

Chapter 2

Environmental Impacts on Plant Volatile Emission

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Abstract Plants in their natural environment are often exposed to a variety of environmental stresses. This chapter emphasises the importance of distinguishing among stress effects on constitutive and stress-induced volatile emissions and, within constitutive emissions, among stress effects on emissions from specialised storage compartments (storage emissions) and de novo emissions. Among constitutive emissions, de novo emissions are typically more sensitive to stress than storage emissions. Depending on stress severity, the emission response is either physiological or the emission response is controlled at the gene expression level. This chapter analyses the impacts of heat, cold, drought and waterlogging stresses on constitutive and induced emissions, highlights similarities and differences of various stresses on volatile release and outlines the gaps in knowledge. We argue that for a fully mechanistic understanding of environmental impacts on plant chemical communication channels, more work is needed to obtain quantitative stress dose versus emission responses for different stresses in species of differing stress tolerance.

2.1 Introduction

Plants synthesise more than 100,000 chemical products and at least 1700 of these are known to be volatile. In the literature, the term *biogenic volatile organic compound* (BVOC) includes organic atmospheric trace gases synthesised by living

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organisms, typically excluding methane (Kesselmeier and Staudt 1999). Vegetation emits a wide array of different BVOC with isoprenoids (Fig. 2.1a), volatile fatty acid derivatives such as different C5 and C6 alcohols, aldehydes and ketones, and various benzenoids being quantitatively the most important compound classes (Arneth and Niinemets 2010; Fineschi et al. 2013; Niinemets et al. 2013).

The plant emissions can occur either under non-stressed conditions (constitutive emissions) or under stressed conditions (induced emissions and constitutive emissions) (Loreto and Schnitzler 2010; Niinemets 2010; Niinemets et al. 2010b). Only a limited number of plants are strong constitutive emitters of volatiles, but these emissions can often dominate the ecosystem, region and global emissions (Fineschi et al. 2013). Nevertheless, biotic and environmental stress can induce BVOC emissions in practically any plant species, and this can have a major impact on BVOC release from stressed ecosystems, with potential large-scale impacts (Arneth and Niinemets 2010; Grote et al. 2013). The induced emission of volatile organic compounds due to mild abiotic stress could prime the defence responses of plants upon exposure to a biotic stress (Conrath et al. 2006; Copolovici et al. 2014; Heil and Kost 2006; Niinemets 2010). On the other hand, plants that have been affected by a biotic stress could be protected from abiotic stresses due to enhanced elicitation of the chemical pathways responsible for the synthesis of protective compounds (Fujita et al. 2006) or due to the direct effect of these induced emissions on abiotic stress resistance (Owen and Peñuelas 2005). Furthermore, plants can signal neighbouring plants an imminent biotic attack using volatile organic compounds, and alteration of this signal by abiotic impacts could importantly affect the plant phenotypic response (Baldwin 2010; Baldwin et al. 2006), underscoring the importance of gaining an insight into the abiotic stress effects on BVOC emissions.

Among the constitutive emissions, volatile isoprenoids, including isoprene (5 carbon atoms, C5) and volatile terpenes such as monoterpenes consisting of two isoprene residues (C10) and sesquiterpenes consisting of three isoprene residues (C15; Fig. 2.1a), have traditionally been considered as the most important class of compounds released from plants due to the overall high contribution to total BVOC release and major roles in photosynthesis, respiration, membrane fluidity and biotic interactions (Fineschi et al. 2013; Harrison et al. 2013; Vranova et al. 2012). Furthermore, from a quantitative point of view, among the volatile isoprenoids, isoprene is globally the most important molecule released by plants into the atmosphere, followed by monoterpenes. The total isoprene emissions are estimated at about 550 Tg C year⁻¹ and the total monoterpene emissions at about 100 Tg C year⁻¹ (Arneth et al. 2008, 2010; Guenther et al. 2012). Due to their high reactivity, isoprene and terpenes play major roles in the determination of atmospheric reactivity and the formation of secondary organic aerosols and cloud condensation nuclei (Carlton et al. 2009; Engelhart et al. 2008; Hallquist et al. 2009; Kulmala et al. 2013).

Isoprenoids form a highly diverse class of compounds that are synthesised via two spatially separated pathways. The mevalonate (MVA) pathway is located in the cytoplasm and is used to synthesise volatile sesquiterpenes (Fig. 2.1) but also nonvolatile metabolites such as phytosterols (Gershenzon and Croteau 1993;

