

Special Issue: Induced biogenic volatile organic compounds from plants

Multiple stress factors and the emission of plant VOCs

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Individual biotic and abiotic stresses, such as high temperature, high light and herbivore attack, are well known to increase the emission of volatile organic compounds from plants. Much less is known about the effect of multiple, co-occurring stress factors, despite the fact that multiple stresses are probably the rule under natural conditions. Here, after briefly summarizing the basic effects of single stress factors on the volatile emission of plants, we survey the influence of multiple stresses. When two or more stresses co-occur their effects are sometimes additive, while in other cases the influence of one stress has priority. Further investigations on the effects of multiple stress factors will improve our understanding of the patterns and functions of plant volatile emission.

Plants and volatile organic compounds: a stressful relationship

While plants are sessile organisms, their metabolic capabilities extend far beyond their borders. Plants release a large variety of volatile organic compounds (VOCs) into the surrounding atmosphere. In addition to simple gases, such as oxygen, carbon dioxide and water vapor, plants emit an enormous wealth of different terpenes, fatty acid derivatives, benzenoids, phenylpropanoids, and amino acid derived metabolites. The release of these substances is frequently associated with a range of biotic and abiotic stress factors. For example, 35 years ago, as part of one of the first efforts to measure plant volatiles, researchers noted that terpene release from sage plants was elevated at high temperatures [1]. Since then, a whole generation of scientists has grown up studying how physical stresses affect the release of terpenes. The discovery that herbivory induces volatile release [2,3] was more recent but no less influential in stimulating many researchers to investigate the role of herbivory in the emission of plant volatiles.

In this review, we begin by briefly summarizing the volatile responses of plants to individual stresses and the evidence that these substances play a role in relieving stress. Then, we focus on how interactions of multiple stresses affect volatile emission and the mechanisms that might explain the patterns observed. We conclude by suggesting how future climate change could impact VOC emission via alteration in plant stress.

Stress brings VOC release

The emission of VOCs from plants varies extensively depending on the species, organ, developmental stage and environmental conditions. Environmental factors, both biotic and abiotic, have an especially large impact on volatiles released from the vegetative parts of plants.

Abiotic stress factors alter the levels of so many different metabolites in plants that it is not surprising that VOCs are also affected. As a generalization, stress can be said to increase VOC emission. This was first recognized for high temperature stress nearly 30 years ago when an exponential increase in VOC emission in pine was described with a linear increase in temperature [4]. Such an increase has been observed for a variety of different terpene volatiles, including isoprene [5], monoterpenes [6] and sesquiterpenes [7], in a range of woody and herbaceous species [8], and in both angiosperms and gymnosperms [9]. Although most studies have concentrated on VOCs from vegetative parts, floral VOC emission also increases with temperature [10]. Elevated emission is in part a physical process due to the increases in the vapor pressure of VOCs at higher temperatures. However, VOC emission often increases more than can be explained by vapor pressure changes, suggesting a higher rate of biosynthesis at elevated temperatures.

Among other abiotic stresses, high light intensity also stimulates VOC emission in a variety of different plant types and growth forms [5,7,8,10–13]. Water stress [14,15], salt stress [16] and oxidative stress imposed via ozone treatment [17,18] have also been reported to increase VOC emission. However, the effects of these other stress factors are not consistent throughout the literature. For example, salt stress had no influence on VOC release in poplar (*Populus × canescens*) [19] and moisture stress did not influence emission of isoprene [20].

Biotic stresses also induce the emission of plant volatiles. Herbivore damage to vegetative parts has been repeatedly shown to cause increased release of inducible VOCs (Figure 1), especially green leaf volatiles (GLVs) and terpenes [21]. The GLVs are C₆ aldehydes, alcohols and esters derived from lipoxygenase cleavage of fatty acids; they take their name because of their typical smell of green leaves. The release of VOCs after herbivory can be a result of the bursting of pre-existing structures in which volatiles are stored, such as resin ducts or glandular trichomes [22,23]. On the other hand, volatiles whose release is not

