

Smelling global climate change: mitigation of function for plant volatile organic compounds

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Plant volatile organic compounds (VOCs) have important roles in plant adaptation to the environment and serve as infochemicals in multitrophic interactions. Global climate change factors, such as increased atmospheric carbon dioxide, ozone and temperature, could alter how insects perceive such compounds. Here we review recent research on the influence of climate change parameters on the ecological functions of VOCs, with specific focus on terpenoids, the best-characterized VOCs. We summarize how emission patterns and concentrations of VOCs could change in future environments, mainly from the perspectives of plant defense and stress responses. We discuss how higher carbon dioxide concentrations, elevated ozone levels and increased temperatures could affect the biological functions of VOCs, particularly their role in plant defense.

VOCs and plant adaptation

Volatile organic compounds (VOCs) are defined as any organic compound with vapor pressures high enough under normal conditions to be vaporized into the atmosphere; many such compounds are released by plants and, although difficult for humans to detect, can inform many other organisms about opportunity and danger. Biogenic VOCs (see [Glossary](#)) are involved in a range of ecological functions, including indirect plant defense against insects [1], pollinator attraction [2], plant–plant communication [3–5], plant–pathogen interactions [3], reactive oxygen species removal [6], thermotolerance [7] and other environmental stress adaptations [8]. Their evolution is complex, affected by interactions of plants with biotic and abiotic factors in constantly changing environments [9].

Whether plant VOCs evolved mainly as a defense against biotic and abiotic stress or to serve plant reproduction as a means of attracting pollinators and seed dispersers is still a matter of speculation. However, VOC production and emission can be affected by abiotic factors, such as temperature and light. In addition, changes in carbon dioxide (CO₂) and ozone (O₃) concentrations in future atmospheres could also have significant effects on the patterns, magnitude and stability of biogenic non-

methane VOC emissions that affect atmospheric reactions contributing to secondary organic aerosol formation, as well as on those emissions released by the actions of predator and parasitoid insects during multitrophic signaling [10].

Given that global CO₂ and tropospheric O₃ concentrations are likely to continue to increase over the coming decades [11], it is important to consider the effects of elevated CO₂ and O₃ as a potential driving force of VOC evolution [12,13]. Atmospheric CO₂ levels are not only already exceeding those from the past 650 000 years [11] but are also associated with changing temperature and precipitation patterns [11]. Biogenic VOC emissions are affected directly by the prevailing temperature, which affects their volatility and humidity and, thus, their movement at the leaf surface [14]. Recent research has highlighted additional effects of climate change factors on the biosynthesis and abundance of VOCs in the atmosphere [15,16], which, in turn, could mitigate their biological and ecological functions [17]. Here we summarize the ecological

Glossary

Biogenic VOCs: compounds released through biochemical actions; commonly used to refer to VOC emissions from vegetation.

Green leaf volatiles (GLVs): green leaf volatiles; fatty acid-derived C₆ alcohols, aldehydes and acetates, for example of hexenol, hexenal or hexenyl acetate origin. These occur universally in plants and are released rapidly from plant surfaces upon wounding through lipoxygenase action; when released in large amounts, they have a characteristic “freshly cut grass” odor.

Indirect defense: the ability of a plant to attract organisms of higher trophic levels for its own benefit. Indirect defense mediated by VOCs involves induced emissions of volatiles upon herbivore attack, which predators or parasitoids perceive and orientate toward. The outcome is beneficial for the emitting plant and the predating or parasitizing insect but harmful for the attacker.

Infochemical: chemical cue that mediates information to a perceiver; they are important for tritrophic and other ecological communications.

Resource availability theory: under nitrogen limitation, more carbon is allocated toward the production of secondary compounds for defense.

Specific leaf area: leaf area per unit of leaf mass. Commonly used as a parameter to determine changes in leaf thickness.

Terpene synthase: a class of enzymes whose gene family consists of >100 currently characterized genes. Some of these produce a single product, whereas others result in the synthesis of multiple terpenoid products.

Terpenoids: isoprenoids are the largest class of secondary metabolites in plants, of which some are volatile. Terpenoids are formed from isopentenylidiphosphate and dimethylallyldiphosphate through the mevalonate or the methyl-erythrol-phosphate pathway. In particular, volatile mono-, sesqui- and homoterpenoids have been linked to biogenic VOC signaling.

