

REVIEW

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Dynamic environmental interactions shaped by vegetative plant volatiles

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Plants shape terrestrial ecosystems through physical and chemical interactions. Plant-derived volatile organic compounds in particular influence the behavior and performance of other organisms. In this review, we discuss how vegetative plant volatiles derived from leaves, stems and roots are produced and released into the environment, how their production and release is modified by abiotic and biotic factors, and how they influence other organisms. Vegetative plant volatiles are derived from different biosynthesis and degradation pathways and are released *via* distinct routes. Both biosynthesis and release are regulated by other organisms as well as abiotic factors. In turn, vegetative plant volatiles modify the physiology and the behavior of a wide range of organisms, from microbes to mammals. Several concepts and frameworks can help to explain and predict the evolution and ecology of vegetative plant volatile emission patterns of specific pathways: multifunctionality of specialized metabolites, chemical communication displays and the information arms race, and volatile physiochemistry. We discuss how these frameworks can be leveraged to understand the evolution and expression patterns of vegetative plant volatiles. The multifaceted roles of vegetative plant volatiles provide fertile grounds to understand ecosystem dynamics and harness their power for sustainable agriculture.

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1. Introduction

Plants shape terrestrial ecosystems by producing and releasing organic chemicals. Chemicals with low boiling points and high vapor pressure can be released as volatiles¹ and mediate interactions with the environment at a distance.^{2,3} Floral volatiles are often constitutively released and can serve as attractants of pollinators and defenses against florivores⁴ but can also mediate interactions with other organisms.^{5,6} Vegetative plant volatiles are often highly inducible by biotic and abiotic

stressors and play important roles in plant interactions with other organisms and the environment.^{2,4,7–9}

Work over the past years has uncovered how vegetative plant volatiles are synthesized and released, how they are modified by their environment, and how they modulate interactions between plants and other organisms.^{10–15} An increasing number of studies have begun to investigate the dynamic patterns that emerge from the multilayered interactions between plants and the biotic and abiotic environment.^{16–18} Understanding the role of vegetative plant volatiles in agroecosystems has become ever more pressing due to climate change, as vegetative volatiles may be used to promote plant resilience in dynamic environments.^{19,20} A robust understanding of the physiological and ecological mechanisms governing volatile-mediated interactions is essential to harness their potential in this context.

Recent reviews have discussed biological functions of vegetative plant volatiles,²¹ the molecular mechanisms of volatile



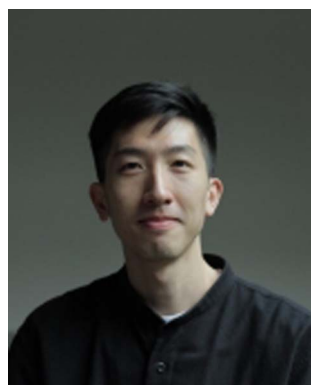
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Dr. Jamie M. Waterman received his PhD from the Hawkesbury Institute for the Environment at Western Sydney University (Australia) in 2021. He is presently an SNSF Swiss Postdoctoral Research Fellow at the Institute of Plant Sciences at the University of Bern (Switzerland). Broadly, his research explores the spatiotemporal, physical and chemical factors that shape interactions between plants and

herbivores; namely, how these factors determine plant defense phenotypes. His current research is focused on identifying how specific spatiotemporal patterns of herbivory influence the kinetics of plant volatile emissions and, consequentially, mediate airborne information transfer between plants.



Dr. Po-An Lin is currently an Assistant Professor in the Department of Entomology at the National Taiwan University. He focuses on understanding how abiotic factors influence the ecology and evolution of plant–herbivore interactions. He is known for his research on stomata-mediated plant–herbivore interactions, water–plant–herbivore interactions, and the role of plant volatiles in these

interactions. He also studies how light, herbivore diel activity patterns, and plant volatile availability influence the evolution of herbivore host range (e.g., the Salient Aroma Hypothesis). He recently received the Asia-Pacific Association of Chemical Ecologists Young Scientist Award due to his contribution to the field.



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Early Career Award of the International Society of Chemical Ecology in 2015. He currently focuses on the role of volatile plant secondary metabolites in plant–environment interactions.



(Fig. 1), all of which are produced *via* distinct biochemical pathways.

Terpenoids comprise over 80 000 known structures.²⁴ They are derived from two five-carbon precursors, the isopentenyl diphosphate (IPP) and its allylic isomer dimethylallyl diphosphate (DMAPP), *via* two independent pathways: the mevalonic acid (MVA) and methylerythritol phosphate (MEP). The MVA pathway gives rise to volatile sesquiterpenes, while the MEP pathway provides precursors to volatile hemiterpenes, monoterpenes and diterpenes. In both pathways, IPP and DMAPP are condensed head-to-tail by short-chain prenyltransferases to form the prenyl diphosphate precursors of various chain lengths, including geranyl diphosphate (GPP, C10), farnesyl diphosphate (FPP, C15), and geranylgeranyl diphosphate (GGPP, C20). These precursors are used as substrates by a family of terpene synthases (TPSs) to generate C5-hemiterpenes, C10-monoterpenoids, C15-sesquiterpenoids, or C20-diterpenoids.^{25,26} Many TPSs can synthesize multiple products from

Plants emit diverse blends of vegetative volatiles. These blends include terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, nitrogen and Sulphur-containing compounds

a single prenyl diphosphate substrate or accept more than one substrate, thus contributing to terpenoid diversity.¹⁰ TPS products can be modified further *via* hydroxylation, dehydrogenation, acylation, or other reactions.^{11,27} For instance, oxidative degradation of the TPS2 products (*E,E*)-geranylinalool and (*E*)-nerolidol by two specific P450 monooxygenases results in the biosynthesis of the acyclic homoterpenes (*E*)-3,8-dimethyl-1,4,7-nonatriene (DMNT) and (*E,E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT).¹¹

Phenylpropanoid and benzenoid compounds are derived from the shikimate pathway. They are defined by their mostly planar and cyclic ring structures with conjugated double bonds and can be classified based on the length of the side chain as phenylpropenes (C6–C3) and benzenoid (C6–C1) compounds.²⁸ The first committed step in their biosynthesis is catalyzed by the *L*-phenylalanine ammonia lyase (PAL) enzyme, which deaminates the aromatic amino acid phenyl alanine to *trans*-cinnamic acid (CA). CA is transformed *via* several enzymatic reactions into *para*-coumaroyl CoA, the general precursor for a wide range of products including anthocyanins, flavonoids, lignin and phenylpropenes. Phenyl propenes are, together with terpenes, major constituents of essential oils, such as methylchavicol or eugenol, which are stored in the trichome glands of basil (*Ocimum basilicum*) leaves.^{29,30} Formation of benzenoids from CA results from the shortening of the propyl side chain by two carbons *via* β -oxidative or non- β -oxidative pathways.²⁸