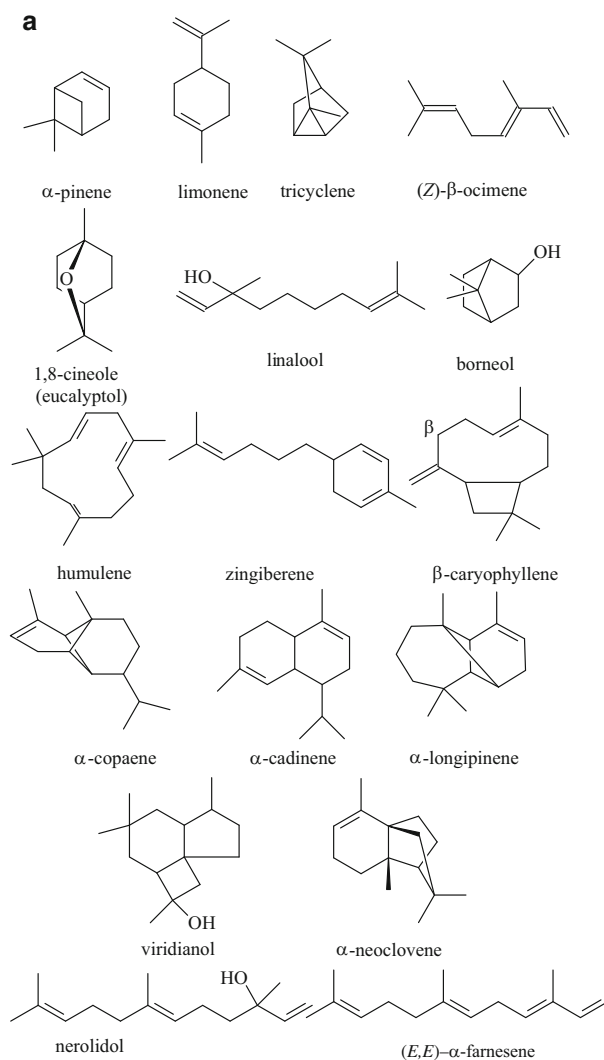


Fig. 2.1 Chemical structures of characteristic monoterpenes, sesquiterpenes and derivatives (**a**) and compartmentalisation of the biosynthetic pathways of volatile isoprenoids in plant cells (**b**). Typically, even single plant emissions consist of a complex blend of chemically heterogeneous volatiles. Often more than 20 different monoterpenes are emitted by a single species (Fineschi et al. 2013; Niinemets et al. 2004; Niinemets and Reichstein 2002). Monoterpenes can have acyclic or mono-, bi- and tricyclic structures. They are typically non-oxygenated with a few exceptions such as 1,8-cineole and linalool. There are a large number of oxygenated monoterpene derivatives. Sesquiterpenes can also be cyclic or acyclic, and there are many oxygenated derivatives. In (**b**), the C_{16} homoterpene (3*E*,7*E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT) and C_{11} homoterpene (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) are also shown. As TMTT is synthesised from the diterpene geranylinalool, its synthesis is expected to occur in the plastids as shown for the herbaceous legume *Lotus japonicus* (Brillada et al. 2013). However, in *Arabidopsis*, geranylinalool and TMTT synthesis occur in the cytosol (Herde et al. 2008)

b

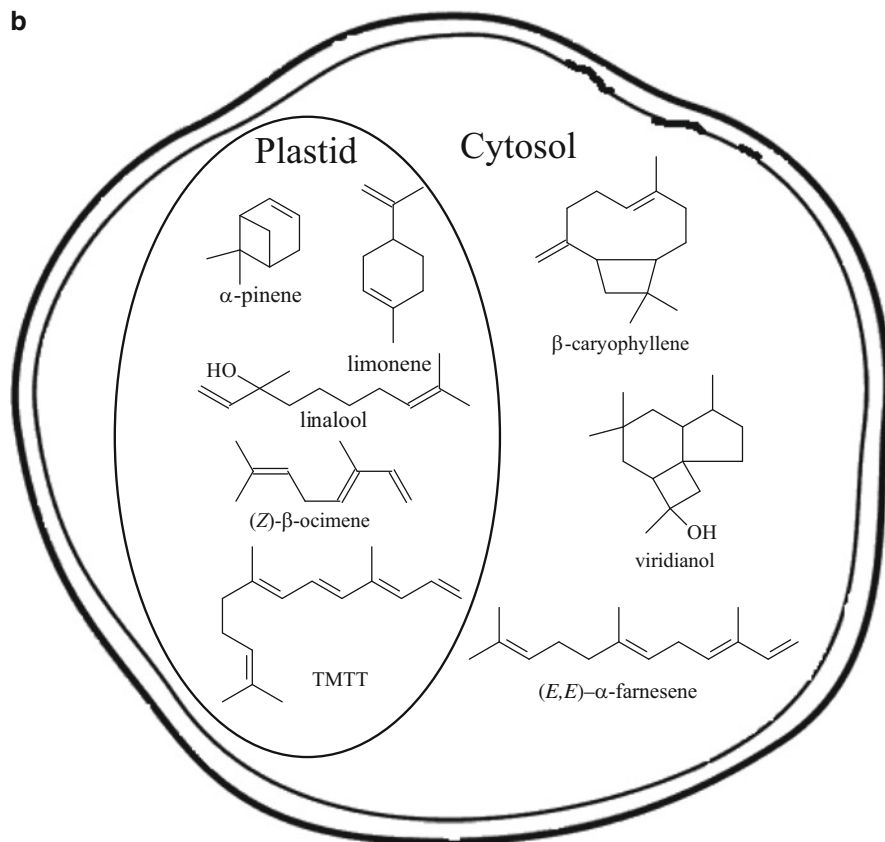


Fig. 2.1 (continued)

Lombard and Moreira 2011; Rosenkranz and Schnitzler 2013). The second pathway, the 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway, is located in plastids and is responsible for the synthesis of volatile isoprene and monoterpenes (Fig. 2.1) and multiple nonvolatile biologically highly relevant compounds such as carotenoids and the phytol residue of chlorophyll (Li and Sharkey 2013; Rajabi Memari et al. 2013; Rosenkranz and Schnitzler 2013). We refer to several recent reviews for details of pathway regulation and enzymatic synthesis of different isoprenoids (Baldwin 2010; Nakamura et al. 2001; Vranova et al. 2012).