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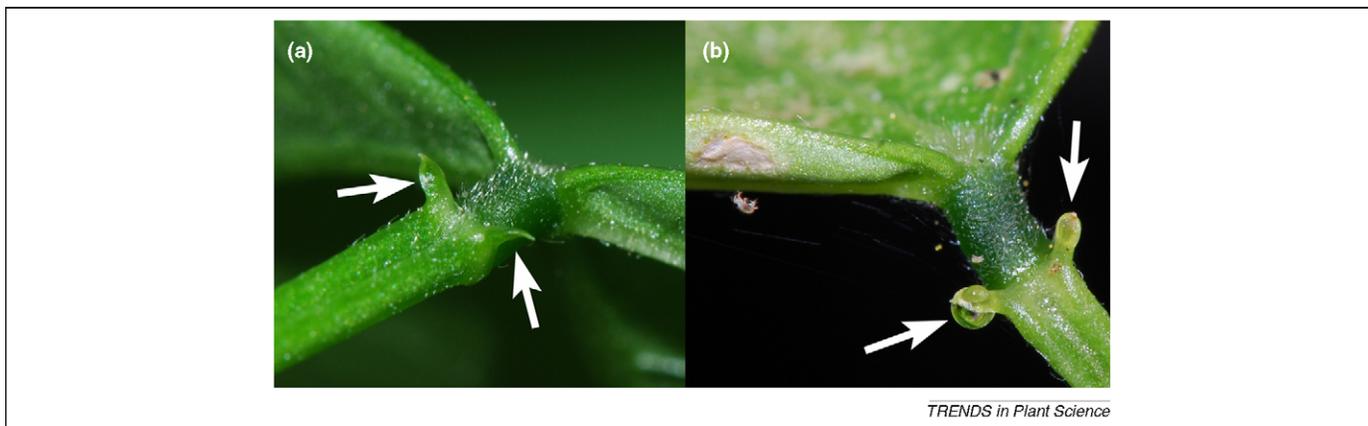


Figure 2. Nectaries (arrows) for production of extra floral nectar (EFN) in lima bean (*Phaseolus lunatus*) petioles. (a) Healthy, non-stressed plants do not produce or produce only trace amounts of nectar. (b) Plants infested by spider mite (*Tetranychys urticae*) produce visible amounts of extra floral nectar. Other biotic and abiotic stresses could interact with herbivory. For instance, VOCs released by spider mite-infested neighboring plants could prime lima bean for increased EFN production on infestation. Abiotic stresses, such as elevated ozone levels can induce production of terpenes and GLVs [18], but also decompose these volatile signal compounds in the atmosphere [75]. Moreover, direct exposure to elevated ozone is capable to increase EFN production in non-infested lima bean plants (James Blande, personal communication).

function in plant protection. Interestingly, methyl salicylate (MeSA), which is known to be inducible by aphid feeding in plants [52,53], is an efficient repellent for migrating aphids [54].

Attraction of herbivore enemies

The first reports on herbivore-induced VOCs focused on how volatile blends released after feeding attracted herbivore predators and parasitoids [2,3]. This phenomenon has now been demonstrated for a variety of plant species, their herbivores and enemies of their herbivores [55,56]. It even occurs below ground where a sesquiterpene released from damaged roots by beetle feeding attracts an entomopathogenic nematode [57,58]. Moreover, enemy attraction also occurs above ground after herbivore oviposition as well as after herbivore feeding, when egg laying alters the volatile blend and egg parasitoids are attracted [24,59]. Experiments with pure VOCs and transgenic plants engineered to produce modified VOC blends have now identified specific terpenes and green leaf volatiles as being involved in enemy attraction [45,57,60–62].

Volatile messages for internal and between plant signaling

VOC emission also functions as an internal plant cue to indicate the presence of herbivores and stimulate the deployment of defense in the region of herbivore attack. For example, a blend of volatiles from lima bean (*Phaseolus lunatus*) leaves damaged by herbivory was shown to induce adjacent leaves [63] to increase their secretion of an extra-floral nectar (Figure 2) that arrests herbivore enemies. Mixtures of terpenes or green leaf volatiles can also induce plants to emit volatiles of their own [28] or increase direct defenses against herbivores [29]. In some cases, VOCs do not trigger immediate responses but prime plants, so that after a subsequent bout of herbivory there are greater responses in comparison with foliage not exposed to VOCs [28–30]. Such volatile signaling among plant parts might be especially important when vascular connections between individual leaves or branches are limited [29,30,64].