Plants also release several nitrogen-containing volatiles that are derived from amino acid biosynthesis. Indole, a precursor of tryptophan biosynthesis, is produced and emitted by many plant species upon herbivory.^{31–33} Indole synthesis and emission have been best characterized in maize (*Zea mays*), where 1-(2-carboxyphenylamino)-*D*-deoxyribulose-5-phosphate is first converted into indole-3-glycerolphosphate by specific indole-3-glycerolphosphate synthases, and then into volatile indole by the action of an indole-3-glycerolphosphate lyase.³⁴ Aldoximes and nitriles occur as intermediates in the biosynthesis of several nitrogenous defense compounds such as cyanogenic glycosides, hydroxynitrile glycosides and camalexin. The biosynthesis of these compounds has been well characterized in Western balsam poplar (*Populus trichocarpa*). Volatile aldoximes such as 2- and 3-methylbutyraldoxime, and nitriles such as benzyl cyanide, which are induced upon herbivory, are derived from amino acids by the action of two cytochrome P450 (CYP) monooxygenases of the CYP79 family.³⁵ Nitriles can be produced by two additional P450 enzymes belonging to the CYP71 family, which catalyze the conversion of aldoximes to nitriles.³⁶

Volatile fatty acid derivatives include green leaf volatiles (GLVs), consisting of C6 compounds including alcohols, aldehydes, esters, as well as the phytohormone methyl jasmonate (MeJA). GLVs and jasmonates are produced *via* the lipoxygenase (LOX) pathway, which begins when C18-polyunsaturated fatty acids, linoleic and linolenic acids, are cleaved from cell membranes by lipases and dioxygenated by either 9- or 13-LOXs to form 9- and 13-hydroperoxides, respectively. These hydroperoxides act as substrates in the hydroperoxide lyases (HPLs) and allene oxide synthases (AOSs) pathways to produce GLVs and jasmonic acid (JA), respectively. For GLV biosynthesis, 13-

hydroperoxy octadecatrienoic acid is cleaved by HPL to form (*Z*)-3-hexenal, which is spontaneously or enzymatically converted into other C6 compounds, including (*E*)-2-hexenal, (*Z*)-3-hexenol and (*Z*)-3-hexenyl acetate.³⁷ Biosynthesis of MeJA is synthesized in the peroxisome from a 13-hydroperoxide intermediate *via* sequential reduction and β -oxidation steps, which results in the formation of JA, and it is followed by the methylation of JA by a JA carboxyl methyltransferase.³⁸

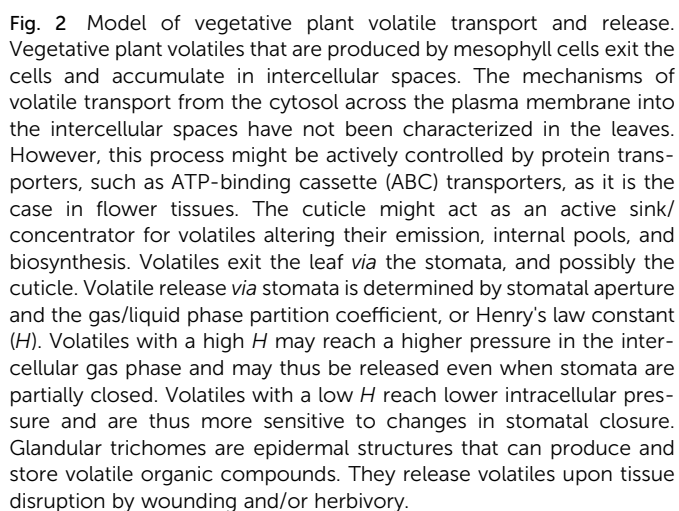
Volatiles can also result from the breakdown of plant secondary metabolites. Isothiocyanates, for instance, are sulfur-containing volatiles that are characteristic of the Brassicaceae and produced by the myrosinase-mediated hydrolysis of glucosinolates.³⁹ Glucosinolates are a structurally diverse group of β -thioglucoside-*N*-hydroxysulfates classified according to their precursor amino acid as aliphatic (from alanine, valine, leucine, isoleucine, or methionine), aromatic (from phenylalanine or tyrosine), or indolic glucosinolate (from tryptophan). Their biosynthesis starts with the modification of the precursor amino acid to form the glucosinolate core. In some instances, side chain elongation or secondary modifications can occur prior to and after core biosynthesis.⁴⁰ Plants producing these compounds also synthesize myrosinases, which are specific β -thioglucosidases that are kept separately from their substrates. When plant tissues are disrupted, the myrosinases hydrolyse the glucose residue of glucosinolates releasing an unstable intermediate, which rearranges to form non-volatile and volatile isothiocyanates and nitriles.⁴⁰

In summary, vegetative plant volatiles are produced through several different pathways and mechanisms. While some volatiles are synthesized from simpler precursors, others are breakdown products of more complex compounds. These diverse origins contribute to the temporal, spatial and environmental complexity of plant volatile blends, and provide many independent attack points for ecological and evolutionary processes to shape these blends.

2.2 Mechanisms of vegetative plant volatile release

The mere production of a volatile organic compound is not sufficient for its release into the environment. Vegetative plant volatiles produced in the epidermal cells of roots²⁵ or in the mesophyll cells of green-leaf tissues have to cross different cellular boundaries such as the cell membrane and wall, the intercellular spaces, and the stomata or cuticle before being released into the environment (Fig. 2).^{41–43} Depending on their physicochemical characteristics, volatile compounds can accumulate in the lipid or aqueous phase.⁴⁴ The emission of volatiles driven solely by diffusion can lead to toxic volatile accumulation in membranes because of preferential partitioning of some of these compounds into lipid bilayers.⁴⁵ To enhance export and avoid toxicity, volatile phenylpropanoid and benzenoid compounds are transported across the plasma membrane by an adenosine triphosphate-binding cassette (ABC) transporter in *Petunia hybrida* flowers.¹² Recent discoveries have furthermore shown that a pleiotropic drug resistance transporter 3 (AaPDR3) from the ABC transporter superfamily is involved in the transport of the sesquiterpene β -caryophyllene in annual mugwort





Some plant species have specialized secretory structures in their aerial tissues such as resin ducts, idioblasts, and/or glandular trichomes where they produce and store volatiles. Glandular trichomes are hair-like epidermal structures that can produce and accumulate essential oils.³⁰ In the tomato clade of the *Solanum* genus, for instance, plants produce leaf glandular

In summary, plants can release volatiles *via* several different routes, including active transport and passive diffusion (Fig. 2). By consequence, plants can potentially regulate volatile release *via* biosynthesis, transporter activity, stomatal opening, and cuticular composition. The latter processes are intimately linked to other biological functions. Transporters, for instance, are likely to transport other small molecules, stomata are essential for gas exchange, and the cuticle provides an important physical barrier against abiotic and biotic stresses. The regulation of volatile release through processes such as stomatal opening and cuticular structure is thus associated with functional trade-offs that may complicate associated evolutionary trajectories. Therefore, the regulation of volatile release for compounds that can be produced *de novo* *via* the production of specific enzymes may be accomplished more effectively by regulating their biosynthesis. Storage and wound release are also an efficient way of tailoring volatile release to environmental stress.