Plants that are considered constitutive emitters of volatile isoprenoids can either be *de novo* emitters or storage emitters (Grote et al. 2013; Niinemets et al. 2010b). *De novo* emitters emit volatiles that have been immediately synthesised without being stored in a significant manner in plant tissues, while the emissions in storage emitters rely on compounds stored in specialised storage compartments and synthesised typically days to months prior to their release into the atmosphere. Constitutive *de novo* emitters mainly emit either isoprene (2-methyl-1,3-butadiene), 2-methyl-3-buten-2-ol (MBO) or monoterpenes, while storage emitters

typically release mono- or sesquiterpenes or both (Azuma et al. 2010; Huang et al. 2012; Jardine et al. 2011; Kesselmeier and Staudt 1999; Staudt and Lhoutellier 2011). Several species have a mixed mode of emission relying both on de novo and storage emissions. In particular, many *Abies*, *Eucalyptus* and *Picea* species can emit simultaneously de novo synthesised isoprene and monoterpenes from storage (Harrison et al. 2001; Street et al. 1997; Westberg et al. 2000; Winters et al. 2009), while several *Pinus* species can emit de novo synthesised MBO and monoterpenes from storage (Gray et al. 2011; Harley et al. 1998).

In the case of de novo emitted compounds, the emission rate is controlled by temperature and light intensity that determine the pool size of precursors for compound synthesis (Li and Sharkey 2013; Rasulov et al. 2009, 2010), while the storage emissions are only dependent on temperature, which alters the diffusion flux out of the storage compartments (Grote et al. 2013; Guenther et al. 2012). Both types of emissions can be modified by compound physicochemical characteristics, and a mixed type of control is also possible (Niinemets et al. 2004; Niinemets and Reichstein 2002). Exposure to stress conditions can alter the rate of volatile emissions by different mechanisms. First, stress can change the rate of constitutive emissions, with the changes in the emission rate being either transient or sustained depending on the intensity and the duration of the stress. Second, stress can induce de novo synthesis of novel volatiles. Thus, stress can profoundly change the blend and overall emission rate of volatiles. Although there is evidence of convergence of early stress responses at the level of oxidative signalling (Fujita et al. 2006; Mittler 2006; Mittler et al. 2011) and there are several ubiquitous stress-dependent volatiles, different stresses can induce the release of different blends of volatiles and differentially affect constitutive and stress-dependent volatile emission rates. In this chapter, we analyse the effects of key abiotic stresses on plant volatile release, considering both the changes in the emission spectrum and the rate of emission. We argue that when analysing the effects of stress on emissions, it is important to clearly separate between the immediate physiological processes that modify the emission rate primarily due to changes in substrate pool sizes and gene expression level responses that lead to changes in the activity of key enzymes controlling the pathway flux and the composition of stress-dependent emissions.

2.2 Emission of Volatiles from Plants Under Abiotic Stresses

2.2.1 Stress-Elicited Volatiles

By definition, constitutively released volatiles are the compounds which are synthesised and released (or stored prior to their release in storage emitters) under normal physiological conditions, while stress-elicited volatiles (or induced volatiles) are produced de novo only in stress conditions. However, stress also elicits

stress volatile release in constitutive emitters [reviewed by (Niinemets 2010)]. This can sometimes blur the separation of constitutive versus induced emissions. Specifically, in the case of constitutive terpene emitters, separation of terpenes released constitutively and upon exposure to stress might be difficult (Niinemets 2010; Niinemets et al. 2010a). Nevertheless, stress typically leads to a release of terpenes that are not emitted from unstressed plants. In particular, 1,8-cineole, linalool and ocimenes are characteristic stress-elicited monoterpenes (Aros et al. 2012; König et al. 1995). In addition, several stresses lead to the emission of the homoterpenes, (3*E*,7*E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT) and (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), and various sesquiterpenes, including β -caryophyllene, α -farnesene and Δ -elemene, although some of these sesquiterpenes can be emitted constitutively in some storage emitters (Blande et al. 2007; Joó et al. 2011; Niinemets et al. 2010b).

Apart from isoprenoids, many stress factors lead to major emissions of methanol as one of the first stress signals (Bamberger et al. 2010; Beauchamp et al. 2005; Filella et al. 2009). In non-stressed plants, especially in growing tissues, methanol is emitted as the result of demethylation of cell wall pectins by pectin methylesterases (Harley et al. 2007; Hüve et al. 2007). It is likely that stress-dependent emissions can be explained by the same mechanism (Peñuelas et al. 2005; Seco et al. 2011), although different pectin methylesterases can be activated upon stress (Pelloux et al. 2007).

Volatile lipoxygenase (LOX) pathway products, mainly consisting of various C6 alcohols and aldehydes (green leaf volatiles, GLV), constitute a ubiquitous class of compounds that are emitted in a variety of plant species during different stress conditions (Heiden et al. 2003; Kask et al. 2013; Niinemets 2010). They are typically emitted when the cellular membrane has been damaged (Kleist et al. 2012). The LOX pathway starts with a release of polyunsaturated fatty acids (octadecanoid acids) from plant membranes through the action of phospholipases (Liavonchanka and Feussner 2006). Further reaction with lipoxygenases produces 9- or 13-hydroperoxylinoleic or 9- or 13-linoleic acid or a mixture of both. Then, a hydroperoxide lyase catalyses the breakdown of 13-hydroperoxylinole(n)ic acid to a C6-compound, (*Z*)-3-hexenal, and a C12-product, 12-oxo-(*Z*)-9-dodecenoic acid. In consecutive reactions, (*Z*)-3-hexenal can be converted to (*Z*)-3-hexenol, (*E*)-2-hexenol, (*E*)-3-hexenol or (*E*)-2-hexenal (Feussner and Wasternack 2002; Matsui 2006). The release of GLV is typically considered de novo emission, although the substrate, polyunsaturated fatty acids, could have been synthesised and incorporated in membranes long before the stress event. In fact, recent experiments with ^{13}C -labelling indicated that the stress-dependent GLV emissions were not labelled by ^{13}C (Kleist et al. 2012).