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Table 1. Known ecological roles of biogenic VOCs

Fields	Roles	Examples	Refs
Plant reproduction	Pollination	Attraction of honeybees and moths	[2,69]
	Seed dispersal	Attraction of seed dispersers	[70,71]
Plant defense	Direct defense against herbivores	Repelling effect on conspecific herbivores	[72]
	Indirect defense against herbivores	Attraction of aboveground and belowground predators and parasitoids	[1,30,73]
	Direct defense against pathogens	Antimicrobial or antifungal effects of volatiles	[5,72,74,75]
Population ecology	Plant–plant signaling	Activation of defenses in neighboring plants	[3,4]
	Allelopathy	Reduced seed germination	[76]
Interactions with environment	Abiotic stress tolerance	Oxidative stress relief	[6]
		Thermotolerance	[7]

functions of VOCs (Table 1) and the effects of global climate change on their production; we go on to discuss how the evolution and ecological functions of VOCs might be altered in future environments, and how organisms might respond to VOCs.

Know your VOCs

VOCs are classified according to their structure and biosynthetic origin [9]. Of current interest to global change research is the simplest terpene isoprene, a five-carbon compound that forms >90% of the total VOC emissions of certain plant species, such as poplar (*Populus*) [18], and contributes to global VOC emissions. Terpenoids [1], green leaf volatiles (GLVs) [4], phenylpropanoids, benzenoids [19] and indole [20] and methyl esters of plant hormones (i.e. methyl jasmonate and salicylate) [21] all contribute to plant–plant, plant–insect and tritrophic interactions that are mediated via VOCs.

With the exception of GLVs, which are ubiquitous and wound induced, genotype is an important determinant of constitutive VOC emissions from plants. The terpene synthase gene family is one of the most diverse gene families, and sequence diversity is common among different cultivars or ecotypes within species [22]. Minimal changes in crucial residues can lead to changes in product profiles and, thus, plants produce suites of volatiles [9,22–24]. This unique feature of the terpene synthase gene family has enabled plants to produce diverse new compounds, which could be important in the adaptation of plants to future environmental change.

The VOC emissions from various plant organs are highly variable and developmentally regulated; for example, differences exist according to circadian rhythms [25] and plant age [26]. Flowers of many plant species emit VOCs in a diurnal or nocturnal cycle-dependent pattern to attract their main pollinators at the most appropriate time [27]. The expression of genes encoding terpene synthase and the emission of volatile terpenoids are both found in *Arabidopsis* flowers, which are almost completely self-pollinated under growth room conditions; however, these compounds had been suggested to be responsible for attracting pollinators in the wild, as the naturally occurring *Arabidopsis* populations have a low percentage of cross-pollination [28]. These compounds were also speculated to have a defensive role against oxidative damage or plant pathogens [28].

The inducible compound emissions involved in plant–insect or plant–plant interactions as infochemicals depend first on the plant species and genotype [29], and second on the type of insect inducer [30]. Other factors such as

nutrient and water availability [31] or atmospheric gas composition [24,32] can set limitations, promote or even interfere with this induction. The evolutionary development potential of VOCs in plant ecology therefore appears highly dynamic. The main known ecological functions of plant VOCs are discussed in Box 1.

Influences of global climate change on the production, emission and stability of VOCs

Altered environments caused by global climate change are expected to influence the emission of VOCs through alterations in plant phenology (differences in growth and maturation) [33], direct physiological factors (i.e. physicochemical properties of VOCs and stomatal function in plants) [14] and allocation of resources (i.e. substrate availability) [15], leading to changes in VOC biosynthesis pathways. Inducible VOC emission as affected by climate change is additionally complicated by herbivore-mediated effects, such as direct and plant-mediated effects on herbivore performance and feeding patterns [34]. For example, elevated CO₂ can increase herbivore feeding damage by compensatory feeding [35], affect herbivore-inducible VOC emissions [32,36] or alter the preferences of herbivores for host species or genotypes when given a choice [37].

