect these patterns as nonself or damaged-self and mount a first layer of immunity called pattern-triggered immunity (PTI). Adapted invaders acquire effector proteins to suppress the PTI. Resistance (R) genes, as a second layer of the immune system, detect effectors and mount a robust defense called effector-triggered immunity (ETI). A network of signaling pathways allows plants to respond appropriately to biotic threats (Heil & Land, 2014; Tsuda & Somssich, 2015). In addition, plants obtain information about their invaders even before direct contact using volatiles as infochemicals (Baldwin *et al.*, 2006; Quintana-Rodriguez *et al.*,

2015). Volatiles symbolize the chemical language of plants, which they use to communicate with other plants and even other members of the phytobiome, such as insects, nematodes and microbes (bacteria, fungi and viruses) (Ali *et al.*, 2012; Pangesti *et al.*, 2016; Simpraga *et al.*, 2016).

In the early 20th century, herbivorous and parasitic insects were found to locate their hosts using plant volatiles. Several plant volatiles, such as α -pinene and isothiocyanate, serve as cues for insect attraction (Elzen *et al.*, 1983). Researchers later found that injured plants emit specific and *de novo* blends of volatiles that are received by neighboring plants or distant parts of the same plant (Baldwin & Schultz, 1983; Frost *et al.*, 2007). These volatiles include green leaf volatiles (GLVs; C6 fatty acid derivatives from the oxylipin pathway), isoprenoids (terpenes) from the mevalonate or methylerythritol phosphate pathways, and metabolites from the shikimic acid pathway, such as methyl salicylate (MeSA) and indole (Simpraga *et al.*, 2016). These compounds were initially known as herbivore-induced plant volatiles (HIPVs) because plants release them immediately after attack by chewing or sucking insects. Plants also emit the same classes of volatiles after pathogen challenge (Quintana-Rodriguez *et al.*, 2015), and, surprisingly, after inoculation with mutualistic microbes such as rhizobia, mycorrhiza and

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plant growth-promoting rhizobacteria (PGPR) (Schausberger *et al.*, 2012; Ballhorn *et al.*, 2013). These volatiles, referred to here as 'microbe-induced plant volatiles (MIPVs)', are the main focus of this review.

Microbe-induced plant volatiles

Airborne counterattack against microbial pathogen attack

Plants emit airborne signals in response to microbial infection, and these play essential roles in both local and systemic plant defense (Kishimoto *et al.*, 2006; Frost *et al.*, 2007). Volatiles are key final components of the salicylic acid (SA), jasmonic acid (JA), and ethylene signaling pathways. Gaseous ethylene, Me-JA, Me-SA and indole also play critical roles in defense (Bailly *et al.*, 2014; Matsui, 2016). Plants release numerous volatiles into the air and soil (Penuelas *et al.*, 2014). Some act as airborne plant defense signals and some make the plant more attractive and susceptible to insect pests and pathogens. This part of the review describes the MIPVs emitted according to the taxonomic position of the pathogen and the type of interaction with the plant.

Cucumber mosaic virus and Barley yellow dwarf luteovirus (virus)-induced plant volatiles

Phloem-limited viruses require vectors to spread between plants. These viruses actively govern the host localization behavior of their vectors by stimulating their olfactory systems. Virus-containing aphids (*Rhopalosiphum padi*) prefer healthy plants (Ingwell *et al.*, 2012), whereas virus-free aphids prefer virus-infected plants, thereby resulting in higher new virus uptake. These viruses modify the volatiles of their host plants to improve their transmission (Fig. 1a). Nonpersistently transmitted viruses can be uptaken rapidly without the need for vector settlement, but persistent (circulative) viruses need long feeding periods to be up taken by vectors. Cucumber mosaic virus (CMV), a nonpersistent virus, elevated the overall emission of volatiles in *Cucurbita pepo* (Mauck *et al.*, 2010). The host plant was more attractive but less palatable to virus vectors, *Myzus persicae* and *Aphis gossypii*. This increased the transmission rate of the virus. Subsequently, it was shown that CMV effector protein 2b is responsible for changing the profile of volatiles. It reduced the amounts of the pollinator repellents 2-carene and β -phellandrene in tomato (Groen *et al.*, 2016). This effector protein also modified the quantity and composition of the volatiles in tobacco (Tungadi *et al.*, 2017). However, it did not change the attraction of *M. persicae* as a virus vector, but increased its feeding time on plant. By contrast, protein 2b increased immigration of *M. persicae* to infected *Arabidopsis* plants, but decreased its settling on virus-infected plants (Wu *et al.*, 2017). Groen *et al.* (2017) proposed that nonpersistent virus has two transmission types in different plant hosts. In type 1, the vector moves rapidly between plants, whereas in type 2, it maintains the population by extending feeding on phloem. So, MIPVs play different roles in CMV transmission based on the host plant species. In persistent viruses, MIPVs increase vector settling on virus-infected plants. Barley yellow dwarf luteovirus (BYDV)

increased the quantity of volatiles, especially (Z)-3-hexenyl acetate, in wheat (Jiménez-Martínez *et al.*, 2004). *R. padi* settle highly on virus-infected plants. *M. persicae* colonize Potato leafroll virus (PLRV)-infected potato plants more than Potato virus X (PVX), Potato virus Y (PVY) and control plants. Volatile profile analysis showed that PLRV-infected potato plants emitted six volatiles differently (Eigenbrode *et al.*, 2002).