In the following, we review the responses of key stress-elicited and constitutive emissions to high and low temperatures and to low and excess water availabilities. Although resolving the immediate and gene expression level effects of stress on different types of volatiles can be straightforward in several cases, processes with different time kinetics can overlap in others. Thus, stresses of different duration and severity can potentially lead to highly complex emission responses with potentially

important consequences for communication of plants with other organisms and for plant-to-plant signalling.

2.2.2 High Temperature Impacts

Climate change involves rising temperature with a dramatic effect on human and natural systems. According to recent estimates, the global surface temperature has risen by about 0.8 °C over the past 150 years, and the temperature is predicted to keep increasing (Fyfe and Gillett 2014; Gillett et al. 2011). High temperatures constitute an important constraint for plants, restricting their productivity and growth and influencing the distribution of species (Loreau et al. 2001). In particular, photosynthesis is highly sensitive to heat stress due to inhibition of photosynthetic electron transport capacity and activity of Rubisco (Hüve et al. 2011; Niinemets and Keenan 2014; Parry et al. 2014; Way and Oren 2010). In addition to direct effects of heat on growth, exposure to heat stress can also critically alter the development of flowers and thereby modify the reproductive success and be therefore particularly important for the productivity of seed crops (Ainsworth and Ort 2010; De Storme and Geelen 2014). In fact, heat stress has a major impact on post-transcriptional and post-translational control systems, as well as on their targets, thereby affecting temperature stress tolerance (Guerra et al. 2015).

Several key plant volatiles have been shown to improve heat stress resistance and have consequently been at the centre of research into heat resistance, although the exact mechanisms of their action are not fully understood (Vickers et al. 2009). In addition to compounds likely involved directly in heat resistance, multiple other compounds are released as the result of activation of ubiquitous stress pathways.

2.2.2.1 Isoprene Emission

In constitutively isoprene-emitting species, even a mild heat stress can enhance isoprene emission due to transient upregulation of the isoprenoid synthesis pathway as the result of greater substrate pools for isoprene synthesis and greater activity of isoprene synthases (e.g. Niinemets 2010; Rasulov et al. 2010). In addition to the transient enhancement of emissions, longer-term increase of temperature leads to acclimation responses typically associated with enhancement of expression of the isoprene synthase gene as well as genes controlling the entire plastidic isoprenoid synthesis pathway (Hanson and Sharkey 2001; Wiberley et al. 2008), but also with leaf structural changes altering the amount of physiologically active, isoprene-producing, leaf biomass per unit leaf area (Rasulov et al. 2015). For example, the rate of isoprene emission was greater from seedlings of the isoprene-emitting deciduous tree species *Populus nigra* (Centritto et al. 2011) and *Populus tremula* × *P. tremuloides* (Rasulov et al. 2015) grown at 35 °C than from seedlings grown at 25 °C. Analogously, in the grass *Phragmites australis*, an increase of soil

temperature also led to increases in isoprene emission rate (Medori et al. 2012). However, increases in night-time temperature did not affect significantly isoprene emission in seedlings of *Populus tremula* (Ibrahim et al. 2010), suggesting that it is not the overall increase in daily temperature but primarily the increase in temperature during the photosynthetic period.

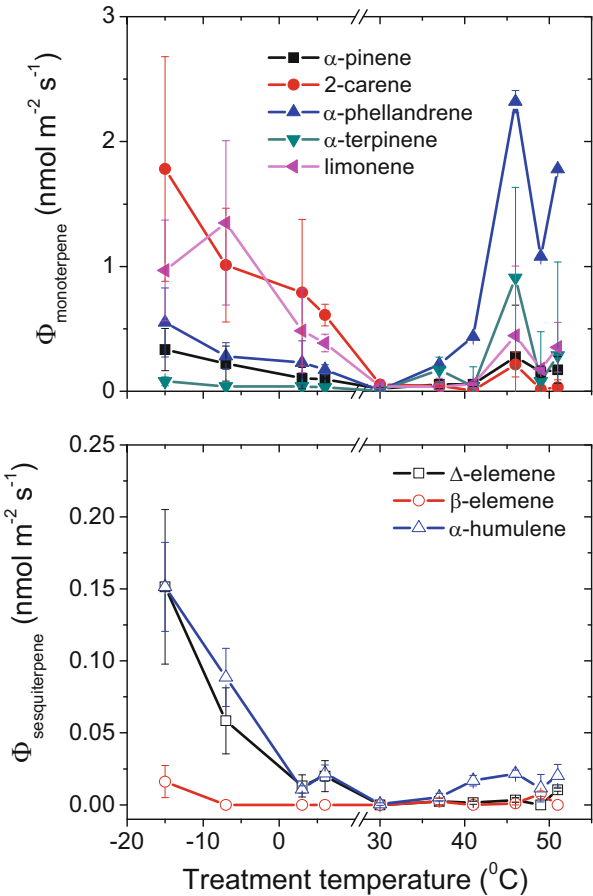
Sharkey and Singsaas (1995) have demonstrated that isoprene can protect photosynthetic apparatus against damage caused by transient high temperature stress, and their finding has been supported by several further studies (Pollastrì et al. 2014; Sharkey et al. 2008; Sun et al. 2013; Velikova et al. 2006; Wang et al. 2014). Furthermore, these results were supported by studies with genetically engineered grey poplar (*Populus x canescens*) lacking isoprene emission due to silencing of the isoprene synthase gene (Behnke et al. 2007, 2013). These researchers demonstrated that non-isoprene-emitting plants were more sensitive to recurrent heat stress simulating heat flecks that can occur upon sudden exposure to full sunlight (Behnke et al. 2007). Heat flecks frequently occur under dynamic light conditions in the field (Sharkey et al. 1996; Singsaas and Sharkey 1998), and in fact, isoprene as a small highly volatile molecule might confer the greatest protection under such dynamic conditions rather than under sustained high temperature conditions (Fineschi et al. 2013; Niinemets and Sun 2015; Sun et al. 2013).