Carbon dioxide increases and VOC emissions

Atmospheric CO₂ concentration is an important factor determining carbon sequestration in plants, and the resulting photosynthesis and carbon fixation are related to VOC production. One hypothesis is that there is a positive relationship between terpenoid volatile production and CO₂ concentration in the atmosphere [38]. Based on resource availability theory, more available carbon would yield commensurately higher terpenoid biosynthesis, resulting in the higher production and emission of monoterpenes and sesquiterpenes [38]. Early studies in conifers suggested that increased CO₂ levels would not lead to a net increase in monoterpene volatile production because of the increase in total biomass and a steady state of emission per unit of biomass [39]. Indeed, the evergreen oak *Quercus ilex* produced lower amounts of monoterpenes (e.g. α -pinene, sabinene and β -pinene) under high CO₂ conditions, possibly as a result of inhibited monoterpene synthases responsible for the biosynthesis of these compounds [40]. By contrast, the emission of another monoterpene, limonene, was enhanced under conditions of elevated CO₂, which corresponded to the increased activity of limonene synthase [40]. This work underlines the dynamic changes in terpenoid metabolism that could

result from the differential response of terpene synthases to higher CO₂ levels. There are also clear indications of decreased isoprene emission at higher CO₂ concentrations [15,41], but uncertainty exists as to whether these findings can be extrapolated to higher terpenoids.

Other studies have revealed VOC patterns [32,42] that might arise from phenological effects. For example,

increased CO₂ levels affect many aspects of plant physiology, including higher growth rates, higher carbon:nitrogen ratios and decreased specific leaf area [39,43], all of which could lead to altered biosynthesis of terpenoids and other VOCs. Response patterns and the developmental effects of elevated CO₂ action on VOC emissions could be better revealed by measuring VOC emissions over the

Box 1. Possible outcomes of increased atmospheric CO₂, O₃ and temperature on the signaling efficiency of VOCs in different ecological interactions

Figure 1 details plant interactions with other species and conspecifics in which VOCs have a signaling role. The positive and negative VOC effects on the emitting plant and on interactive species in each case are indicated by plus and minus signs, respectively. A positive effect will enhance the activity of interactive species, and vice versa. Letters indicate points of interactions as defined in Table 1.

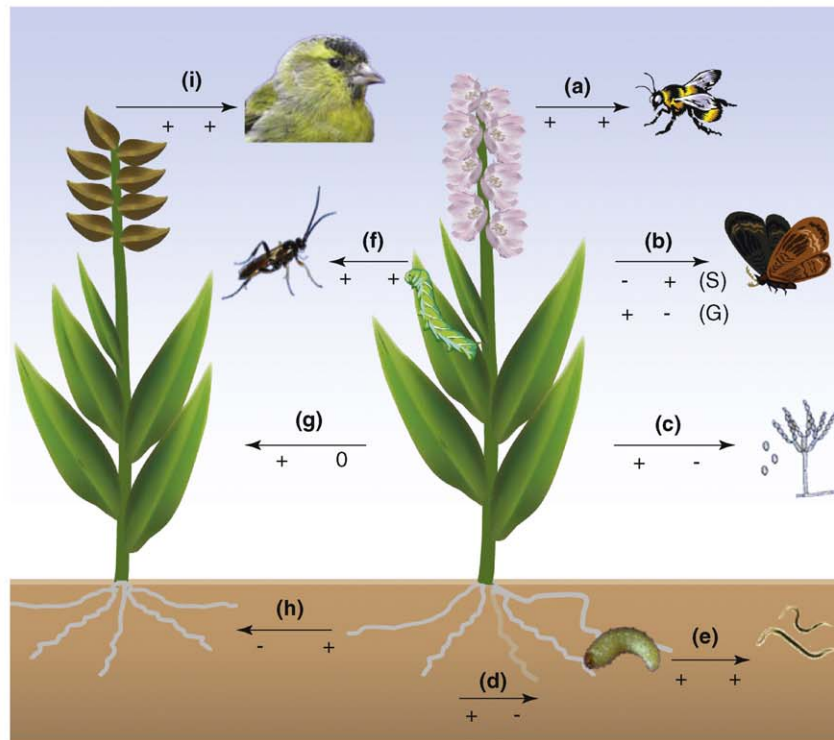
Higher VOC production and volatility under elevated temperatures [49] might enhance plant–pollinator interactions (Figure 1a), alter the ability of specialist herbivores (Figure 1b,d), predators or parasitoids (Figure 1e,f) or frugivores (Figure 1i) to locate their hosts and increase pathogen defense (Figure 1c) and/or alter plant–plant interactions (Figure 1g,h). Higher atmospheric O₃ concentration degrades certain biogenic VOCs [17] and could reduce pollination efficiency and disturb herbivores, higher trophic-level and plant–plant interactions aboveground [60]. Phytotoxic O₃ levels could also induce the production of other inducible VOCs [45], which might mask herbivore-induced VOCs as cues. Elevated CO₂ leads to reduced seasonal terpenoid emissions [15,39,40], which decrease VOC signals for higher trophic levels, although this generalization appears to depend on the tritrophic system in question [32,36]. CO₂ effects on floral VOC production are largely unknown.