Pseudomonas syringae (bacteria)-induced plant volatiles

Bacteria and their elicitors induce volatile emissions in plants, which is completely dependent on the virulence status of the pathogen (Fig. 1a). Inoculation of tobacco with avirulent *P. syringae* pv. *tomato* DC3000 and *P. syringae* pv. *maculicola* ES4326 increased SA accumulation within 6 h in tobacco (Huang *et al.*, 2003). Volatile emissions peaked at 36 h, with MeSA, MeJA and sesquiterpenes representing the main volatiles produced in response to these avirulent strains. By contrast, treatment of tobacco with virulent *P. syringae* pv. *tabaci* did not induce early and strong SA production and the same volatile emissions peaked at 60 h post-inoculation (hpi). In another study, inoculation with an avirulent strain of *P. syringae* pv. *maculicola* increased MeSA emissions, whereas a virulent strain induced the emission of two terpenes, β -ionone and α -farnesene, in *Arabidopsis* (Attaran *et al.*, 2008). The terpene trimethyl tridecatetraene was prevalent in volatile blends induced by the two strains (Attaran *et al.*, 2008). Thus, the MIPV profile can give information about the type of plant-microbe interaction.

MIPVs play a critical role in establishment of pathogenic bacteria and host susceptibility. Inoculating common bean with *P. syringae* pv. *phaseolicola* induced the emission of (E)-2-hexenal and cis-3-hexenol at 15–24 hpi (Croft *et al.*, 1993). (E)-2-hexenal was bactericidal at concentrations > 16.5 nl per agar plug, and even low concentrations led to bacterial cell lysis. In contrast to common bean, GLV emissions make *Arabidopsis* more susceptible to *P. syringae* pv. *tomato*. In the GLV *Arabidopsis* hydroperoxide lyase mutant, which has impaired GLV production, the *P. syringae* population was reduced 4.6-fold and JA levels were 3-fold lower than in the wild type, whereas SA levels were elevated. Pretreatment with 3 μ M (E)-2-hexenal increased the susceptibility of *Arabidopsis* to the bacteria, whose population increased > 5-fold (Scala *et al.*, 2013).

Puccinia striiformis and *Colletotrichum lindemuthianum* (fungi)-induced plant volatiles

Plants also produce a blend of volatiles in response to pathogenic fungi. The production of volatiles is dependent on the susceptibility of the plant to a given pathogen. Resistant wheat inoculated with stripe rust emits diverse volatiles, mainly sesquiterpenes such as β -ocimene (Castelyn *et al.*, 2015). In susceptible wheat, oxylipin derivatives are predominant in the volatile profile. These two cultivars are near isogenic, suggesting that plant volatiles are regulated by a single R gene in resistant plants. Interestingly, the exposure of a susceptible cultivar to volatiles from a resistant cultivar significantly reduced disease severity in wheat (Castelyn