Volatile composition and emission by plants vary depending on the identity of the attacker. For example, feeding by thrips (cell content-feeder), spider mites (cell content-feeder), or aphids (phloem-feeder) in cucumber (*Cucumis sativus*) leaves induces the expression of different terpene synthases, which translates into different volatile emission patterns.⁵⁸ In addition, attacks by chewing herbivores tend to trigger higher emission of volatiles than by piercing-sucking insects, suggesting that different types and levels of damage induce distinct volatile responses in plants.^{8,59} Simultaneous or sequential

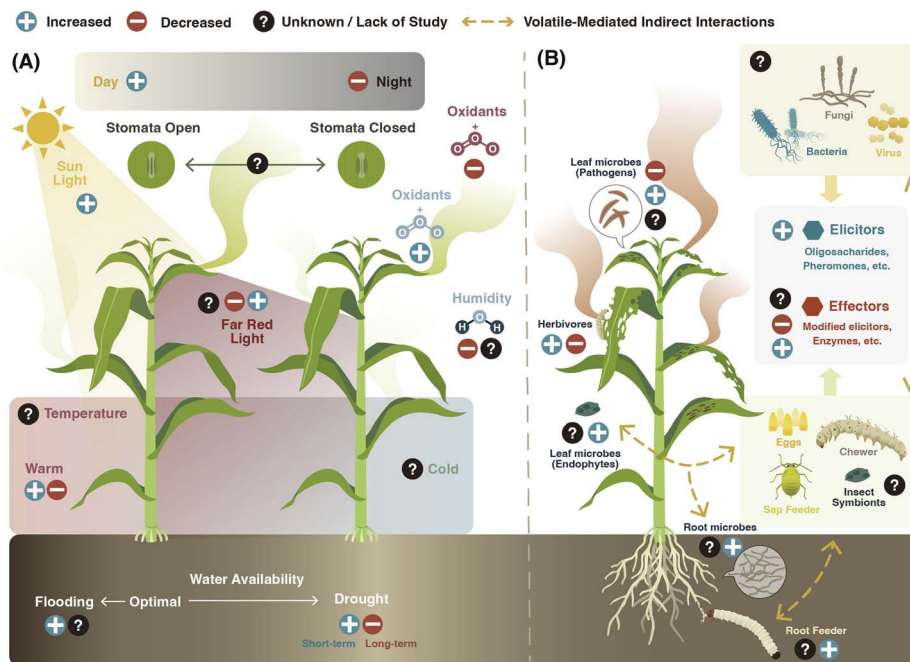


Fig. 3 Environmental regulation of vegetative plant volatiles. Induction (+) or suppression (–) of vegetative plant volatile emission can be modulated by (A) abiotic and (B) biotic factors. (A) Light intensity and spectrum, photoperiod, temperature, water availability, air humidity, and oxidants such as ozone (O_3) can control constitutive and inducible volatile biosynthesis and release. (B) Herbivores and microorganisms can use elicitors and effectors to either induce or suppress the biosynthesis and emission of vegetative plant volatiles. Furthermore, they can wound plants and thereby trigger volatile release. Root and leaf herbivores and microbes can interact via the plant and thereby trigger distinct volatile responses.

attack by multiple herbivores can result in distinct volatile emissions as well.^{60,61} Aboveground attack by the fall armyworm (*Spodoptera frugiperda*), for instance, induces volatile emission in the roots of maize (*Zea mays*) plants that repels Western corn rootworm (*Diabrotica virgifera virgifera*) larvae. Yet, when the Western corn rootworm feeds on the plant first, the induction of the repellent volatiles is suppressed.⁶¹

The modulation of vegetative plant volatile emission by herbivores is mediated by the recognition of damage-associated molecular patterns as well as herbivore-associated molecular patterns present in the oral secretions, saliva, ovipositional fluids, digestive waste products, and pheromones of the herbivore.⁶² Depending on their ability to induce or suppress plant defense responses, these are called elicitors or effectors.⁶³ Herbivore-derived elicitors like β -glucosidases,⁶⁴ *N*-acylglutamines such as volicitin,⁶⁵ and cyclic disulfide-bridged inceptin-related peptides⁶⁶ found in the oral secretions of lepidopteran larvae, as well as monounsaturated disulfoxy fatty acids (caeliferins) present in the oral secretions of non-lepidopteran insects,⁶⁷ have all been shown to induce volatile emissions in plants. Recently, four oligosaccharides detected in the oral secretions of the cotton leafworm (*Spodoptera littoralis*) larvae induced volatile emissions in Tansy (*Tanacetum vulgare*) plants.⁶⁸ Herbivore-derived proteins from eggs^{69,70} and frass⁷¹ modulate volatile emissions as well. For instance, an annexin-like protein “diprionin” isolated from egg-associated secretions in sawfly (*Diprion pini*) was recently found to trigger (*E*)- β -farnesene emission in Scots pine (*Pinus sylvestris*).⁷⁰

Interestingly, volatiles released by insects, such as sexual and aggregation pheromones, can also modulate volatile emissions by enhancing herbivory-induced plant defense responses⁷² and volatile release.⁷³