Nonspecific VOCs such as GLVs appear to be important in plant–plant signaling [3], and their responses to abiotic variations are more unpredictable than are those of terpenoids. Volatile terpenoids in allelopathic root exudates affecting competing plant species could be

increased under elevated CO₂ [76]. Higher root allocation and higher temperatures can increase herbivore-deterrent terpenes in roots [77], but the belowground VOC responses to O₃ [78] are hard to predict, because these signaling interactions, in general, are poorly understood. However, belowground, O₃ is unlikely to affect VOC distribution in soil pores, as O₃ is easily dissolved in the water film on soil particles.

Under higher temperatures, insects (herbivores, predators and parasitoids) have higher metabolic activity and might be more receptive to plant infochemicals. Herbivorous insects experience abiotic stress, including high temperatures and elevated CO₂-mediated reduction in plant quality [35]. Moderately elevated temperatures or elevated CO₂ have been shown to enhance feeding by certain herbivores [35,79] and this, in turn, could increase inducible VOC emissions [31,32].

Plant diseases caused by bacteria and fungi could be less virulent under warmer and drier conditions, whereas these conditions favor the spread of virus pathogens and their vectors. O₃ can directly harm the growth of fungal hyphae and increase levels of phenolics and other antifungal compounds in plant tissues. Also, elevated CO₂ could increase stomatal closure and cause structural changes that reduce fungal penetration [33]. Increased O₃ might also induce VOCs resembling the hypersensitive response found after pathogen attack [45]; thus, induced VOCs in the stomatal cavity and leaf boundary layer [80] could decrease fungal pathogen growth and even enhance plant defenses against such pathogens.



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Figure 1. Plant interactions with other species and conspecifics for which VOCs have a signaling role. G = generalist herbivores; S = specialist herbivores.

Table 1. Possible effects of changing climate on VOC-mediated signals

Interaction type ^a	Elevating temperature	Elevating CO ₂	Elevating O ₃
(a) Pollination	Increase due to higher VOC synthesis and/or volatility	Difficult to predict	Decrease due to VOC degradation, leading to reduced reach of floral scent trails [60]
(b) Aboveground herbivory (specialist herbivores [S]; generalist herbivores [G])	Decrease due to interference of specific signals or increase in VOC cue abundance (S) No effect (G)	Decrease in cue abundance [15,40]	Decrease due to VOC degradation
(c) Fungal pathogens	Increase due to higher VOC synthesis and/or volatility	Difficult to predict	Increase by induced VOCs in leaf inner space
(d) Belowground herbivory	Difficult to predict	Difficult to predict	Difficult to predict
(e) Belowground predation	Difficult to predict	Difficult to predict	Difficult to predict
(f) Aboveground predation	Species specific; interference possible; e.g. higher isoprene emission due to increased temperature could lead to a negative (or no) effect on parasitoids [81]	Species specific; decrease [36], no effect [36] or increase in herbivore-induced VOCs [32]	No effect [17,45] or a decrease in parasitoid attraction by induced VOCs [32]
(g) Plant–plant signals	Increase due to higher VOC synthesis and/or volatility, but interference possible	Difficult to predict	Decrease due to VOC degradation
(h) Root–root signals	Increase due to increased root allocation	Increase due to increased root allocation	Difficult to predict
(i) Frugivory	Increase due to higher synthesis and/or volatility	Difficult to predict	Decrease due to VOC degradation

^aLetters in parentheses refer to corresponding letters in Figure 1.

complete life cycle of a species. Alterations in stomatal density and conductance, along with the physicochemical factors affecting volatility and diffusion of different VOCs from the leaves [14], could also affect the abundance of VOCs in CO₂-enriched atmospheres in addition to changes in their rate of biosynthesis. For example, emission of the oxygenated monoterpene linalool is more restricted by stomatal control than is that of the non-oxygenated, water-insoluble (*E*)- β -ocimene [44]. The emission of VOCs other than terpenoids, such as hydrocarbons 2-undecanone and 2-tridecanone, are also increased by higher CO₂ concentrations [42], although we know even less about their regulation by elevated CO₂. An important caveat at this point is that many of the existing studies have been performed under artificial conditions; therefore, more research is needed on responses of different taxa in undisturbed natural settings, but with modified atmospheres. These studies are necessary to verify the impact of terpene synthase regulation and terpene emission.