Clearly, within-plant VOC signaling also has the potential to be detected by neighbors. Recent reports document

several examples in which plants have responded to VOCs emitted from herbivore-attacked neighbors by increasing their own defenses immediately or being primed to respond in an enhanced manner after actual herbivory [65,66]. For example, volatiles from damaged lima bean leaves induce extra-floral nectar in adjacent plants as well as in adjacent leaves on the same plant [67]. The mechanism by which plants perceive other volatile signals from attacked neighbors remains largely unsolved although membrane-bound ethylene receptors are well known [68]. For methyl salicylate, there is some evidence that salicylic acid binding proteins are able to bind this compound [69] and convert it to salicylic acid initiating defense signaling in the receiver plant.

Impact of multiple stresses on VOC emission

Under natural conditions, plants rarely experience single stress factors one by one, but are much more likely to be exposed to multiple stresses simultaneously. However, very few studies have attempted to investigate VOC emission under multiple stresses, either in the laboratory or the field. Such research is essential because the response of plants to multiple stress combinations cannot always be extrapolated from responses to individual stress factors [70].

Interaction of biotic and abiotic stresses

The application of different biotic and abiotic stress factors simultaneously could have additive or opposing effects on VOC emission [71–77] (Table 1, Fig. 3). A good example of additive response comes from work on maize which releases volatiles after herbivory by lepidopteran larvae. In a laboratory setting, maize plants were induced to emit VOCs in a regulated manner by simulation of herbivory through application of lepidopteran oral secretions to mechanically damaged leaves [71]. They were also challenged by different temperature regimes. As reviewed above, high temperatures increase the VOC emission rate in many plant species. In maize, the combination of high temperature and simulated lepidopteran herbivory resulted in greater VOC emission than when either stress was applied alone [71].

Table 1. Impact of selected abiotic stresses on emitted amounts of known herbivore-inducible plant volatiles^a

Plant species ^b Abiotic stress	Zm	Zm	Zm	Zm	Zm	Bn	Gh	PI	PI	Bo	Bn	Bo	Bn	
	Drought	High temperature	Low light intensity	Nutrient deficiency	Nitrogen deficiency	Nitrogen deficiency	Nitrogen deficiency	AIR POLLUTANTS	Elevated O3	O3-rich atmosphere	O3-rich atmosphere	O3-rich atmosphere	Elevated CO2	Elevated CO2
Plant volatile														
Fatty acid derivatives														
(Z)-3-Hexenal (C6)	nd ^c	nd	nd	nd	nd	nd	↔ ^d	nd	nd	nd	nd	nd	nd	nd
(E)-2-Hexenal (C6)	nd	nd	nd	nd	nd	nd	↔	nd	nd	nd	nd	nd	nd	nd
(Z)-3-Hexenyl acetate (C6)	↔	↑	↑	↓	↔	↓	↑	↑	nd	↓	↔	↔	↔	↔
(Z)-3-Hexen-1-ol (C6)	nd	nd	nd	nd	nd	↓	nd	↔	↓	↓	nd	nd	nd	nd
1-penten-3-ol (C5)	nd	nd	nd	nd	nd	nd	nd	↑	nd	nd	nd	nd	nd	nd
Phenyl propanoids														
Indole (C8)	↑	↔	↓	↓	↑	nd	↔	nd	nd	nd	nd	nd	nd	nd
Methyl salicylate (C8)	nd	nd	nd	nd	nd	↔	nd	nd	↔	nd	nd	nd	nd	nd
Isoprenoids														
Myrcene (C10)	↔	↔	↔	↔	↔	↔	↔	nd	nd	↓	↔	↓	↔	↔
Linalool (C10)	↓	↔	↔	↔	↔	nd	nd	nd	↓	↓	nd	nd	nd	nd
β-Ocimene (C10)	nd	nd	nd	nd	nd	↔	↑	↔	↓	nd	nd	nd	nd	nd
DMNT (C11)	↑	↔	↔	↓	nd	↔	↔	↑	nd	↓	↓	↔	↔	↔
Geranyl acetate (C15)	↔	↓	↓	↓	↔	nd	nd	nd	nd	nd	nd	nd	nd	nd
β-Caryophyllene (C15)	↔	↑	↔	↓	↑	nd	↑	nd	nd	nd	nd	nd	nd	nd
α-Bergamotene (C15)	↔	↔	↔	↔	↑	nd	↑	nd	nd	nd	nd	nd	nd	nd
(E)-β-farnesene (C15)	↔	↔	↔	↔	↑	nd	↑	nd	nd	nd	nd	nd	nd	nd
α-Farnesene/β-Bisabolene (C15)	↔	↔	↑	↓	↔	↓	↑	nd	nd	↓	↓	↔	↔	↔
(E)-Nerolidol (C15)	↔	↑	↓	↓	↔	↓	nd	nd	nd	nd	nd	nd	nd	nd
TMTT (C16)	↔	↑	↓	↓	↔	nd	↓	↔	↓	nd	nd	nd	nd	nd
Refs	[71]	[71]	[71]	[71]	[72]	[73]	[74]	[18]	[75]	[75]	[77]	[76]	[77]	[77]