Herbivore-derived effectors can suppress volatile emissions.⁶³ Silkworms (*Bombix mori*),⁷⁴ the fall armyworm (*S. frugiperda*),⁵⁷ velvet bean caterpillar (*Anticarsia gemmatilis*),⁷⁵ tomato fruitworm (*Helicoverpa zea*), and tobacco hornworm (*Manduca sexta*)⁷⁶ have been all reported to suppress induced volatile emissions in plants. In *B. mori* larval oral secretions, a fatty acid hydroperoxide dehydratase (BmFHD) suppresses GLVs production.⁷⁴ Similar enzymes are present in the oral secretions of other lepidopteran species.⁷⁷ The truncated form of inceptin (Vu-In^{−A}) produced by the legume-specialist velvet bean caterpillar antagonizes inceptin-induced responses, including the production of the homoterpene DMNT in cowpea (*Vigna unguiculata*).⁷⁵ Recently, in *H. zea*, the salivary enzyme glucose oxidase has been shown to inhibit volatile emission in different host plants.⁴³ This inhibition was linked to the suppression of stomatal aperture.⁷⁸ Besides the induction or suppression of volatile emissions, some herbivores can modulate the chemical profile of the released plant volatile compounds. In *M. sexta*, the larval oral secretions are enriched in an (3Z):(2E)-hexenal isomerase that modulates the release of plant GLVs by re-arranging (Z)-3-hexenal to (*E*)-2-hexenal.⁷⁹

In summary, the release of plant volatiles following herbivore attack is strongly influenced by the action of elicitors and effectors (Fig. 3B). Elicitors act by activating the biosynthesis of



plant volatiles, but to what extent these compounds also regulate transport and release processes is not well established. Herbivore effectors are known to target both the biosynthesis and volatile release processes. Understanding the interplay between elicitors and effectors in regulating volatile release is an important research frontier.

3.1.2 Microorganisms. Similar to their response to herbivores, plants can emit specific blends of volatiles when coming into contact with pathogenic or beneficial microbes⁸⁰ (Fig. 3B). Emission of microbe-induced volatiles is regulated by the recognition of microbial-associated molecular patterns and the activation or suppression of plant defense signaling pathways.

Pathogenic bacteria can modulate volatile release in plants. A virulent strain of *Pseudomonas syringae*, for instance, increases the emission of TMTT, β -ionone, and α -farnesene in Arabidopsis.⁸¹ In tobacco (*Nicotiana tabacum*), both avirulent and virulent *P. syringae* strains induce the emission of MeSA, monoterpenes, and sesquiterpenes in infected plants.⁸² Gram-negative bacterial pathogens such as *P. syringae* have a type III secretion system (a molecular syringe) that injects effectors into the host cell to suppress the plant immune system and promote bacterial infection. Tobacco plants treated with *P. syringae* mutants deficient in this secretion system emit less volatiles upon infection.⁸² More recently, it has been shown that plant recognition of one of these injected *P. syringae* effectors, *AvrRpm1*, triggers the emission of vegetative volatiles in Arabidopsis.⁸³

Vegetative plant volatile emissions can be also regulated by fungal infections.⁸⁴ Infection with fungal pathogens elicits greater GLVs emissions than wounding alone or insect herbivore attack.⁸ Although the mechanisms of this phenomenon are still unknown, it has been suggested that enhanced GLVs production might be controlled by the action of fungal effectors. In nature, however, pathogen infections can co-occur with herbivore attacks resulting in distinct volatile profiles.⁸⁵ These patterns may be explained by hormonal cross-talk.^{85–87} For instance, the rust fungus (*Melampsora laricipopulina*) reduces the biosynthesis and emission of herbivore-induced plant volatiles in black poplar (*Populus nigra*) by activating the SA pathway and suppressing JA associated defenses.⁸⁷

Plant viruses regulate vegetative plant volatile emissions as well.⁸⁸ For instance, the Tomato spotted wilt virus (TSWV), mainly transmitted by Western flower thrips (*Frankliniella occidentalis*), reduces the expression of terpene synthases and emission of monoterpenes in thrips-infested pepper (*Capsicum annuum*) plants. This suppression is mediated by a non-structural protein of TSWV that directly interacts with the MYC2 transcription factor, a JA signaling regulator.⁸⁹ MYC2 is also targeted by the viral genetic factor β C1 of Tomato yellow leaf curl China virus, which suppresses plant terpene biosynthesis in Arabidopsis and *Nicotiana benthamiana* plants.⁹⁰ In a recent study, infection with the Cucumber mosaic virus was found to reduce the production of the monoterpenes 2-carene and β -phellandrene through the action of a viral 2b RNA silencing suppressor protein in tomato (*Solanum lycopersicum*), implicating microRNAs in the regulation of volatile emissions as well.⁹¹

Apart from pathogens, microbes that live in symbiosis with plants and herbivores can also influence constitutive and stress-induced vegetative plant volatiles. Root colonization by nitrogen-fixing rhizobia, for instance, increases indole and MeSA emission while suppressing β -caryophyllene production in leaves of JA-induced lima bean plants (*Phaseolus Lunatus*).⁹² Soil inoculation with the rhizobacteria *Pseudomonas fluorescens* WCS417r and *P. putida* SJ04 enhances aboveground emissions of menthone, menthol, and pulegone terpenoid compounds in peppermint (*Mentha $\times$ piperita*) plants.⁹³ In addition, colonization with rhizobacteria alters the expression of genes responsible for the synthesis of sesquiterpenes and indole in maize roots.⁹⁴ Similar systemic effects have been also observed for aboveground colonizing microbes. The endophytic fungus *Neotyphodium uncinatum*, which colonizes the aerial parts of the grass hybrid *Festuca pratensis $\times$ Lolium perenne*, can reduce the emission of root volatiles.⁹⁵ Effects of beneficial microbes might be mediated by the increased N availability and other resources needed for volatile biosynthesis,⁹⁶ but also by the modulation of defense signaling.⁹⁷ In the case of insect symbionts, the presence of the endosymbiont *Hamiltonella defensa* in pea aphid (*Acyrtosiphon pisum*) has been shown to compromise plant indirect defenses (*i.e.*, parasitoid attraction) by altering volatile emission upon aphid feeding.⁹⁸

In summary, plant pathogenic and beneficial microbes can induce and suppress plant vegetative volatiles, locally or systematically, *via* microbial elicitors and effectors that target plant defense signaling. Recent studies have shown that microbes present in herbivores and parasites of herbivores can also affect the volatile emissions of their host plant, thus adding an additional layer to the biological regulation of plant volatile release.⁹⁹

3.2 Regulation by abiotic stressors

3.2.1 Temperature. Environmental temperature is an important determinant of vegetative plant volatile emissions (Fig. 3A). Long-term increased temperature, for instance, enhances the emission of plant-derived terpenoids and GLVs in subarctic ecosystems.^{16,100} The effects were more pronounced in the presence of herbivores.¹⁶ Synergism between warming and herbivory was also observed in dwarf birch (*Betula nana*).¹⁷ These synergistic interactions might be explained by temperature effects on plant defense signaling, volatile biosynthesis, volatilization and diffusion, herbivore physiology, oil organic matter mineralization rates, and increased nutrient availability.^{19,101} In *Empetrum hermaphroditum*, *Cassiope tetragona*, and *B. nana*, warming treatment did not affect volatile emissions directly, but it was affected by increased nutrient availability.¹⁰²