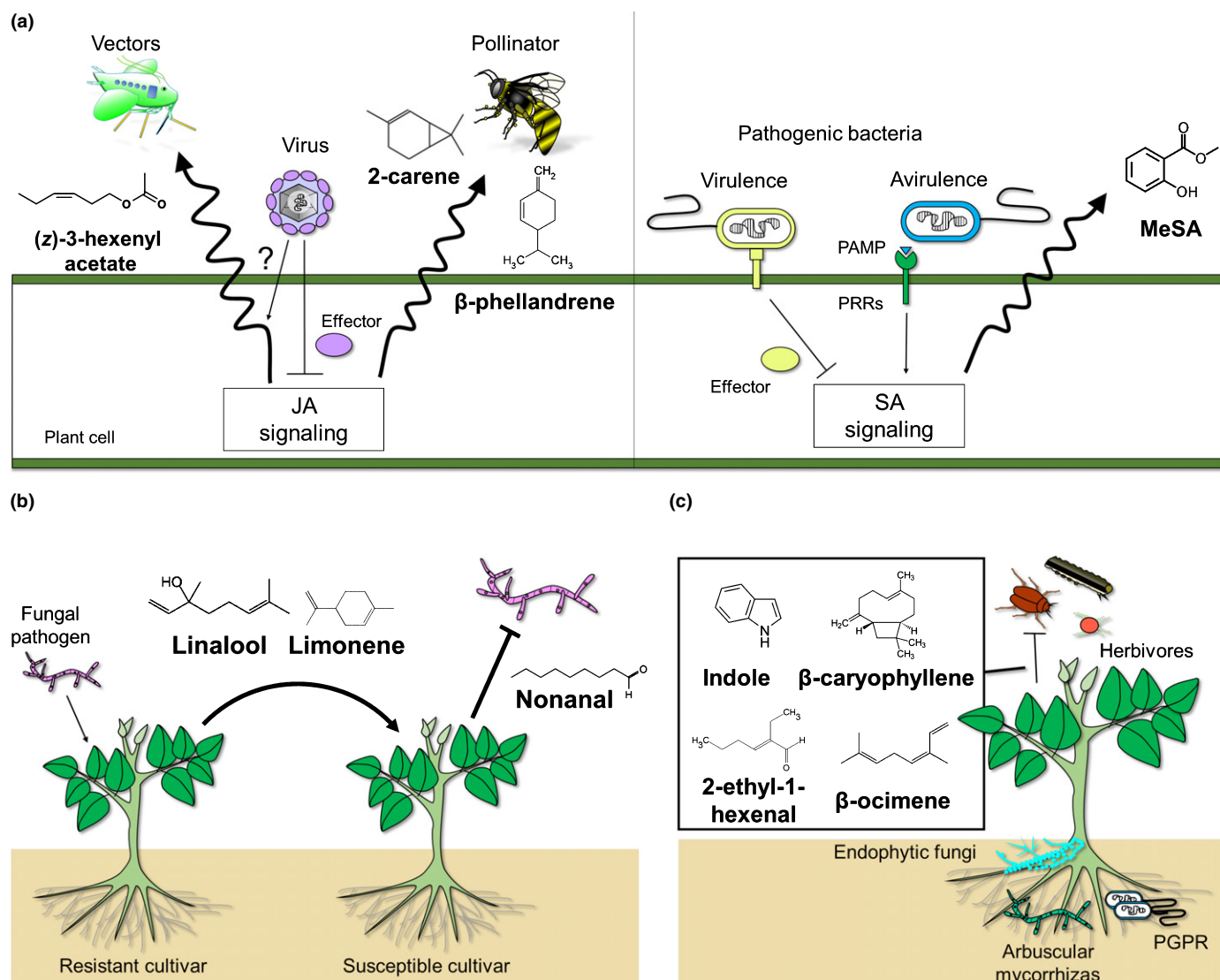


Fig. 1 Microbe-induced plant volatile act as infochemicals in plant communication with other members of the phytobiome. (a) Pathogenic microbes directly or indirectly affect the host plant to elicit the emission of plant volatiles. A virus effector protein such as *Cucumber mosaic virus* (CMV) 2b suppresses jasmonic acid (JA) signaling in the host plant to attract its vector. CMV-infected tomato plants emit reduced amounts of pollinator repellents 2-carene and β-phellandrene. *Barley yellow dwarf luteovirus* infection in wheat increased a plant volatile (Z)-3-hexenyl acetate to recruit its vector insect. Bacterial pathogens can induce volatile emissions depending on the virulent states of the pathogens. Virulent strains suppress salicylic acid (SA) signaling and volatile production by injecting effector proteins into the cytosol. However, the pathogen-associated molecular pattern (PAMP) of avirulent strains is recognized by pattern recognition receptors (PRRs), which increase SA signaling and the production of methyl salicylate (MeSA) to activate plant defense. (b) The production of volatiles depends on the susceptibility of the plant to fungal pathogens. Limonene and linalool are dominant in resistant cultivars and nonanal is dominant in susceptible cultivars. Susceptible cultivars exposed to volatiles from resistant cultivars suppress fungal disease. (c) Beneficial microbes also induce plant volatile emissions, thereby suppressing insect herbivory. Treatment with plant growth-promoting rhizobacteria (PGPR) induces the production of volatiles such as indole and β-caryophyllene that affect defense responses. Symbiotic fungi, including endophytic fungi and arbuscular mycorrhizas (AM), can modulate volatile emissions from the host in response to insect pests. The colonization of endophytic fungi can alter volatile emissions such as 2-ethyl-1-hexenal. AM-treated plants release a blend of volatiles, including β-ocimene, in response to insect pests.

et al., 2015) and lima bean (Quintana-Rodriguez *et al.*, 2015). The molecular response of a susceptible lima bean cultivar to an anthracnose-causing fungus *C. lindemuthianum* became similar to that of a resistant cultivar exposed to MIPVs from inoculated resistant plants or Benzothiadiazole (BTH)-treated plants (Fig. 1b). Exposure to volatiles from a resistant cultivar can prime the expression of defense-related genes *PR1*, *PR2* and *PR4* in the susceptible cultivar. Limonene, linalool, β-ocimene and farnesene

are dominant in the resistant cultivar, whereas susceptible plants mainly release aldehydes, such as nonanal and decanal.