^aCarbon content of each compound is given in parentheses.

^bPlant species Zm = *Zea mays* [71,72], Bn = *Brassica napus* [73,77], Gh = *Gossypium hirsutum* [74], PI = *Phaseolus lunatus* [18,75], Bo = *Brassica oleraceae* [75,76].

^cnd = not detected

^d↔ = no effect, ↑ = significant increase, ↓ = significant decrease.

The additive effects of biotic and abiotic stresses were also noted in a study on lima bean subjected to spider mite feeding and ozone treatment [18]. Both spider mites and ozone were observed to induce a similar volatile profile dominated by the GLV, (Z)-3-hexenylacetate, and the homoterpenes, 4,8-dimethylnona-1,3,7-triene (DMNT) and 4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT). When spider mites and ozone were applied together, the responses were nearly additive. Curiously, the ozone treatment caused visible tissue damage that closely resembled the piercing caused by mite feeding. Thus, for these stresses, VOC emission may be primarily a consequence of a particular type of physical damage.

The interaction of ozone and herbivory on volatile release has been examined in other plant species as well. An experiment on the hybrid aspen (*Populus tremula* × *tremuloides*) grown in a free-air ozone concentration enrichment facility employed a lower ozone dose than in the lima bean work [79], and this dose had virtually no effect on the VOC emissions of aspen induced by feeding of a lepidopteran larvae and a curculionid weevil. In contrast, a laboratory study on oilseed rape (*Brassica napus*) given a higher, long-term dose of ozone revealed that ozone reduced insect-induced VOC emission 45–50% [77]. In this experiment, the long-term dose probably reduced the apparent emission rate by degrading VOCs after their release from the plant via gas phase reactions.

Additive effects of stresses on VOC emission might also be expected for combinations of abiotic stresses, including high temperature, high light and ozone, all of which induce higher VOC emission rates when applied singly. These three stresses all appear to act through a common biochemical mechanism in plants resulting in elevated levels of reactive oxygen species (ROS), including singlet oxygen, superoxide and hydrogen peroxide [38]. Such reactive oxygen species cause damage by reacting with lipids, proteins or other cellular components. Certain VOCs have been shown to react rapidly with reactive oxygen species *in vitro*, and plants may exploit this chemistry to protect themselves *in vivo* against the negative effects of light, temperature and ozone stresses. Thus, combinations of these three reactive oxygen-generating stresses would be predicted to increase VOC emission in an additive manner depending on reactive oxygen species levels, but further research is needed to test this expectation.

The co-occurrence of multiple stresses may significantly limit energy or nutrient supplies, and so it may not be possible for a plant to respond to every stress factor impinging on it at a single time. Instead, response may be prioritized against stresses deemed most severe, those representing the greatest threats to survival, or those for which the most resources are available for mitigation. For example, field experiments on herbivore-attacked plants that were simultaneously under abiotic stress demon-