Short periods of high temperature can affect plant volatile emissions. In the Mediterranean shrub (*Halimium halimifolium*), a 10 days heat wave resulted in an increase in volatile emission during the first two days.¹⁰³ A ¹³C-labeling approach revealed that plants allocated more carbon into *de novo* biosynthesis of plant volatiles. Carbon investment for *de novo* volatile biosynthesis was also enhanced in *Salix* and *Betula* spp



MeJA-induced volatile emissions.¹¹⁸ In tomato, water deficit can increase the emission of herbivore-induced vegetative plant volatiles that function as repellents to insects.¹¹⁹ By contrast, water deficit reduces the emission of MeSA upon infection with the bacterial pathogen *Candidatus Liberibacter* in citrus plants.¹²⁰ In general, drought can be expected to suppress the emission of leaf volatiles with a low Henry's law constant (H) by increasing stomatal resistance (see Section 2.2).

Compared to water deficit, less is known about the effect of water saturation and flooding on vegetative plant volatile emission. Flooding significantly changes the quality of the volatile blend in maize plants and reduces total volatile emission in certain maize genotypes but not others. However, when flooded maize plants are damaged by *S. frugiperda* caterpillars, they produce a significantly higher amount of volatiles.¹²¹

3.2.3 Light. The light environment can strongly modulate vegetative volatile emission in plants *via* different mechanisms (Fig. 3A). Light controls the metabolic flux from photosynthesis to terpenoid biosynthesis, as the Calvin cycle delivers the starting substrates for the MEP pathway.¹¹¹ Accordingly, the promoters of many TPSs contain multiple motifs related to light responsiveness and circadian rhythmicity.⁵⁸ This can partially explain the diurnal fluctuations in terpene biosynthesis rates that translate into greater emissions during the day than during the night.¹²² Apart from this strong regulatory mechanism over the volatile biosynthetic machinery, light can control the emission of volatiles with a low Henry's law constant (*H*) (see Section 2.2) *via* diurnal changes in stomatal aperture.^{42,49} Increasing light intensity has been shown to augment type-VI glandular trichome density and, concomitantly, the production of trichome-derived volatile terpenoids in tomato plants,¹²³ indicating that light can not only control volatile production but their storage structures as well.

Changes in light spectral composition can also modulate vegetative plant volatile emissions. In dense canopies, the absorption of red (R) and reflection of far-red (FR) light by photosynthetic tissues causes a decrease in R to FR ratios. Plants respond to this light shift by investing in growth to outcompete their neighbors¹²⁴ and suppressing defenses.¹²⁵ Both constitutive and inducible volatile emission are decreased in *Arabidopsis thaliana* upon low R:FR ratio treatment.¹²⁶ In tomato, the JA-induced production of volatile compounds is also modulated by low R:FR ratios or genetic inactivation of the FR-associated photoreceptor, resulting in specific volatile blends.¹²⁷ In addition, decreased proportions of ultraviolet radiation A, blue and green-yellow light, together with increases in R and FR, can decrease the concentrations and emissions of the phenylpropanoid eugenol and the monoterpenes linalool and 1,8-cineole in basil (*Ocimum basilicum*).¹²⁸ Enhanced blue light treatment, however, can decrease the emission rates of monoterpenes in Norway spruce (*Picea abies*).¹²⁹ FR supplementation can enhance the emission of maize (*Z. mays*) volatiles in response to herbivory or volatile cues emitted by neighboring plants.¹³⁰ These effects may be in part explained by the positive impact of supplemental FR on stomatal conductance and photosynthetic rate.¹³⁰ Similar effects have also been found in goldenrod (*Solidago altissima*), where FR enhanced

Drought can also modulate herbivore- and microbial-induced plant volatile emissions by itself.¹¹⁷ In tea (*Camellia sinensis* var. *sinensis*) plants, for instance, water deficit enhances

O₃.¹⁴⁸ It is estimated that forest-emitted isoprene contributes to the generation of 15–18% of the tropospheric ozone.¹⁴⁹

Atmospheric oxidants are also involved in reducing the availability of plant volatiles.¹⁵⁰ Ozone fumigation reduces the atmospheric concentration of mono- and sesquiterpenes released by oilseed rape (*Brassica napus*). The reduction in sesquiterpene concentration was likely linked to ozonolysis at the leaf surface, whereas reduction in monoterpene concentration was linked to reactions with ozonolysis-derived OH radicals in the air.¹⁵¹ It was also shown that increased ambient ozone reduces the adsorption of the monoterpene myrcene in white cabbage (*Brassica oleracea* convar. *capitata* var. *alba*).¹⁵² The reactivity of vegetative volatiles in the atmosphere is compound-specific, with reaction lifetimes that range from days to seconds.¹⁵⁰

4.2 Air humidity

Air humidity can influence the availability of volatiles in the atmosphere by regulating their breakdown processes and the formation of secondary aerosols.^{153,154} In addition, a negative relationship between ozone levels and humidity is constantly observed in air quality data. High vapor pressure deficit (VPD) has a strong correlation with higher ozone levels.^{155–157} This correlation is partly caused by the lower dry deposition of ozone by plant stomata due to stomatal closure under high VPD.¹⁵⁸ Since the late 1990s, there has been an increase in VPD consistently associated with the decrease in primary production, which can offset the positive effect of elevated CO₂ on plant growth.¹⁵⁹ This high VPD can affect the concentrations of ozone in the atmosphere and, therefore, also the chemical interactions between plant vegetative volatiles and ozone (see Section 4.1). The dynamics of these interactions, however, are still unknown and need further research especially in the context of plant ecological interactions.