Elevated tropospheric O₃ and VOC emissions

O₃ reacts directly with VOCs in the atmosphere, leading to rapid degradation of certain volatiles, including terpenoids and GLVs [17]. The atmospheric lifetimes of VOCs are highly variable, depending on their chemical structure and reactivity with O₃ (Figure 1). Elevated O₃ either as chronic higher background concentrations or as increasingly frequent high O₃ episodes causes oxidative stress to plants [11]. Given that some VOCs, including isoprene, have important roles in reactive oxygen stress relief by scavenging reactive oxygen species in leaf inner space [7], increased O₃ in the atmosphere could have substantial impacts on plant VOC emission. Higher O₃ levels have been found to lead to higher constitutive and herbivore-induced emissions of terpenoids, GLVs and isoprene as well as total VOCs [45–47]. O₃ also induces systemic acquired responses in plants and could lead to emission of other induced VOCs [3]. Furthermore, it is feasible that known variability in O₃ sensitivity of plant genotypes might affect the evolution of

induced VOC responses to O₃. If VOC induction protects from oxidative stress, genotypes with the highest capacity for VOC induction (and highest O₃ sensitivity) could thus have increased fitness. However, further work is required to investigate this hypothesis further.

Combined elevated CO₂, O₃ and VOC emissions

Increased O₃ and CO₂ in future atmospheres could have synergistic effects on VOC emissions. When grown in a free-air carbon dioxide enrichment (FACE) experiment, an O₃-sensitive clone of aspen, *Populus tremuloides*, had decreased isoprene emissions with elevated O₃ or CO₂ alone and CO₂ and O₃ combined; by contrast, an O₃-tolerant clone had a higher capacity to maintain isoprene emission under these variations [13]. This shows first that O₃ could overcome the expected higher CO₂ effect [16], and second that the overall pattern could also depend on O₃ sensitivity [13].

Impact of increased temperature and related environmental stress on VOC emission

Elevated temperature has long been known to increase biogenic VOC emissions and is used as a variable of algorithms to standardize terpene emission rates [48]. The abundance of biogenic VOCs is also affected by physicochemical factors, such as volatility and diffusion, which respond significantly to temperature differences [14]. The strong correlation of terpene emissions with temperature indicates that there is likely to be increased emissions under warmer climate conditions [49]. Some VOCs, such as monoterpenes and isoprene, have important functions in plant adaptation to heat stress and increased temperature (Table 1) [7,31,49,50]. For example, isoprene fumigation increased the recovery of bean, *Phaseolus vulgaris*, leaves from a short-term (2 min at 46 °C) heat stress by 20–40% [7]. Thus, temperature-dependent increase of VOC emissions might be expected to be important in the future evolution of thermotolerance of plants.