2.2.2.2 Terpene Emissions

Constitutive terpene emissions from storage pools usually increase with increasing temperature, reflecting the exponential temperature dependency of diffusion and terpene vapour pressure (Grote et al. 2013; Guenther et al. 1993). Analogously to isoprene emissions, immediate effects of high temperatures on terpene emissions by de novo emitting species can result from enhanced precursor pool sizes and enhanced terpene synthase activities. Indeed, de novo synthesis of volatiles often increases due to temperature effects on the enzymes responsible for volatile synthesis (Grote et al. 2013; Niinemets et al. 2010b). Emission of de novo synthesised monoterpenes has been shown to improve foliage heat resistance (Copolovici et al. 2005; Llusà et al. 2005; Loreto et al. 1998), suggesting that monoterpenes operate similarly to isoprene, although different monoterpenes have differing capacities for heat protection (Copolovici et al. 2005). However, in contrast to storage emissions, the release of de novo synthesised monoterpenes has a temperature optimum that is generally lower, at around 35 °C (Copolovici et al. 2005; Loreto et al. 1998), than the temperature optimum for isoprene synthesis of around 40–45 °C (Rasulov et al. 2010, 2015). Nevertheless, less volatile monoterpenes can be nonspecifically stored in leaf liquid and lipid phases (Niinemets and Reichstein 2002; Niinemets et al. 2002) and, thus, could protect leaves for longer periods than isoprene. In addition, due to maintenance of significant concentrations in leaf tissues, they can still be involved in protection from heat flecks under dynamic light conditions at temperatures exceeding the optimum temperature for their synthesis.

Apart from the effects on constitutive emission rates, heat stress elicits expression of multiple terpenoid synthase genes (Mazzucotelli et al. 2008). In the conifer *Pseudotsuga menziesii*, heat stress-enhanced emissions of sesquiterpenes, the monoterpene alcohol linalool and the benzenoid methyl salicylate and the increases were much less for other monoterpenes (Joo et al. 2011). Analogously, heat stress led to emission of sesquiterpenes and selective effects on different monoterpenes in the herb *Solanum lycopersicum* (Fig. 2.2, Copolovici et al. 2012). These changes in the emission composition have been associated with altered gene expression profiles. However, alterations in emission composition by heat stress in *P. menziesii*, where terpenoids are stored in resin ducts, and in *S. lycopersicum*, where terpenoids are stored in glandular trichomes, can partly reflect stronger increases in the volatility of C15 relative to C10 compounds as well as effects of temperature on the permeability of cuticle and cellular structures. On the other hand, in the deciduous broad-leaved tree *Quercus rubra*, a constitutive isoprene emitter, heat stress resulted in elicitation of de novo monoterpene emissions that increased after

Fig. 2.2 Illustration of the effects of high and low temperatures on the release of mono- and sesquiterpenes from the foliage of the herb *Solanum lycopersicum* (modified from Copolovici et al. 2012)



the first hour of mild stress (45 °C) and were maintained at the induced level for the rest of the treatment (Copolovici et al. unpublished data). In a similar manner, in the evergreen broad-leaved *Quercus ilex*, a constitutive de novo monoterpene emitter, heat stress led to synthesis of ocimenes, linalool and sesquiterpenes (Staudt and Bertin 1998).

2.2.2.3 Release of Green Leaf Volatiles

As discussed in Sect. 2.1, green leaf volatiles (GLV) constitute a ubiquitous class of compounds released in response to virtually any stress (for a review, see Niinemets 2010). Given that the release of GLV is associated with membrane-level damage, it is expected that GLV is emitted upon severe heat stress. However, a certain elevation of GLV emission can already occur upon a moderate increase in temperature, e.g. in *Betula pendula* (Hartikainen et al. 2012) and *Picea abies* (Filella et al. 2007). In *S. lycopersicum* (Copolovici et al. 2012) and in a number of tree species (Kleist et al. 2012), it has been further demonstrated that the emission rate of GLV can be correlated with the stress strength, indicating that GLV release can serve to quantify the severity of damage upon heat exposure. Overall, it is expected that future heat waves will result in enhanced release of constitutive and induced terpenoids and GLV emissions.

2.2.3 Low Temperature Impacts

The yield potential and geographic range of crops is importantly modulated by low temperatures (Harley 2011), especially by early and late season frosts (Kalisz et al. 2014; Kim et al. 2013; Luo et al. 2014). Studies have mainly investigated the responses of photosynthesis to chilling and frost stress (Adams et al. 2001; Küppers and Küppers 1999; Savitch et al. 2002), and there is much less information available of low-temperature effects on the emission of volatile organic compounds.