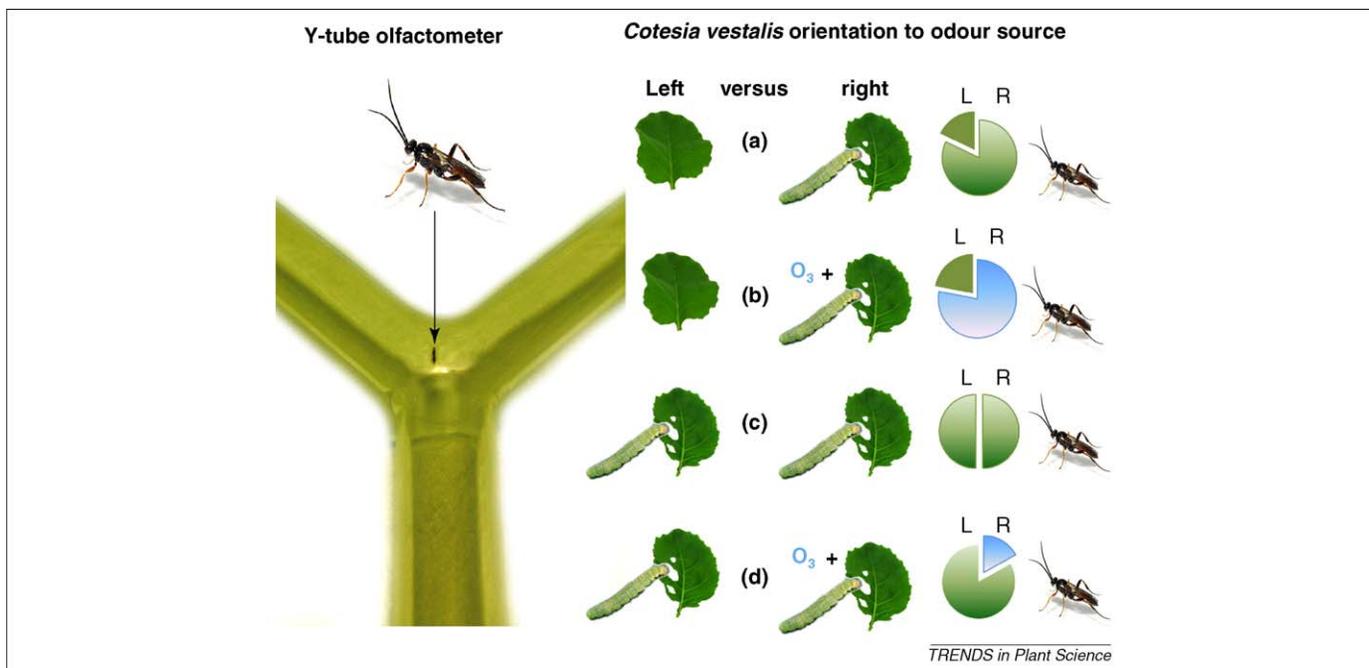


Figure 3. Example of interaction of biotic and abiotic stress factors. The behavior of the larval parasitoid (*Cotesia vestalis*) of diamondback moth (DBM, *Plutella xylostella*) in a Y-tube olfactometer is influenced by herbivory and ozone. Many of the typical herbivore-induced VOC compounds released from DBM-damaged cabbage plants (see Table 1 and reference [75]) were reduced in the plant headspace, when plants were exposed to elevated O_3 levels (60 and 120 ppb). VOC emissions from DBM-damaged cabbage plants and from intact plants were released into the arms of olfactometer and the number of female parasitoids selecting either left or right arm of the olfactometer were counted. (a) More *C. vestalis* females preferred VOC emissions from a DBM damaged plant (R) when compared with emission released from an intact plant (L) when both plants were in filtered air. (b) VOCs from DBM-damaged plant growing at 120 ppb ozone (R) were preferred by *C. vestalis* females when compared to VOC bouquet from healthy plant in filtered air (L). (c) DBM-damaged plants both grown in filtered air were equally attractive to *C. vestalis*. (d) When the damaged plant was growing at 120 ppb O_3 (R), significant reduction of preference was observed when compared to attraction of damaged plant in filtered air (L). Redrawn (with permission) from data published by Pinto *et al.* [78].

strated that herbivory has a stronger impact on VOC emission than stresses, such as elevated ozone concentration [18] and UV-B radiation [80]. However, it is easier to manipulate multiple stresses in the laboratory than in the field. Laboratory experiments on maize subjected to simulated herbivory and nutrient stress showed that nutrient stress appeared to have a higher priority than herbivory. Nutrient deficiency decreased herbivore-induced VOCs by approximately 75% [71]. Similar results were obtained for oilseed rape grown simultaneously under diamondback moth larvae infestation and nutrient stress [73]. Here low nutrient soils resulted in substantial declines in herbivore-induced VOC emission. These responses suggest that nutrient deficiency acted to channel plant resources away from anti-herbivore defense perhaps to mitigate low nutrient status (e.g. by enhanced root growth). Alternatively, volatile formation may have been limited by the lack of specific nutrients (e.g. iron, sulfur, manganese or phosphorus required for intermediates, cofactors or enzymes of volatile biosynthesis).