In addition to atmospheric humidity, the humidity in the soil can influence the diffusion and degradation of below-ground vegetative plant volatiles.¹⁶⁰ In maize, for instance, the diffusion of β -caryophyllene produced by roots was found to be much faster in drier soils.¹⁶¹

4.3 Other organisms

Vegetative volatiles can be absorbed or degraded by other organisms after their release.¹⁶² In tomato, (Z)-3-hexenol from damaged neighboring plants can be taken up and converted into (Z)-3-hexenylylcianoside, which negatively influences herbivores.¹⁶³ Uptake of plant volatiles by plants can also be observed at larger scales.¹⁶⁴ In a winter wheat (*Triticum aestivum*) field, volatile emissions were observed to differ significantly across the growing season.¹⁶⁵ Different types of vegetative volatiles exhibited specific bi-directional exchanges between the field and atmosphere, involving plants, soil, or both.¹⁶⁵ Similar to the role of plants as volatile sinks, soil microbes can rapidly mineralize volatiles, a process that is highly dependent on the microbial community and specific volatile compounds.¹⁶⁶

Vegetative volatiles can stick to the surface of other plants. This absorption can lead to reductions in atmospheric volatiles

Plant volatiles can react with oxidants (*e.g.*, OH, NO₃, O₃) in the atmosphere (See ref. 148 for detailed graphics). For example, isoprene has been shown to be reactive with OH¹³ and terpenoids with O₃.^{143,144} These oxidative processes are responsible for the majority (68–69%) of biogenic secondary aerosols,¹⁴⁵ which are important for absorbing radiation from the sun, the formation of cloud droplets, precipitation patterns and humidity in general.^{146,147} Vegetative plant volatiles can also contribute to the generation of atmospheric oxidants. The oxidation of plant volatiles can generate peroxy radicals that react with NO to form NO₂, which is then photolyzed to generate



Indole is a nitrogen-containing volatile that is also emitted relatively early after attack.³² Indole can prime defense responses to herbivory or pathogen infection.^{31,32,173,177} In rice (*Oryza sativa*) and tea (*Camelia sinensis*) indole-mediated priming was shown to be dependent on mitogen-activated protein kinase and downstream WRKY transcription factors, suggesting that this priming occurs in a JA-dependent fashion.^{31,178} In maize, pre-treatment with indole primed up-regulation of anti-necrotrophic fungal defense genes and significantly reduced disease severity upon exposure to *Fusarium graminearum*.¹⁷⁷ Indole also exhibits synergistic priming effects together with GLVs,¹⁷³ demonstrating that different volatiles can act in concert to reprogram plant defenses.¹⁷⁹

5.2.3 Pollinators and seed dispersers. The behavior of pollinators and seed dispersers is often determined by vegetative plant volatiles.⁴ Interactions between stress-induced volatile emission and pollinators can yield complex ecological outcomes. When infected by *Cucumber mosaic virus* (CMV), resultant changes in volatile emission from tomato plants increased attractiveness of plants to pollinating bumble bees (*Bombus terrestris*). This increase in attraction further led to enhanced pollination of infected tomato flowers, which counteracted the negative impact of CMV infection on seed production.⁹¹ Volatiles can also have multiple functions for a single herbivore species. Although stress-induced volatiles have been shown to deter foliar oviposition by tobacco hornworm (*Manduca sexta*) adults on tobacco plants, the same volatiles were also shown to attract foraging *M. sexta* adults to flowers and thus enhance pollination.²¹² In agarwood (*Aquilaria sinensis*), GLVs released from seeds can attract *Vespa* hornets, which are important seed dispersers. Additionally, many of these volatiles are similar to those induced during foliar herbivory; this has been suggested to be a repurposing of plant defense to facilitate effective seed dispersal.²¹³ Herbivore-induced vegetative volatile emissions can also have negative impacts on plant-pollinator relationships. Vegetative plant volatiles released from wild tomato (*Solanum peruvianum*) plants under both real and simulated (MeJA application) herbivory conditions reduced the plant attractiveness to

Vegetative plant volatiles influence interactions of plants with multitude of microorganisms, such as viruses, bacteria, archaea, protozoa, fungi, algae, and nematodes.^{230–232} Plant-derived terpenoids, benzenoids, and aldehydes can all exert antibacterial or antifungal effects. For instance, the monoterpenes limonene and β -pinene, and several aldehydes, which are major constituents of the volatile bouquet emitted by pine trees, display antimicrobial activities against airborne bacteria.²³³ Similarly, GLVs such as (*E*)-2- and (*Z*)-3-hexenal show antimicrobial effects against plant pathogenic bacteria *in vitro*.²³⁴ Yet, exceptions to this pattern have been reported for

the sesquiterpene (*E*)- β -caryophyllene, which can directly stimulate the growth of the hemi-biotrophic fungus *Colletotrichum graminicola*.²³⁵ In rice, the induced emission of the monoterpene (S)-limonene upon infection with the pathogenic fungus *Magnaporthe oryzae* can inhibit the germination of *M. oryzae* spores.²³⁶

Besides antimicrobial activities, vegetative plant volatiles can influence the establishment of microbial communities by acting as attractants, nutrients, or substrates to produce bioactive compounds.²³⁷ Linalool, 2-phenylethanol, and nonanal emitted by strawberry (*Fragaria ananassa*) plants can be chemically transformed by leaf epiphytic bacteria and enhance their competitive performance in the presence of the pathogenic fungi *Botrytis cinerea*.²³⁸ Root-derived volatiles emitted by tomato plants can attract certain soil bacteria.²³⁹ These authors also observed that some bacteria might be more strongly attracted by plant volatiles under soil nutrient limitation, implicating root volatiles as info-chemicals that provide information about a nearby nutrient-rich environment. Whether active recruitment of microorganisms by vegetative plant volatiles affects plant performance or resilience against biotic and abiotic stressors, however, is not well explored.

In addition to direct effects, microbial communities can indirectly be affected by the interplay of vegetative plant volatiles with other plants or higher trophic organisms. For instance, pathogen-induced emission of aboveground vegetative volatiles in infected plants can alter the responses of non-infected neighbors to the same microbial pathogen either by increasing or reducing susceptibility.²⁴⁰ More recently, vegetative volatiles emitted aboveground by tomato plants inoculated with beneficial root-associated bacteria were shown to modulate the rhizosphere microbiota of surrounding conspecific plants *via* volatile-induced changes in root exudates.²⁴¹ The ecological and physiological implications for both the emitter and receiver plants, as well as their associated soil microbiota, were not further investigated. Still, this novel phenomenon adds further support for the potential use of above- and/or below-ground volatiles to fine-tune the rhizosphere microbiota in agricultural systems.

6. Synthesis: biological frameworks to explain patterns of vegetative plant volatile release

Vegetative plant volatiles are produced *via* a multitude of pathways and follow different routes to end up in the environment. The biosynthesis and release of volatiles is modulated by both biotic and abiotic factors. Together, this results in highly dynamic and diverse volatile release patterns. Once the volatiles have left the plant, they interact with organisms of all known kingdoms, both at behavioral and physiological levels. These interactions again shape the genetics of volatile release and production over evolutionary time. Given this substantial physiological and ecological complexity, one has to wonder whether there are any specific biological frameworks beyond the most fundamental physical, chemical, and biological

principles that explain vegetative volatile release patterns. Over the last years, a number of frameworks have started emerging that may help to explain volatile release patterns (Fig. 5).