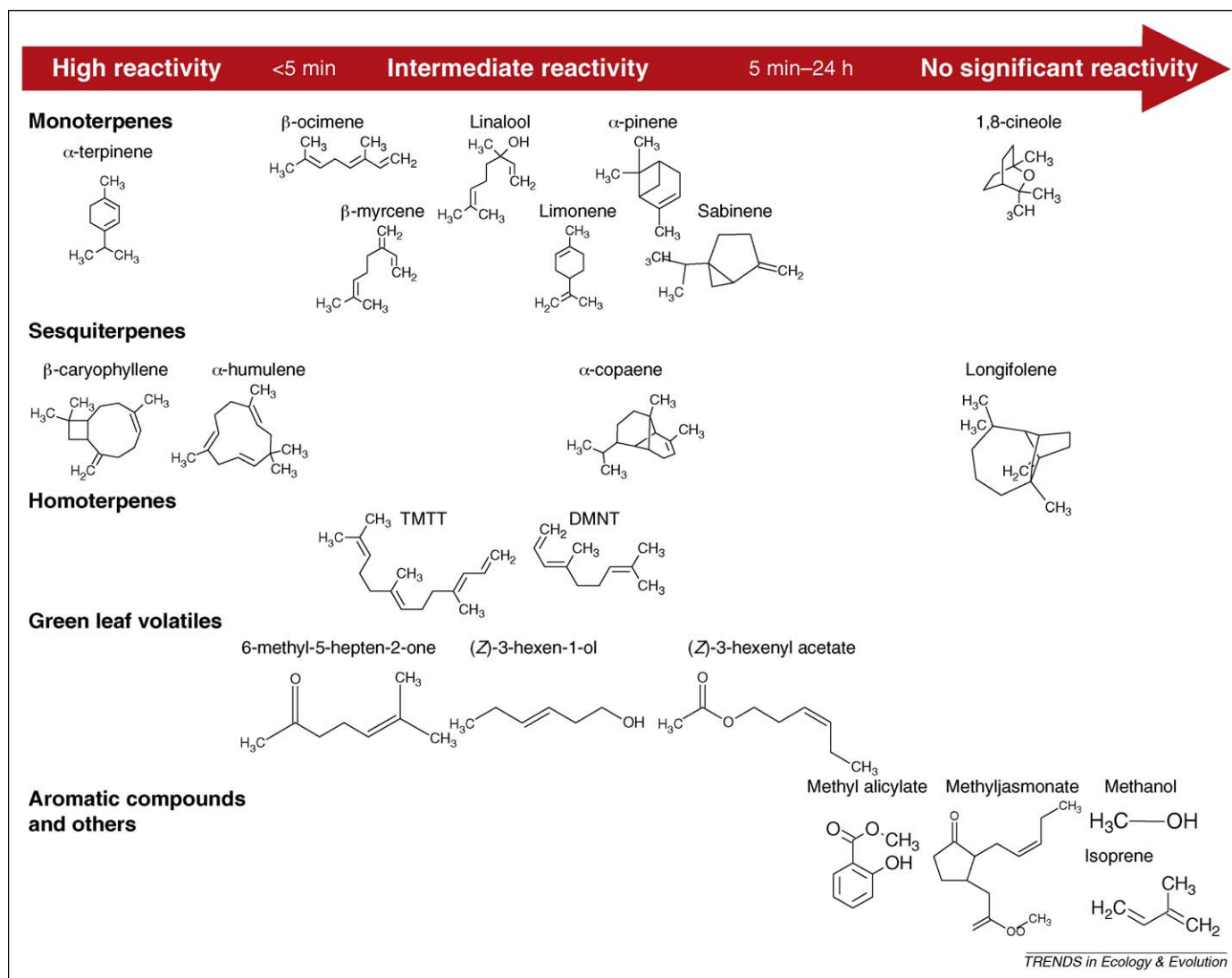


Figure 1. Reactivity (based on atmospheric lifetimes) with O_3 of selected compounds representing different VOC groups [14,47,50]. The degree of O_3 reactivity is based on the structural properties of VOCs, such as the presence of double bonds in the carbon skeleton to which O_3 can initially add [68]. DMNT = (*E*)-4,8-dimethyl-1,3,7-nonatriene; TMTT = (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene.

The effects of drought stress, another expected regional effect of global climate change, on terpenoid emission partly depends on the type of water loss. Short-term water loss decreased sesquiterpene emission, but increased monoterpene emission in Mediterranean species [51]; however, long-term water stress decreased all terpenoid production [51]. Severe drought stress was recently shown to reduce isoprene emission from black poplar, *Populus nigra* L., leaves with reduced recovery even after watering under high-growth temperature (35 °C) [52]. Thus, it still seems that the overall effects of drought and higher temperature on VOC production depend on the degree of temperature increase, the plant species, the compound group and the season [53].

In addition to temperature and drought, VOC emission from plants might also be altered by environmental factors that are not directly related to climate change but that contribute to these responses by interacting with elevated CO_2 and temperature levels, such as nutrient availability [39] and within-plant allocation, or light conditions [31]. Overall, despite consensus that elevated temperature increases VOC emissions [48,49], phenological effects, such

as altered seasonality and leaf duration and associated interactions with water and nutrient availability, might lead to alterations in VOC emission capabilities, for example, in drought-stressed plants [51,53].

The impact of global climate changes on the ecological functions of VOCs

Overall, global climate change could have a substantial influence on the emission and production of VOCs, which could, in turn, have highly variable ecological effects that are currently difficult to predict. Although only a few studies address these effects, we examine the current ecological roles of VOCs and speculate on possible patterns of future change, as illustrated in Box 1.