In addition to their signaling role, plants use MIPV compounds as natural antibiotics at sites of wounding. These volatiles directly inhibit fungal growth, spore germination and spore production, with C9 oxylipins exhibiting strong antifungal activity at natural concentrations. C9 aldehydes inhibit *Fusarium oxysporum* and *Botrytis cinerea* growth in *Arabidopsis* (Matsui *et al.*, 2006). Most

oxylipins have inhibitory actions against plant pathogenic fungi and oomycetes (Prost *et al.*, 2005). Of the 43 oxylipins (at 100 μ M) investigated against 13 plant pathogens, 26 had inhibitory activity against at least three pathogens. Terpenes also have fungicidal activity. Pontin *et al.* (2015) reported that, among eight microbially induced terpenes from garlic, nerolidol and terpinolene had negative effects on mycelial growth and on sclerotia production in *Sclerotium cepivorum*.

Airborne plant reactions due to beneficial microbes

Plant defense priming by soil bacteria

Plant growth-promoting rhizobacteria improve plant growth and health by providing nutrients or modulating phytohormone production or signaling (Sharifi & Ryu, 2017). They can also induce direct and indirect defense responses against plant insect pests by modifying the plant volatile profile (Fig. 1c). Ballhorn *et al.* (2013) reported that rhizobia + JA treatment reduced the total volume of volatile emissions but increased the production of the shikimic acid derivative indole. Indole was the only nitrogen-containing volatile induced by rhizobia in their experiment. It plays important roles in bacterial pathogenesis and plant growth and health (Baillly *et al.*, 2014; Lee *et al.*, 2015). It primes defense responses against herbivores by increasing terpenes and JA-isoleucine biosynthesis in systemic leaves. An indole mutant plant is more attractive to *Spodoptera littoralis* caterpillars than the wild type, and adults prefer this mutant for oviposition (Veyrat *et al.*, 2016). *Pseudomonas simiae* WCS417r primes the ORA59 branch of the JA/ethylene signaling pathway in response to leaf chewing by *Mamestra brassicae* (Pangesti *et al.*, 2016). Pretreatment with *P. simiae* WCS417r increases the attractiveness of plants to the parasitoid *Microplitis mediator* and significantly reduces the release of MeSA, (*E*)- α -bergamotene and linal (Pangesti *et al.*, 2015). *Pseudomonas putida* KT2440 alters the expression of several genes and metabolic pathways to increase defense against plant pathogens, including key genes in oxylipin volatiles and JA biosynthesis, acting in direct and indirect defense responses to different pests and pathogens (Planchamp *et al.*, 2014). Strain KT2440 also induces the production of two key volatiles in plant defense, indole and β -caryophyllene (Planchamp *et al.*, 2014).

Symbiotic fungi help plants avoid pests

Plants have a mutual relationship with highly specialized endophytic fungi such as *Neotyphodium* (Teleomorph: *Epichloë*) and mycorrhizas, and unspecialized endophyte genera such as *Colletotrichum*, *Acremonium* and *Fusarium*. *Neotyphodium* can modulate host volatile emissions in response to insect pests (Fig. 1c). African black beetles prefer perennial ryegrass free of endophytic fungi (Qawasmeh *et al.*, 2015). However, different *Neotyphodium* strains have different effects on plant volatiles. The volatile 2-ethyl-1-hexenal is prevalent in plants treated with effective strains of this fungus. Above-ground endophyte colonization can also alter volatile emissions in below-ground plant parts (Rostás *et al.*, 2015). The root herbivore *Costelytra zealandica*

prefers endophyte-free hybrids of *Festuca* (by up to 90%). Endophyte-infected plants released 22% less of total volatiles than noninfected plants. It appears that lower volatile emission make these plants less detectable by herbivores compared with endophyte-free plants. Pretreatment of *Vicia faba* with arbuscular mycorrhizas (AM) diminishes release of sesquiterpenes (Babikova *et al.*, 2014). β -Farnesene and (*E*)-caryophyllene concentrations are notably reduced in AM-inoculated plants, making them more attractive to aphids. However, pretreatment with aphids reduces root colonization by AM. Root colonization with AM primes indirect defense responses to the mite *Tetranychus urticae* in *Arabidopsis* (Schausberger *et al.*, 2012). AM-treated plants release *de novo* β -ocimene, β -caryophyllen and MeSA after mite challenge. Unspecialized endophytes also modify volatile emission by regulating defense signaling pathways (Navarro-Meléndez & Heil, 2014).