Cold stress in *Populus tremula* led to reductions in constitutive leaf isoprene emissions, but after the cold stress, isoprene emissions partly recovered due to increases in the pool size of the immediate isoprene precursor and the fraction of carbon going into isoprene synthesis (Sun et al. 2012a). Induction of the release of certain stress-dependent mono- and sesquiterpenes has been observed after a cold shock treatment in *S. lycopersicum* (Copolovici et al. 2012). In this species, the emission of (*E*)- β -ocimene was quantitatively correlated with the severity of temperature stress, with emissions at levels higher than 1 pmol m⁻² s⁻¹ only observed after severe stress (temperatures <1 °C) (Copolovici et al. 2012). The emission of sesquiterpenes, especially β -caryophyllene, after cold shock treatment was quantitatively correlated with stress strength during the treatment (Copolovici et al. 2012). Both induction of terpenoid synthesis after stress and breakage of

primarily sesquiterpene-containing structures could have played a role in enhanced sesquiterpene release in this study. In fact, Copolovici et al. (2012) demonstrated that exposure of *S. lycopersicum* leaves to freezing temperatures led to the release of GLV including (Z)-3-hexenol, (E)-2-hexenal, 1-hexanol and 1,4-hexadienal, whereas the emissions increased drastically below a temperature threshold. Cold shock treatments in the deciduous vine *Vitis vinifera* resulted in a similar enhancement of GLV production as well as enhanced production of nonvolatile GLV condensation products with glutathione (S-(3-hexan-1-ol)-glutathione) and cysteine (S-(3-hexan-1-ol)-L-cysteine) (Kobayashi et al. 2011). These nonvolatiles of *V. vinifera* are known precursors of S-containing aroma compounds such as 3-mercaptohexan-1-ol (Peyrot Des Gachons et al. 2002), implying that cold shock can have major impacts on species-specific smell bouquets.

2.2.4 Influence of Drought on Plant Emissions

Temporal or chronic drought is a major stress factor worldwide. According to the Food and Agriculture Organization (FAO) of the United Nations, chronic limitations of water availability affect at least 40 % of the Earth's surface (Bodner et al. 2015; FAO 2003). The negative impact of drought on photosynthesis, due to reduced CO₂ entry into chloroplasts as the result of decreases in stomatal and mesophyll diffusion conductances, and reductions in Rubisco activity and photosynthetic electron transport rate are well-known (Flexas et al. 2014, 2016; Galmés et al. 2012; Niinemets and Keenan 2014). However, as demonstrated in the following sections, the effects of drought on constitutive isoprenoid emission are somewhat controversial.

2.2.4.1 Effects of Drought on Isoprene Emission

In the case of constitutive isoprene emissions, there might seem to be no clear trend across studies if one does not consider that the effects of drought depend on species, stress intensity and timing (Niinemets et al. 2010a; Peñuelas and Staudt 2010). Peñuelas and Staudt (2010) summarised the available evidence and indicated that in about 25 % of studies, isoprene emission rates increased; in about 50 % of studies, the emissions decreased; and in about 25 % of studies, the emission rate was not changed.

Indeed, the response of constitutive isoprene emissions to drought includes both direct physiological responses as the result of drought effects on CO₂ concentration in chloroplasts and acclimation responses as the result of changes in isoprene synthase gene expression. Regarding the physiological response, isoprene emission depends on ambient CO₂ concentration according to a curve with an optimum at relatively low intercellular CO₂ concentrations of 100–150 μmol mol⁻¹ (Rasulov et al. 2009; Sun et al. 2012b; Wilkinson et al. 2009). Thus, mild water stress that

leads to moderate reductions in stomatal conductance can lead to increases in isoprene emission, as demonstrated in several studies (Funk et al. 2004; Genard-Zielinski et al. 2014; Niinemets et al. 2010a; Pegoraro et al. 2004; Sharkey and Loreto 1993). Moderate drought during the middle of the summer can even cause a doubling of isoprene emission compared with well-watered periods (Monson et al. 2007). With further advancement of drought, isoprene emission rate typically decreases (Fang et al. 1996; Sharkey and Loreto 1993). When this happens, the recovery upon watering can be time-consuming, taking 4 days or more, and indicating that drought has led to a reduction of isoprene synthase activity such that recovery critically depends on changes in expression of isoprene synthase activity. On the other hand, recovery can result in overcompensation such that the emissions after stress are higher than before the stress (Niinemets 2010, 2016; Sharkey and Loreto 1993).

The direct impacts of drought-dependent changes in isoprene emission are not clear. Experiments with isoprene-emitting transgenic *Nicotiana tabacum* plants demonstrated that drought-stressed non-isoprene-emitting plants had increased foliar concentrations of reactive oxygen species (ROS) and greater lipid peroxidation level, while no change in ROS and lipid peroxidation occurred in isoprene-emitting plants (Ryan et al. 2014). Thus, increases in isoprene emission upon moderate drought stress could play a role in maintenance of membrane integrity in drought-stressed plants.

2.2.4.2 Drought Influences on Terpene Emissions

Similar to constitutive isoprene emissions, effects of drought on monoterpene emissions are variable. In the constitutive de novo monoterpene emitters *Quercus ilex* and *Fagus sylvatica*, drought enhanced the emission rate (Blanch et al. 2009a; Wu et al. 2015). In contrast, drought-dependent reductions in monoterpene emission have been observed in other studies with *Q. ilex* (Lavoie et al. 2009; Plaza et al. 2005; Staudt et al. 2002). The study of Wu et al. (2015) indicates that this discrepancy likely reflects differences in the severity of drought. In their study, monoterpene emission in both *Q. ilex* and *F. sylvatica* was initially enhanced and then severely curbed as the drought period continued (Wu et al. 2015). We suggest that the initial increase of monoterpene emissions reflects the effects of low intercellular CO₂ concentrations on the substrate pool size similar to isoprene (see above), while the severe stress leads to reductions in monoterpene synthase activity, although the latter effect has not always been found (Grote et al. 2010). Similar to isoprene, overcompensation of monoterpene emissions upon rewatering has sometimes been observed (Peñuelas et al. 2009).