6.1. Multifunctionality

There is now ample evidence that the same volatile can have multiple functions for plants²⁴² (Fig. 5). GLVs, for instance, act as within-plant defense signals, antimicrobials, and attractants of natural enemies.⁸ Indole primes plant defenses, it acts as a repellent at high doses, and it can directly intoxicate herbivores.^{18,32,196,204} The homoterpene DMNT can act as an herbivore toxin when ingested, and it also interferes with the location of the herbivore's host plant when perceived by olfactory receptors.^{201,203} β -caryophyllene has been implicated in biotic interactions as a volatile cue both above- and below-ground, where the impacts on plants range from beneficial to detrimental. For example, β -caryophyllene can attract herbivores' natural enemies²⁴³ or help *Diabrotica virgifera virgifera* larvae to locate their host plant roots.²⁰⁶ β -caryophyllene has also been implicated as a critical defense against the fungal pathogen *Pseudomonas syringae*.²⁴⁴ The regulation of the production and release of these compounds likely mirrors their multiple roles and benefits for plants. During insect herbivory, biosynthetic similarity between compounds is associated with higher covariance between compounds, suggesting that there may be constraints at the biosynthetic level for covariation patterns between different volatile groups.²⁴⁵ For example, multiple compounds can be produced from a single enzyme/substrate pair. Further, conditions such as catalytic metal ion availability and pH can influence the relative abundances of terpene products *in vitro*.²⁴⁶ It is thus possible that, under variable conditions within plant tissues, the relative abundance of products of the same substrate/enzyme might vary. Developing a deeper understanding of the multifunctionality of volatiles can thus help to uncover ecological and evolutionary rationales for their biosynthesis and emission.

6.2. Chemical communication displays and the information arms race

Vegetative plant volatiles can provide information to beneficial organisms such as herbivore natural enemies, but also to antagonists such as herbivores. These conflicting functions and effects can be described as an information arms race, whereby the plant tries to hide from herbivores while being visible to herbivore natural enemies.²⁴⁷ In this framework, the ability of plants to produce volatiles that are protective but not necessarily unique (*i.e.*, other nearby plants are also producing them) is most effective for minimizing fitness costs associated with volatile emission.²⁴⁷ Volatile emission can be considered as a chemical communication display that serves as information (Fig. 5B). In plants, covariation between volatiles is relatively low, particularly following herbivory, suggesting that single or few compounds are likely responsible for mediating a particular information transfer between a plant and another organism.²⁴⁵ If herbivores rely on fixed ratios of compounds, then the further reduction of covariance among herbivory-induced plant



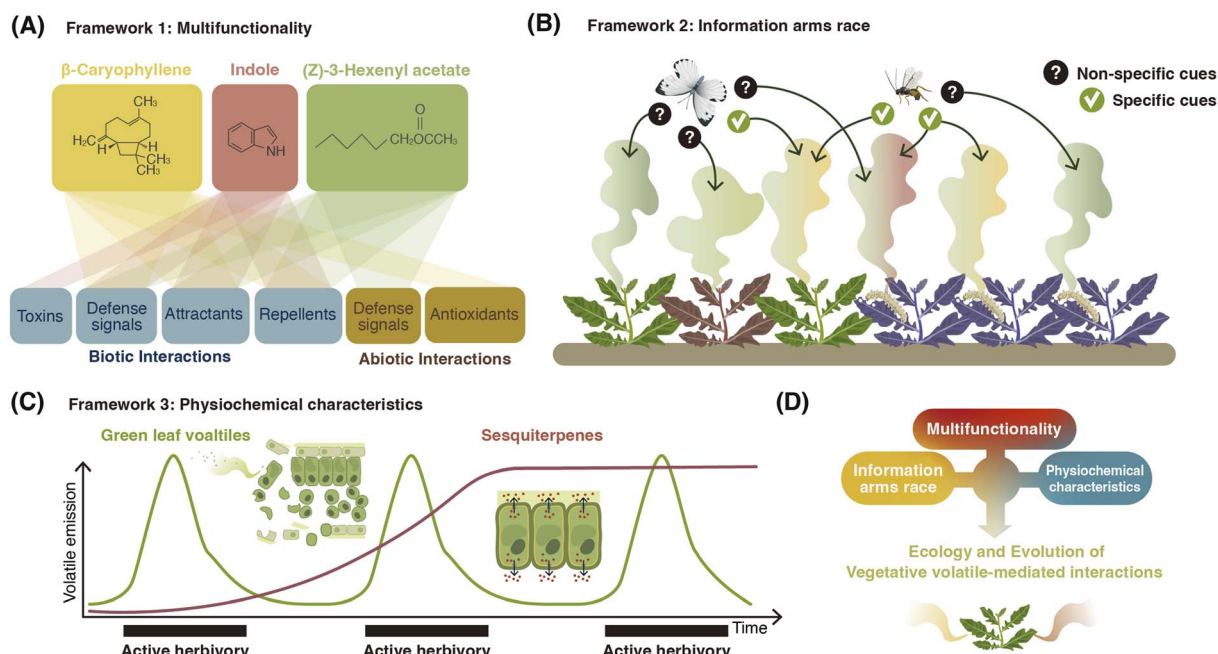


Fig. 5 Biological frameworks that help to explain release patterns of vegetative plant volatiles. (A) Multifunctionality: plant volatiles can serve multiple purposes for plants, and this multifunctionality is mirrored in the regulation of their production and release. (B) Vegetative volatiles provide information to both allies and antagonists, which may result in an information arms race that shapes the composition of plant volatile bouquets. Different colors depict different blends of volatiles, some of which contain useful information only for beneficials and others can act as useful signals for both beneficials and enemies. (C) Physiochemical characteristics such as the biochemical origin, the volatility, the stability and the toxicity of vegetative volatiles influence their production and release kinetics, which again determines potential functions and environmental effects. (D) Interactions between A, B, and C will influence the evolution of vegetative plant volatiles, and thus help to explain spatiotemporal production and release patterns that are observed in nature.

volatiles may interfere with the host location of subsequent herbivores.²⁴⁸ Further exploration regarding how multifunctionality, not only of the volatile pool but also of individual compounds, influences the ecological interactions in complex ecosystems is essential to identify how volatiles ultimately impact plant fitness and evolutionary trajectories.