In contrast to the results above, the deficiency of a single nutrient, nitrogen, led to a dramatic increase in sesquiterpene emission from maize seedlings in which herbivory was simulated by application of jasmonic acid, mechanical damage or the insect elicitor, volicitin [72]. This response was attributed to the effect of nitrogen shortage on defense signaling pathways in maize. Both jasmonic acid and ethylene are believed to be involved in signal transduction pathways for volicitin-induced volatile emission. Nitrogen deficiency caused an increase in the level of jasmonic acid and an increase in ethylene sensitivity, and hence may

have stimulated signaling leading to volatile emission [72]. Despite these intriguing results, most combinations of herbivory and abiotic stress factors remain to be tested for their effects on VOC emission. Additional studies using a variety of plant species are needed before further generalizations are possible.

Interaction of biotic stresses: pathogens and herbivores

Under natural conditions, plants are often subject to simultaneous attack by both herbivores and pathogens, but the combined effect of these stress factors on VOC emission has rarely been investigated [81]. In maize, fungal infection reduced the emission of VOCs induced by lepidopteran herbivory alone by about 50% [82]. This may represent a diversion of plant resources from anti-herbivore to presumptive anti-pathogen defenses. A plausible mechanism is that fungal infection could stimulate the salicylic acid-based signal transduction pathway which would reduce signaling through the herbivore-triggered jasmonic acid pathway because of negative crosstalk [82].

Pathogen infestation by itself sometimes results in a different blend of volatiles than that seen after herbivore attack. For silver birch (*Betula pendula*), VOCs released after herbivore damage include the terpenes (*E*)- β -ocimene, (*Z*)-ocimene, α -farnesene, linalool, DMNT, plus methyl salicylate [83]. However, infestation by a fungal leaf pathogen on this species induced only the first three compounds in the list. In peanut, herbivore damage induced only DMNT, while pathogen infection led to release of DMNT, 3-octanone and methyl salicylate [84,85]. Aphid infestation has some similarity to pathogen

attack and on soybean aphids caused emission of methyl salicylate and α -farnesene [53]. On silver birch and black alder saplings, aphid infestation also increased methyl salicylate emissions substantially [52]. Since both pathogen and aphid attack often trigger activation of the salicylate signaling pathway in plants, it is perhaps not surprising that the emission of methyl salicylate increases under these conditions. When this compound is included in an herbivore-released VOC blend, it could function as a reliable signal (for other herbivores and herbivore enemies) of the presence of another biological stress factor: pathogens or aphids. In general, aphids and other phloem-feeding insects can significantly alter the blend of VOCs released by leaf-chewing herbivores [81].

Multiple stresses and the role of isoprene

Whether different stress factors cause changes in VOC composition should depend on the specific roles of individual volatile compounds in alleviating particular stress conditions. In our present state of knowledge, it is unclear why a single volatile compound could not mitigate against various stresses at the same time. In this section, we consider isoprene, which after nearly 30 years of research is widely accepted to function in plant resistance to abiotic stresses, such as high temperature and oxidative stress [20]. Could isoprene also function in resistance to herbivores, as other terpene volatiles do? On the contrary, most evidence indicates that isoprene is not involved in resistance to herbivory. For example, isoprene does not appear to repel a leaf beetle specializing on poplar (*Populus* \times *euroamericana*) from landing on the plant [86]. And, when expressed ectopically in *Arabidopsis* (*Arabidopsis thaliana*), isoprene reduces the attraction of an herbivore enemy that normally seeks its lepidopteran host on wild-type *Arabidopsis* [87]. In fact, herbivore damage to poplar causes an increased allocation to monoterpene and sesquiterpene emission at the expense of isoprene [79,86]. This pattern is in keeping with the relative reactivity of these terpenoids in the atmosphere. Most of the monoterpenes and sesquiterpenes involved in herbivore defense have a much shorter lifetime than isoprene [88], and thus may provide more ephemeral, but more accurate close-range signals for insect orientation. All of these lines of evidence indicate that individual volatiles have specific roles in various stress responses. Hence a recent report on the anti-herbivore effects of tobacco engineered to emit isoprene at a rate found naturally in other species was quite surprising [47]. This transgenic tobacco line and an artificial diet emitting isoprene both significantly deterred feeding by tobacco hornworm larvae suggesting that isoprene might function in response to both biotic and abiotic stresses. Further investigation is needed to determine if isoprene is actually toxic to this lepidopteran, if the compound alters host quality in another way, or if isoprene just serves to signal the insect that it is on the wrong host plant.