In the case of the constitutive storage monoterpene emitters *Cistus albidus*, *Pinus halepensis*, and *Rosmarinus officinalis* drought stressed for 11 days, drought initially had a minor effect on monoterpene emissions, but there was a surprising enhancement at day 7, followed by a reduction during the remaining days of the experiment, whereas the emissions still remained higher at the end of the

experiment than the emissions in non-stressed plants (Ormeño et al. 2007). In contrast, storage emissions in *Picea abies* and *Pinus sylvestris* were weakly affected by drought (Wu et al. 2015). The drought-dependent increase of monoterpene emissions observed in some storage emitters has been suggested to indicate greater investment in secondary carbon-rich chemicals, including terpenes, in conditions that lead to an arrestment of primary metabolism and growth (Blanch et al. 2009a; Delfine et al. 2005). Indeed, increases in monoterpene content upon a moderate water stress have been observed in *R. officinalis* and *Mentha spicata* (Delfine et al. 2005), in *P. halepensis* (Blanch et al. 2009b) and in two *Eucalyptus* species (McKiernan et al. 2014). However, upon a severe stress, the investment of carbon into secondary chemistry also declines and the storage pools for terpenes decrease, leading to reduced terpene content as has been observed, for example, in the conifer *Cupressus sempervirens* (Yani et al. 1993).

Much less data are available for drought effects on constitutive sesquiterpene and stress-induced volatile emissions. In the storage emitter *R. officinalis*, sesquiterpene emissions decreased drastically under drought stress, but minor effects were observed for *C. albidus* and *P. halepensis* (Ormeño et al. 2007). However, it is unclear as to what extent sesquiterpene emissions in their study reflected emissions from storage or induction of emissions. In the de novo emitter *Q. coccifera*, sesquiterpene emissions decreased with advancing drought, but there was a certain increase at the end of the experiment under most severe water stress conditions (Ormeño et al. 2007). In wheat (*Triticum aestivum*) plants, sustained drought was associated with the release of monoterpenes, benzaldehyde and geranyl acetone, and these emissions were smaller in bacterially primed plants (i.e. inoculated with biofilm-forming bacteria) that were more resistant to drought (Timmusk et al. 2014). Only a moderate drought effect was observed on induced mono- and sesquiterpene emissions in the broad-leaved deciduous species *Quercus robur* and *Prunus serotina* (Bourtsoukidis et al. 2014). In the latter study, methanol emissions were reduced and GLV emissions were either reduced or unchanged upon drought exposure (Bourtsoukidis et al. 2014). In contrast, in broad-leaved deciduous species *Betula pendula*, drought enhanced both GLV and monoterpene emissions (Pag et al. 2013). There is evidence that drought can enhance methyl salicylate emissions (Bourtsoukidis et al. 2014; Copolovici et al. 2014), and there is further evidence that drought might prime volatile defences for a stronger response upon biotic attack (Copolovici et al. 2014). We conclude that more experimental work is needed on drought effects on induction of isoprenoids and on emission of immediate stress volatiles.

2.2.5 Influence of Flooding on Plant Emissions

The effects of flooding on different plant species depend on plant waterlogging tolerance and on the intensity of stress, stress timing and site conditions (Kozłowski and Pallardy 2002). Some species can only tolerate short episodes of flooding,

while others can grow in permanently flooded soils. Anoxic conditions elicit a plethora of physiological stress responses including reductions in photosynthesis rates and stomatal conductance (Jackson et al. 2009). The key adaptations to cope with flooding include modifications that improve oxygen availability such as root regeneration, facilitation of oxygen uptake and transport and metabolic adjustments (Bertolde et al. 2012; de Oliveira et al. 2014; Yu et al. 2015).

Although flooding is a major stress in several ecosystems, flooding effects on BVOC emissions have received little coverage in the literature (Kreuzwieser and Rennenberg 2013), except for the classical increases of emissions of ethanol and acetaldehyde from foliage of waterlogged plants (Holzinger et al. 2005; Kreuzwieser et al. 1999, 2000, 2001) that arise as the result of anaerobic metabolism of sugars in the roots. In addition to major emissions of ethanol and acetaldehyde, flooding elicits a release of a series of volatile stress marker compounds including methanol (Bourtsoukidis et al. 2014; Copolovici and Niinemets 2010; Rottenberger et al. 2008), and GLV (Fig. 2.3) (Bourtsoukidis et al. 2014; Copolovici and Niinemets 2010). Apart from the C6 GLV, Bourtsoukidis et al. (2014) observed significant emissions of the C9 oxylipin nonanal—an indicator of degradation of lipid membranes—in *Quercus robur* and *Prunus serotina*. In addition to carbon-based volatiles, Copolovici and Niinemets (2010) observed significant emissions of NO upon flooding in three deciduous species: *Alnus glutinosa*, *Populus tremula* and *Quercus rubra*. The rate of NO emissions correlated with the rate of GLV release, and the rate of emissions of both NO and GLV increased with decreasing species flooding tolerance (Copolovici and Niinemets 2010).