Microbe-induced signaling cascades conciliate plant volatile synthesis

JA is the main hormone that regulates volatile biosynthesis in plants (Arimura & Pearce, 2017). Therefore, invaders use several strategies to control JA signaling and subsequent volatile emissions in plants (Krumm *et al.*, 1995; Wu *et al.*, 2017). JASMONATE ZIM DOMAIN (JAZ) is a key target of microbes in their effort to induce or suppress JA-dependent volatile biosynthesis. JAZ represses JA-dependent genes, but JA activation by external stimuli causes JAZ to be degraded by the 26S proteasome (Wasternack & Hause, 2013). The degradation of JAZ releases JA-dependent transcription factors from JA-dependent genes such as volatile synthase genes, allowing them to be expressed (Taniguchi *et al.*, 2014b; Wu *et al.*, 2017). Some pathogens actively target JAZ to modify plant volatile emissions. CMV produces 2b effector protein, which alters plant volatile emissions (Wu *et al.*, 2017). Effector protein 2b interacts physically with several members of the JAZ family, including JAZ1, which represses JA signaling in *Arabidopsis*. This effector protein competes with COI1 for the same binding domain on JAZ1 and inhibits the degradation of JAZ1 by the COI1-dependent 26S proteasome pathway, thereby suppressing JA signaling (Fig. 2). By contrast, *P. syringae* activates JA signaling by secreting the polyketide toxin coronatine (Wasternack & Hause, 2013), which acts as a glue for the physical interaction of JAZ with the F-box domain of COI1 in the 26S proteasome pathway (Fig. 2). JAZ degradation activates JA-dependent genes and induces the emission of plant volatiles. Coronatine treatment increases GLVs, terpene and MeJA emissions (Krumm *et al.*, 1995). Furthermore, biotrophic pathogens can suppress the JA pathway via activation of SA signaling. The SA pathway suppresses the JA pathway via the nonexpressor of PR1 (NPR1) (Sharifi & Ryu, 2017). Treatment of black poplar with the biotrophic fungus *Melampsora laricipopulina* or MeSA increased SA but decreased MeJA biosynthesis (Eberl *et al.*, 2018). The pretreated trees released lower levels of GLVs and sesquiterpens after caterpillar attack and were more attractive to caterpillars.

PAMPs act as elicitors that alter MIPV emissions; the bacterial flagellin peptide flg22 is a well-characterized PAMP of bacteria.