Multiple stresses and global climate change

Knowledge of how multiple stresses affect biogenic VOC emission could help in anticipating the effects of global climate change [89]. Current models predict that anthropogenic impact will not only increase mean temperature,

but also increase the frequency of drought and flooding [90], and increase oxidizing conditions due to continuous elevation of background O₃ levels [91]. The additive effects of these stresses might lead to substantial increases in isoprene, monoterpene and sesquiterpene emission from vegetation. The increased photosynthetic rate and increased leaf area index predicted under future climatic conditions [92] could also enhance this trend. Global warming is additionally expected to trigger more frequent biotic stresses, such as extensive insect outbreaks in forested temperate areas [93]. These could also promote increased VOC release on an ecosystem or landscape scale. A recent study on conifers demonstrated that herbivory increases monoterpene and sesquiterpene emission from undamaged as well as damaged tissues [80].

The effects of climate change on VOC emission could feed back on future conditions in unexpected ways. For example, when herbivore-inducible monoterpenes and sesquiterpenes react with ozone, aerosol particle formation in the atmosphere is activated [94]. Aerosol particles in the range 60–100 nm form nuclei which promote cloud condensation and reduce solar radiation [95]. Thus, an increase in insect outbreaks could have the potential to alter global weather by promoting reactive aerosol-forming volatile emissions and cloud formation. On the other hand, abiotic stresses, particularly high temperature that induces higher quantities of isoprene emission from vegetation [12] could have an opposite effect. Recently it has been shown that a greater proportion of isoprene in the atmosphere relative to other VOCs reduces the nucleation of other VOCs leading to a decline in the formation of aerosol particles [96]. If these results are extrapolated to the vast forested areas of isoprene-releasing species, abiotic stresses may actually end up reducing cloud formation. Thus, future changes in the relative proportion of isoprene-emitting species and the frequency of herbivore outbreaks might affect our climate in different ways via alterations in the composition of volatile emissions.

Conclusions and future perspectives

The relationship between plant stress and VOCs has been studied for several years in many ways, but stresses have usually been considered as single, independent factors. As this review has shown, the interaction of multiples stresses, both biotic and abiotic, has great potential to alter VOC emission. Unfortunately, there is still too little experimental evidence to draw any wide-ranging conclusions on the topic. But since the occurrence of multiple, rather than single stresses, is probably the rule under natural conditions, it is hoped that investigators will give this topic more attention in the future. Knowledge of how multiple stresses affect VOC emission will also provide more information to evaluate the biological roles of VOCs in mitigating stress [88].

One stress combination worthy of particular study in the future is the effect of herbivory and temperature on VOC emission. Plant volatiles with relatively low vapor pressures, such as sesquiterpenes and methyl salicylate, might play different biological functions at low temperatures because of their low volatility. At temperatures below 20 °C, these compounds tend to condense on the surfaces of

plants rather than remaining in the atmosphere [97,98]. They may also partition into the particle phase [99] or condense on the surfaces of aerosol particles [100,101] in the atmosphere immediately surrounding the plant causing increased particle size, aggregation and eventual deposition back on the plant surface [89]. Whether on the plant surface or in the atmosphere, the high reactivity of VOCs can be expected to give rise to organic acids and other reaction products as demonstrated in gas phase studies [101]. The accumulation of VOC reaction products on plant surfaces could serve as an unanticipated new mode of defense against herbivores or pathogens. The levels of such reaction products could be especially abundant in environments where the concentrations of atmospheric oxidants (e.g. OH, NO₃ and O₃) are high [101]. Only the study of plant volatile emission under realistic, multiple stress regimes will be able to determine the natural occurrence of such VOC reaction products and their importance in plant function.

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