6.3. Physiochemistry

Depending on their physiochemical characteristics, vegetative plant volatiles show distinct spatiotemporal release and transfer patterns. Some are breakdown products and thus released rapidly from wounded tissues, while others are synthesized *via* enzymatic cascades and thus produced more slowly^{8,32} (Fig. 5C). Some are stable and diffuse across large distances, and others are unstable and rapidly degraded.²⁴⁹ Thus, vegetative plant volatiles have distinct physiochemical fingerprints, which constrain their adaptive plasticity and ecological effects. GLVs, for instance, are breakdown products rapidly released following stress, mostly from wound sites.²⁵⁰ They thus provide a timely, but unspecific cue of active damage, and may be used by natural enemies accordingly.²⁵¹ Similarly, the above properties predispose GLVs to act as damage-associated molecular patterns in plant defense regulation.²⁵² Volatiles such as terpenes, on the other hand, diffuse slowly and take longer periods to be produced because of dedicated biosynthetic machinery. Accordingly, they can act as highly specific cues for certain

herbivores and other plants, as well as constitutive defenses or phytoanticipins. Hence, terpenoids might be less suited as rapid, localized defense signals (Fig. 5C). There are, however, exceptions to this; terpenes stored in trichomes for instance can be released rapidly upon damage (see Section 2.2).

In summary, we propose that the release patterns of a given class of volatiles can be explained, at least in part, by their multifunctionality, the information arms race, and their physiochemical properties. A better understanding of the physical properties and ecology of individual volatile classes is indispensable to leverage the power of these frameworks (Fig. 5D).

7. Open questions and future research on vegetative plant volatiles

Although the field is rapidly gaining a deep understanding of the physiology and ecology of vegetative plant volatiles, several important open questions remain.

7.1 Mechanisms of transport and release

While the biosynthesis of vegetative plant volatiles is understood in substantial detail, the mechanisms governing transport and release are not well known yet (Fig. 2). Most molecular work so far has focused on floral volatiles,²⁵³ and it remains to be seen whether vegetative volatile release is governed by the same mechanisms. A particular challenge will be to understand



the relative importance of transport and/or diffusion across cell membranes, cuticular barriers, stomata, trichomes, and wounds. Given the vast diversity of physiochemical characteristics across vegetative plant volatiles, it is likely that different volatiles will have different preferred release pathways mediated by the physiological characteristics of plant tissues.^{41,44} Understanding the major transport routes of individual volatiles will be imperative to investigate their regulation, ecology, and evolution in an environmental context.

7.2 Interactions of multiple stresses on volatile production and release

Plant volatile responses to individual biotic and abiotic factors are well described, and we have also gained more detailed understanding on how different abiotic factors interact in this context.²⁵⁴ However, much remains to be learned regarding the impact of multivariate environments on plant volatile production and release. Interactions between multiple abiotic factors at different levels of stress severity, for instance, are not well known. Severe stress might trigger completely different responses in comparison to mild stress. Climate change has led to an increase in multi-stress scenarios worldwide,¹¹⁴ which will most likely affect plant volatile emissions and plant interactions as well. Investigating how plant volatiles profiles respond to these dynamic abiotic pressures will help to predict plant performance in the context of herbivory and beyond.

7.3 Transmission dynamics in the field

A number of methods has been developed to detect, identify, and quantify plant volatiles.²⁵⁵ The pros and cons of various plant volatile measurement techniques are reviewed in detail by Tholl *et al.*²⁵⁶ Most of these methods rely on collection approaches with low temporal resolution and/or involve highly restricted headspace environments such as glass bottles.^{257,258} For example, volatiles are often collected and concentrated over time (often several hours) and collections are then analyzed using techniques such as gas chromatography coupled with mass-spectrometry (GC-MS).²⁵⁶ As samples are pooled, the precise time point in which these volatiles are emitted is difficult to determine. Even if samples are collected for shorter periods of time, materials and lengthy analytical program run times can cause temporal experimental bottlenecks. Techniques such as proton-transfer reaction time-of-flight mass spectrometry (PTR-ToF-MS) do not require a time-consuming separation phase and allows for direct injection of airborne volatiles into the mass spectrometer. Still, PTR-ToF-MS cannot differentiate chemical structures with identical molecular weights, *e.g.*, different monoterpenes.

It is clear that there is high spatial variability in vegetative plant volatile emissions, whether it be differing plant tissues and plant species or between plants under variable environmental pressures.^{259–261} Capturing this variation in more detail will be important in the future. Recently, technological advancements have allowed for real-time measurements of volatiles across multiple plants, however this has yet to be implemented in a field setting.¹³⁰ By consequence, we lack

a detailed understanding of spatial and temporal volatile dynamics at the plant and interplant scale within plant canopies.²⁵⁶ Developing our understanding of how vegetation creates a “volatile landscape” in terrestrial ecosystems is important to understand how ecosystem-scale volatile dynamics mediate ecosystem functioning. The development of adequate devices/technologies will play an essential role in the study of plant volatiles at the canopy level.

7.4 Mechanisms of uptake, perception, and physiological responses

Plant volatiles are perceived and, in some cases, taken up by plants and other organisms.^{163,179,262–265} The mechanisms underlying these processes, however, are not well understood. Volatile uptake by plants, for instance, is thought to occur through the stomata or *via* diffusion through the leaf cuticle,^{253,266} but neither of these mechanisms have been explored in detail. To date, a receptor-based mechanism in plants has only been reported for the volatile phytohormone ethylene.²⁶⁷ Volatile perception has been explored at the molecular level for a number of insects, and different mechanisms are being validated for plants.^{164,268,269} Outside of perception, volatiles' targets that may trigger physiological responses in insects and mammals are unknown and deserve further study to harness the potential of plant volatiles as pest control agents and drugs.

7.5 Identifying major evolutionary forces driving vegetative plant volatile patterns

Given the many functions and effects of vegetative plant volatiles, understanding the major forces that govern their evolution remains challenging. Volatiles have been implicated as driving forces in shaping resistance to herbivory in receiver plants, sometimes in a taxa specific manner. There is also genotype-specific information transfer between plants, where signals from kin have been shown to result in the highest level of resistance to herbivory in receiver plants.^{14,270} The existence of elicitors and effectors produced by both arthropods and microbes modulating volatile emissions has reinforced the idea that vegetative plant volatiles are important actors in the ecology of plant biotic interactions and might have shaped the evolution of these traits.^{43,271} In nature, however, plants are exposed to all these components either simultaneously or sequentially through their lifetime. Thus, it is likely that volatile-related traits have evolved under the influence of a dynamic environment. Understanding how vegetative plant volatiles respond to multiple biotic factors is, therefore, essential to unravel their ecological functions.

8. Author contributions

All authors conceived the idea for this review. REB, PAL and JMW contributed equally to the writing of the first draft (order of authorship determined by alphabetical order of last name). ME wrote additional sections and made critical revisions to



subsequent drafts. All authors made substantial contributions to the final draft.

9. Conflicts of interest

The authors have no conflicts of interest to declare.

10. Acknowledgement

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