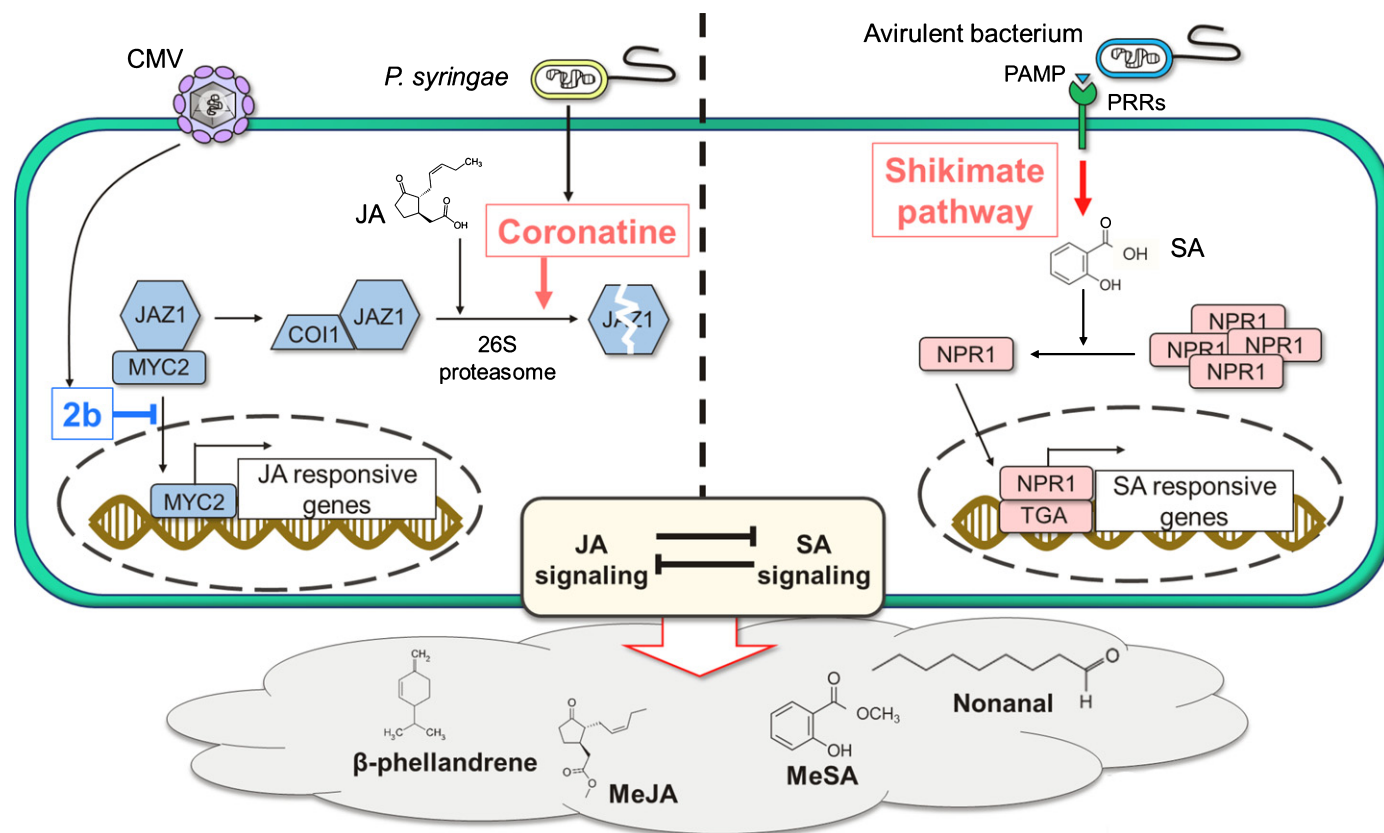


Fig. 2 Molecular mechanism via which microbes modulate volatile emissions. *Cucumber mosaic virus* (CMV), *Pseudomonas syringae* and bacterial pathogen-associated molecular pattern (PAMP) induce the production of plant volatiles such as β -caryophyllene, methyl jasmonate (MeJA) methyl salicylate (MeSA) and nonanal. Microbe-induced plant volatile (MIPV) emission is modulated through jasmonic acid (JA) – salicylic acid (SA) signaling antagonistic crosstalk. The 2b effector of CMV and coronatine toxin of *P. syringae* modulate JA signaling by promoting or suppressing COI1-dependent degradation of JASMONATE ZIM-DOMAIN (JAZ) through the 26S proteasome. JAZ protein has a negative effect on JA signaling by inhibiting the MYC2 transcription factor and, subsequently, JA-dependent volatile emissions. Moreover, a PAMP derived from avirulent bacteria is recognized by the pattern recognition receptor (PRR) and activates the biosynthesis of SA via the shikimate pathway. Accumulation of SA results in the monomerization of nonexpressor of pathogenesis-related gene 1 (NPR1). The translocation of monomeric NPR1 to the nucleus activates SA responsive genes via the TGA transcription factor.

flg22 was shown to induce H_2O_2 accumulation after 5 min, thereby increasing the production of free fatty acids, which in turn act as substrates for oxylipin volatile production. Plant volatile nonanal levels are 20-fold higher in flg22-treated plants (Tu *et al.*, 2017). Sulfated laminarin also increases the emission of terpenes and MeSA but reduces MeJA and (*Z*)-3-hexenyl acetate in grapevine emissions, which results in resistance to *Plasmopara viticola* (Chalal *et al.*, 2015). In addition to PAMPs, several chemical compounds, for example BTH, nonanal and JA, induce systemic plant defense responses by altering plant volatile emissions. JA treatment induces the release of β -ocimene, linalool, indole and MeJA in *Arabidopsis* (Yi *et al.*, 2009) and β -elemene, β -bisabolene, linalool and (*Z*)-3-hexenol in rice (Taniguchi *et al.*, 2014b). These volatiles suppress the pathogens *Magnaporthe oryzae* and *Xanthomonas oryzae* in rice. Nonanal reduces the *P. syringae* population by inducing the JA signaling pathway (Yi *et al.*, 2009). Several inducers, such as BTH and Me-SA, repress the JA pathway by eliciting the SA signaling pathway through antagonistic signaling crosstalk (Fig. 2). BTH induces the emission of 2-ethylhexanol, nonanal and MeSA in *Arabidopsis* (Yi *et al.*, 2009).

Applications of MIPVs: airborne protection via MIPVs

Volatiles can act as airborne signals in plant–plant interactions at a distance of < 1 m or as below-ground signals at a distance of 15–30 cm (Simpraga *et al.*, 2016; Arimura & Pearce, 2017). These observations could be used to develop management strategies for plant pests and diseases by intercropping and cultivar mixing. Volatiles from plants inoculated by virulent or avirulent pathogens confer immunity to neighboring susceptible cultivars (Huang *et al.*, 2003; Yi *et al.*, 2009; Castelyn *et al.*, 2015; Quintana-Rodriguez *et al.*, 2015). However, the use of pathogens to elicit MIPV emissions is limited due to their potential effects on susceptible plant species around the target plant.