The influence of VOC emission changes by climate change factors on tritrophic interactions

Infochemical signaling in tritrophic interactions are intricate, and should not be underestimated when considering how changes of volatile emissions could affect ecological function. The amount and composition of VOCs released from plants differ both among plant species and within

plant growth stages [28] and depend on the attacking insect species [30]. A change in volatile production or even in the ratio of particular VOCs as a result of abiotic stress could result in miscues by parasitoid and predator species, which might decrease their abundance through lower forage efficiency and lower recruitment. For example, in the system consisting of cabbage, *Brassica oleracea*, the herbivore insect *Plutella xylostella* and the generalist predator *Podisus maculiventris*, as well as the specialist parasitoid *Cotesia plutellae*, elevated CO₂ appeared to have minimal effects on terpenoid production, with a slight decrease in emissions of farnesene and the homoterpene DMNT [36]. However, the minor VOC decreases translated to higher trophic-level effects in the system, because both predator and parasitoid species failed to respond to the volatile signal sent by damaged cabbage grown under elevated CO₂ concentrations [36]. In a similar laboratory study with young oilseed rape *Brassica napus* plants, elevated CO₂ levels increased constitutive and herbivore-inducible terpenoid emissions, but did not negatively affect the orientation of *C. plutellae* to *P. xylostella*-damaged plants [32]. Percy *et al.* [54] found higher natural enemy abundance under elevated CO₂ on *P. tremuloides*, but the role of VOCs in this context was not determined. Laboratory studies are only the first phase of assessing the actual CO₂ effects on natural enemy orientation, so more field data from FACE experiments are needed, including data from variable tritrophic systems, before conclusions can be made about the effects of elevated CO₂.

Investigations into the effects of O₃ on tritrophic interactions have shown that O₃ alters volatile emission patterns, but does not change parasitoid responses in specialized tritrophic interactions [17,45]. These results also suggest that relatively rare O₃-reactive, herbivore-induced VOCs could act as attractants for parasitoids in O₃-rich atmospheres [10]. However, the degree of herbivore feeding damage is an important factor for the maintenance of tritrophic interactions under elevated O₃. In the case of insect-resistant *B. napus*, reduced feeding damage led to the attraction of fewer *C. plutellae* under elevated O₃ compared with ambient conditions [32]. Given that significant changes in volatile contents and composition can occur under increased O₃ levels, more research is needed in different ecosystems and experimental settings to examine whether increased O₃ will mitigate tritrophic interaction in a predictable manner [10,17].

Multitrophic VOC signaling has been studied by examining induced VOC emissions over ranges of temperatures [31]. One complication is that elevated temperature often directly enhances insect activity [34], which could lead to altered geographical distributions of parasitoids and their host insects, and also altered fitness landscapes, which could affect tritrophic interactions [55,56]. Given the complexity, increased temperature effects on multitrophic communication are currently best regarded as system specific, and general predictions are thus difficult to make.

The influence of climate change on other functions of VOCs

As compared to VOCs involved in tritrophic interaction, less research has been conducted on the changes of VOC

content in flowers as the result of global climatic change factors and the VOC effect on the interaction between plants and pollinating insects. In addition, global warming is likely to change flowering timing and fruit development, which could result in changes in the relationship between plants and pollinating insects, for example, altering frequency distribution of overlap between flower phenology and insect availability for pollination [57–59]. A recent modeling study suggests that current tropospheric O₃ could reduce the maximum downwind distance of highly reactive floral scents from kilometers during pre-industrial times to no more than 200 m during the more polluted conditions of the present [60]. This might lead to reduced searching and foraging efficiency of pollinators during O₃ episodes.

The role of VOCs in relieving abiotic stress such as temperature and reactive oxygen species is expected to be enhanced in future climates when the abundance of high temperature or O₃ episodes is predicted to be more frequent [11]. Moreover, given the plant–plant communication role of terpenoids, the altered volatile content and composition as a result of climate change might alter these relationships by either weakening or strengthening the signals for neighboring plants. Plant–plant communication research under global climate change factors should be a ripe area of future research. Thus, some VOCs, such as terpenoids, have been implicated in multi-trophic interactions involving plants, pathogens and two trophic levels of insects, and the changes in plant VOCs might also mitigate or stabilize these interactions [61]. For example, plant volatiles from cassava, *Manihot esculenta*, which are produced during herbivore damage by green mite, *Mononychellus tanajoa*, trigger the sporulation of some isolates of the mite-pathogenic fungus *Neozygites tanajoa*, but not others [61]. Furthermore, these multitrophic effects vary by atmospheric conditions, making it difficult to determine a general response pattern [61].