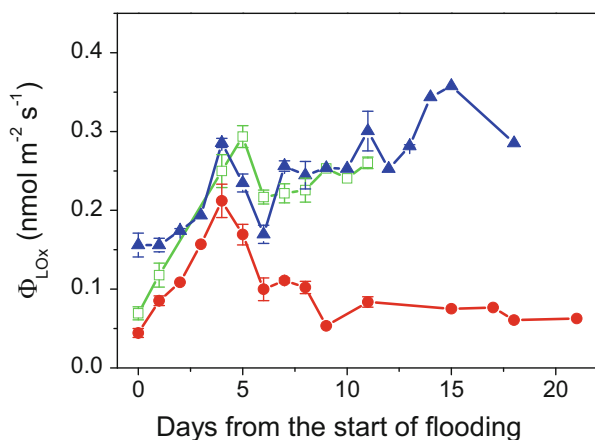


Fig. 2.3 Time-dependent changes in lipoxigenase (LOX) pathway products (green leaf volatiles) in three temperate deciduous tree species *Alnus glutinosa* (red line and symbols), *Populus tremula* (green line and symbols) and *Quercus rubra* (blue line and symbols) after the onset of a waterlogging treatment. *Alnus glutinosa* is the most and *Q. rubra* the least waterlogging-tolerant species (Niinemets and Valladares 2006). Data are modified from Copolovici and Niinemets (2010)

In general, flooding results in reductions in constitutive isoprene emission as the data for *Q. rubra* and several Amazonian species (Bracho Nunez et al. 2009) demonstrate. However, in *P. tremula* that is more resistant to waterlogging than *Q. rubra*, isoprene emission was marginally affected and even fully recovered during the flooding treatment (Copolovici and Niinemets 2010). Surprisingly, no effect of flooding was evident on isoprene emissions in a relatively flooding-intolerant species *Q. robur* (Bourtsoukidis et al. 2014). Given that flooding results in simultaneous reductions in both stomatal conductance and net assimilation rate such that intercellular CO₂ concentration remains essentially unaltered (Copolovici and Niinemets 2010), no increase of isoprene emissions even under mild stress are expected, and the time-dependent reduction of isoprene emission rate under sustained flooding likely reflects decreases in isoprene synthase activity.

Few data are available for constitutive and induced terpene emissions. In several constitutive monoterpene-emitting Amazonian species (Bracho Nunez et al. 2009), flooding reduced emissions. In contrast, for induced monoterpenes, the flooding effect was not significant, but there was a moderate increase in induced sesquiterpene emissions in two temperate deciduous species (Bourtsoukidis et al. 2014). More studies on the effects of flooding on constitutive isoprene and monoterpene emitters are needed to gain conclusive insight into the species and stress severity controls on emissions.

Different to other stresses, the release of NO from flooded plants can lead to the interesting possibility of altered air reactivity without anthropogenic pollution. Both reactive hydrocarbons that are primarily biogenic, and NO_x (NO and NO₂) that are primarily anthropogenic are needed for ozone formation in the troposphere (Fall 2003). Thus, sustained high-level NO emissions from flooded isoprene-emitting *Q. rubra* trees (Copolovici and Niinemets 2010) suggest that ecosystems dominated by this species may be significant producers of ozone in the absence of human-driven NO_x production. Although flooding significantly reduced isoprene emissions in *Q. rubra*, the emissions still remained at a level of 30–50 % after sustained flooding (Copolovici and Niinemets 2010), implying that flooded forest ecosystems keep altering air quality. In addition, oxygenated compounds, ethanol, acetaldehyde, GLV and methanol are emitted from flooded plants (Bourtsoukidis et al. 2014; Bracho Nunez et al. 2009; Copolovici and Niinemets 2010). Although the reactivity of these compounds is lower than that of non-oxygenated non-saturated hydrocarbons (Jiménez et al. 2007), they still significantly contribute to atmospheric OH radical and O₃ formation. Quantitative relationships between flooding tolerance, and time of flooding are needed to predict emissions of NO and oxygenated and non-oxygenated BVOC from flooded forests.

2.3 Conclusions and Suggestions for Future Work

This chapter demonstrates that a variety of emission responses are observed from stressed plants. Although all environmental stresses bear similarities, e.g. any stress typically leads to reductions in leaf photosynthesis rates, different stresses

differently affect volatile emission rates, and the responses can be different for constitutive and induced emissions. In addition, for any stress, the effects depend on stress severity and duration. Mild stress characteristically first results in physiological responses that are quickly reversible upon a return to non-stressed conditions. Such physiological responses typically result from changes in substrate availability for all stresses and from changes in enzyme activity for temperature stresses. Thus, the effects can be positive, e.g. due to enhanced substrate availability for isoprene emission upon mild drought stress or due to enhanced substrate availability and enzyme activity upon mild heat stress. For other mild stresses, the effects can be negative or occasionally no effects can be observed. Mild stress seldom elicits release of stress volatiles, or if it does, the elicitation is minor. More severe stress typically leads to major reductions in constitutive emissions and release of characteristic stress volatiles. The available evidence demonstrates that the release of stress volatiles is stress dose dependent.

This chapter indicates the existence of important gaps in understanding the mechanisms of action of several stress factors and also indicates that there is a limited coverage of stress effects on emissions of several compound classes. The major limitation in a number of past studies has been that stress severity has not been objectively assessed, making it difficult to judge whether a certain phenomenon observed in a given study reflects a physiological response or a severe stress response. We argue that more experimental work is needed to fill the gaps in knowledge on stress responses of volatile compound classes with limited measurements, such as sesquiterpenes. We also suggest that for fully mechanistic consideration of environmental stress effects on BVOC emissions, stress dose versus emission relationships need to be developed using quantitative approaches to characterise the severity of stress.

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