Three possible methods were suggested for eliciting MIPVs as plant protectant compounds (Fig. 3a). (1) Instead of using virulent pathogens, their PAMPs could be used to modulate plant volatile emissions. PAMPs such as flg22 (Tu *et al.*, 2017), glucan (Leitner *et al.*, 2008) and laminarin (Chalal *et al.*, 2015) induce the emission of plant volatiles in various plants (Fig. 3a). (2) Plant volatile emission could be induced by chemical compounds and even specific volatiles. Treatment with nonanal and (*E*)-2-hexenal

activated defense pathways and induced volatile emissions in several plants (Kishimoto *et al.*, 2006; Yi *et al.*, 2009; Scala *et al.*, 2013). Yi *et al.* (2009) found that field application of nonanal induced the emission of specific blends of volatiles, which primed effective defense mechanisms in neighboring plants. (3) MIPVs could be directly applied to control pathogens, insect pests and pathogenic nematodes (Fig. 3a). (*E*)-2 hexenal was successfully used as a fumigant nematicide under field conditions to control *Meloidogyne incognita* in tomato (Lu *et al.*, 2017). The optimum dose was 500 l ha⁻¹. The effect of this volatile was the same as that of 400 kg ha⁻¹ of the commercial soil fumigant Dazomet (Basamid®). The yields of plants treated with this plant volatile were 20% higher than those of the untreated control (Lu *et al.*, 2017).

MIPVs have great potential for use in plant biotic stress management. However, the nature of these compounds makes them sensitive to evaporation or to reaction with other compounds, making it necessary to develop effective formulations for commercial use. Recently, new technologies were reviewed for formulating volatiles as natural pesticides (R. Sharifi and C.-M. Ryu, unpublished). Briefly, volatiles could be encapsulated in biodegradable biopolymer shells to allow the slow release of volatiles over several days. These formulations could be applied with a conventional sprayer or seeder in the farm or glasshouse (Fig. 3b). Since the best time to apply priming agents is at sowing, seed priming using the proper MIPVs should be considered.

Future perspective

Plants release distinct sets of volatiles depending on the nature of the interactions in the phytobiome, such as with insects and

microbes. Despite the similarity of the emitted compounds, the quality of the blend, concentration of individual volatiles and emission time for their release are probably microbe-specific (Portillo-Estrada *et al.*, 2015; Jiang *et al.*, 2016). The type of plant–microbe interaction appears to determine the MIPV profile, but there is not yet any clear view on the microbe specificity of MIPVs. More studies should be performed using plants and microbes from different taxonomic groups to determine the role of MIPVs in ecological communication in the phytobiome. Comparing microbes with similar lifestyles, such as those that colonize nonhosts, avirulent microbes, necrotrophs and biotrophs, will provide a clearer view on the effects of interaction type on MIPVs. Meta-analyses, such as that of Rowen & Kaplan (2016), could help interpret this growing body of information, including how many volatiles show specificity for different types of interactions. Furthermore, few studies have focused on the molecular mechanisms by which microbes mediate plant volatile emissions. Although plant volatiles belong to different metabolic pathways, they appear to be regulated by major signaling pathways such as those of SA and JA (Taniguchi *et al.*, 2014a,b; Eberl *et al.*, 2018). The effects of elicitors and effectors that induce or suppress plant defense pathways upon MIPV emission should be investigated in more detail. Plant receptors and R genes also play a significant role in MIPV emissions. In wheat and rust fungi, a single R gene is responsible for modulating plant volatiles (Castelyn *et al.*, 2015), but the molecular mechanism is not fully understood. Additional analysis should uncover how R genes activate downstream pathways for volatile emissions.

More attention should be paid to MIPVs in breeding programs for new cultivar development. Meta-analysis has revealed that