Focus for future research

Based upon the work reviewed above, we can be reasonably sure that global climate change will have an impact on VOC emissions and their ecological functions, but our knowledge about the details is still limited, partly because of the complexity of the problem and that most of the research has been performed using small-scale studies with potted plants. We therefore propose several points that could help guide future research on ecological functions of VOCs during predicted climate change.

First, the changes of VOC ecological function might depend on system resource availability [15,31,38]. Although the original hypothesis of resource availability directly affecting carbon-based secondary metabolism [38] appears not to be directly applicable for terpenoids, competition for growth and higher photosynthesis versus VOC production [15] could be affected under future CO₂- and O₃-enriched atmospheres. It has been shown that high nitrogen availability might increase VOC emissions [31]. Therefore, competition for nitrogen under excess carbon, enhancing growth or allocation of resources under O₃ stress could also affect VOC biosynthesis.

Second, the tradeoff between the two different ecological roles of VOCs in mitigating plant stress (i.e. abiotic versus biotic) needs to be better understood. In the case of terpenoids, it is generally assumed that the evolution of the terpene synthase gene family has been driven primarily by plant defense against insects and pathogens. However, with increased O₃ and temperature levels, the evolution of terpenoid volatiles for the protection of plants against abiotic stress will become increasingly important. The evolution between plants and pathogens or herbivores and their predators might be perturbed by the evolution of plant response to abiotic stress. For example, given that terpenoids and isoprenes help relieve temperature stress, their overproduction could affect multitrophic signaling pathways.

Third, the learning ability of natural enemies of herbivorous insects and pollinating insects could largely define the plasticity of an ecosystem [62]. Many insects, including parasitoid species, possess highly evolved olfactory systems that can detect variations among amounts and compositions of volatile compounds, which enhances their capacity to learn and adapt to changing environments. One important class of insect parasitoids is parasitic wasps, which have the most advanced learning ability among insects [63]. Pollinators, such as moths and bees, have differing olfactory capacities, with moths typically using VOC cues over longer distances and requiring higher emissions [64], whereas bees can distinguish between small differences in ratios of compounds [65]. If parasitoids and pollinating insects evolve quickly enough to react to new compositions and ratios of volatile compounds produced by plants, ecosystems could be expected to be less perturbed by changing climates, and the functions of volatile terpenoid compounds might not significantly change [66]. Failure to adapt could result in the disruption of plant defense and reproduction.

Conclusions

As with many aspects of global climate change, the roles of VOCs in ecology and evolution are influenced by many factors. As data emerge on the genetic, biochemical and physiological controls of VOC emissions associated with climate change, new models are needed for leaf-level, whole-plant or vegetation-level systems [67]. Currently, there are many gaps in our understanding of VOC signaling interactions, even under current climatic conditions. The infochemical flow among organisms could be altered if abiotic climate change factors do cause significant changes in pools and the timing of emissions of VOCs. The content and composition of VOCs, the abundance and biodiversity of relevant insects in the system and the biotic and abiotic stresses are interacting to shape indirect defense systems. These different roles and effects of volatiles represent valuable research opportunities. For example, more investigations are needed to elucidate how insect-mediated pollination might alter during global climate change and how plant–plant communications could be affected by altered volatile terpenoid emissions. Changes in volatile signal production might have a more profound impact on plant–plant communications as compared to plant–insect interactions,

given the absence of the olfactory organs in plants that are present in insects.

Overall, the changes of terpenoid volatile production, emission and function with climate change are likely to alter plant–insect interactions, and the resulting ecosystem evolution should be a fruitful field for research. Most valuable are research setups that are long-term field-based model systems that enable the incorporation of phenological data, detecting changes in VOC emission profiles throughout the growth season, measurement of relevant insect abundances (natural and introduced) and a means to integrate year-to-year and seasonal effects. However, laboratory-based first-phase experimentation is crucial to elucidate the underlying specific mechanisms for plant responses. Systems biology and transgenic approaches could thus be ideally suited to detangle the complexities of VOC signaling.

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