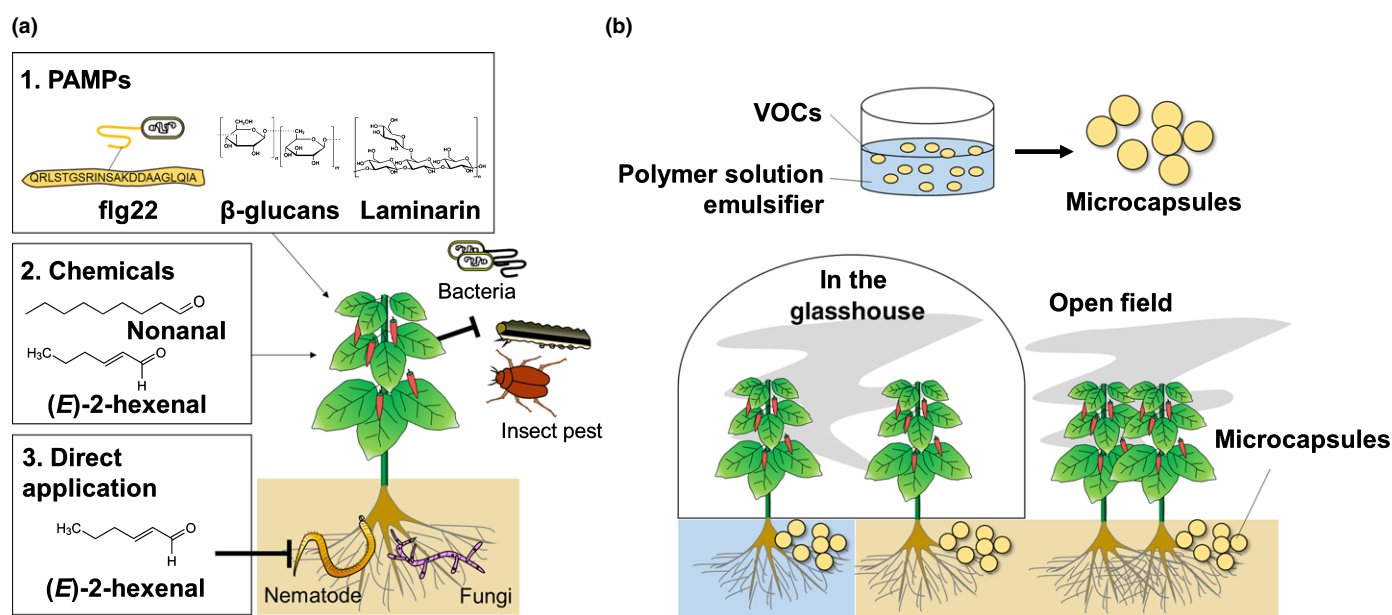


Fig. 3 Practical applications of microbe-induced plant volatiles (MIPVs). (a) Three possible methods for MIPV-mediated plant protection. (1) Elicitation of MIPV emission by pathogen-associated molecular patterns (PAMPs) such as flg22, β-glucan and laminarin could lead to the emission of plant volatiles in the field. (2) Elicitation of MIPV emissions by other plant volatiles such as nonanal and (*E*)-2-hexenal. (3) Direct application of an MIPV such as (*E*)-2-hexenal to control pathogens, insect pests and pathogenic nematodes. (b) For open field and glasshouse application of volatiles, MIPVs and volatile organic compounds (VOCs) can be encapsulated in a biodegradable biopolymer (polymer solution and emulsifier) for the generation of microcapsules.

cultivated crops have less complex inducible volatiles than their wild ancestors (Rowen & Kaplan, 2016), indicating that breeding has a negative impact on the ecological competence of plants. For instance, *Poncirus trifoliata* constitutively produces volatiles that attract entomopathogenic nematodes, but the hybrid crop, *Swingle citrumelo*, has lost this ability (Ali *et al.*, 2011). Similarly, North American maize lines have lost genes for β -caryophyllene synthase, which is responsible for attracting natural enemies of the root-feeding pest *Diabrotica virgifera* (Köllner *et al.*, 2008). Therefore, breeders should not only measure induced volatiles in new lines, but should also consider introducing lost volatile genes as part of rewinding programs.

The same volatiles could unexpectedly confer susceptibility against other pathogens; for example, (*E*)-2-hexenal suppresses root knot nematode infection in the field but induces susceptibility to *P. syringae* (Scala *et al.*, 2013). However, a very high concentration of (*E*)-2-hexenal is needed to observe nematocidal activity (Lu *et al.*, 2017). Furthermore, (*E*)-2-hexenal activates the JA pathway in *Arabidopsis*, which improves resistance against the necrotrophic pathogen *Botrytis cinerea* but promotes susceptibility to *P. syringae* pv. *tomato* (Kishimoto *et al.*, 2006; Scala *et al.*, 2013). In addition, methanol induces resistance against *Ralstonia solanacearum*, but increases susceptibility to *Tobacco mosaic virus* (TMV), as it facilitates cell-to-cell movement of virus particles (Dorokhov *et al.*, 2012). Generally, volatiles should be considered double-edged swords and may have negative effects on nontarget pathogens. Therefore, it is necessary to collect data about their positive and negative effects before applying them in the field.

The idea that volatiles serve as the chemical language of plants was proposed 38 yr ago. Since then, scientists have confirmed this idea and unraveled many of the details. Plants emit odors to other organisms in their niche, and these chemicals are also recognized by other members of the phytobiome, including diverse microbes. The total biomes of plants and microbes were recently recognized as 'holobiomes', which have been co-developing for a long period of time. Volatiles act as a universal language in this interaction (Mithöfer & Boland, 2016; Simpraga *et al.*, 2016). In addition to MIPVs, the adaptation of plant physiological responses to microbial volatiles represents the next important topic to investigate. In-depth studies will help to decode this sophisticated language to make better decisions about crop management.

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