

Emission of volatile organic compounds as a signal of plant stress

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Plant volatiles

During growth and development plants produce around 100 000 chemical products out of which 1700 are known to be volatile (Dicke and Loreto, 2010). Plant volatile organic compounds (VOCs) are released by various plant organs such as flowers (Colquhoun et al., 2013), fruits (Laothawornkitkul et al., 2009), roots (Köllner et al., 2004; Crespo et al., 2012) and leaves (Owen et al. 2001). Among all the VOC-s, isoprene (Laothawornkitkul et al., 2008; Sharkey et al., 2008; Darbah et al., 2010; Li and Sharkey, 2013), mono- and sesquiterpenes (Chen and Pawliszyn, 2003; Martin et al., 2003; Tholl, 2006; Chen et al., 2011; Rajabi Memari et al., 2013), fatty acid cleavage products known also as green leaf volatiles (GLV-s)(Hatanaka, 1993) and aromatic volatiles (e.g., methyl benzoate and methyl salicylate) (Dudareva et al., 2000; Cardoza et al., 2002; Dudareva et al., 2004; Zhao et al., 2010; Holopainen et al., 2013) are the most studied ones. The rate of plant volatile release can depend on environmental drivers including temperature (Guenther et al., 1993; Bertin et al., 1997; Staudt and Bertin, 1998; Niinemets et al., 2010b; Hu et al., 2013) and light (Guenther et al., 1993; Staudt et al., 1997; Niinemets et al., 2010b; Kesselmeier and Staudt, 1999; Hu et al., 2013; Monson, 2013) and atmospheric CO₂ concentration (Vourinen et al., 2004; Räisänen et al., 2008; Velikova et al., 2009; Rasulov et al., 2009; Monson, 2013; Sun et al., 2012) and endogenous drivers including circadian rhythms (Wilkinson et al., 2006; Loivamäki et al., 2007), leaf age (Mayrhofer et al., 2005; Guenther et al., 2006; Sun et al., 2009; Niinemets et al., 2010a; Sun et al., 2012) and plant age (Shiojiri and Karban, 2006).

Plant stress factors and defenses

During the growth, plants have to cope with various abiotic and biotic stress factors (Mittler, 2006; Loreto and Schnitzler, 2010; Niinemets, 2010a; Niinemets, 2010b; Copolovici et al., 2011). Among these, herbivores (Fatouros et al., 2012), plant viruses (Eigenbrode et al., 2002) and pathogens (Huang et al., 2012) are the key biotic stressors, while temperature

(Velikova and Loreto, 2005; Possell and Loreto, 2013; Sun et al., 2013), drought and flooding (Rennenberg et al. 2006; Kreuzwieser and Rennenberg, 2013), light (Loreto et al. 2006), ozone (Beauchamp and Wisthaler, 2005; Pinto et al., 2010; Calfapietra et al., 2013) and nutrient availability (Lopéz-Bucio et al., 2003) are the main abiotic stress factors. In addition, the severity of stress can be importantly modified by elevated atmospheric CO₂ concentrations (Vourinen et al., 2004; Räisänen et al., 2008; Calfapietra et al., 2013; Sun et al., 2013).

Multiple stress factors can affect plants' resistance simultaneously or consecutively. In canopy top high leaf temperature and radiance can cause leaf necrosis, which in turn endangers the survival of low-growing trees (Valladares and Pearcy, 1995). Meanwhile in areas of low soil nutrient availability development of root system of young seedlings is blocked and seedlings experience drought stress (Oliet *et al.*, 2013). Additionally soil nitrogen content affects frost injury of plants, because nitrogen contributes the biosynthesis of anti-freeze proteins in apoplast and prevents ice crystal formation (Lambers et al. 2008), otherwise breakage of cell membranes triggers immediate release of GLVs (Copolovici *et al.*, 2012).

Plants have developed physical and chemical defense systems to protect themselves against stressors. Among physical defense systems, spines, thorns and hardened leaves play a major role in several plants species (Milewski *et al.*, 1991; Cooper and Ginnet, 1998; Hanley *et al.*, 2007), while enhanced investment in waxes and secondary plant metabolites is a common direct defense response across plants (Halitschke *et al.*, 2000; Arimura *et al.*, 2005; Leitner *et al.*, 2005; Howe and Schaller, 2008; Kessler and Heil, 2011). In contrast, stress-induced volatile compounds that can be attractants of predators and parasitoids belong to indirect defense, when the attacked plant is „calling for help“ against herbivores (Dicke, 1994; Dicke *et al.* 2009; Dicke and Baldwin, 2010; Holopainen and Gershenzon, 2010; Fatouros *et al.* 2012). There are numerous recent studies demonstrating that indirect chemical defense systems do increase the fitness of attacked plants (for reviews see Dicke and Baldwin, 2010; Trowbridge and Stoy, 2013), and thereby constitute an important rapidly induced defense system.

Induced stress volatiles

Volatiles are biosynthesized mainly via four biochemical pathways: the lipoxygenase pathway for green leaf volatiles (GLV-s) (Hatanaka, 1993), shikimic acid pathway for aromatic volatiles (Paré and Tumlinson, 1996), methylerythritol pathway (MEP) for isoprene and monoterpenoids (Pichersky *et al.*, 2006; Rajabi Memari *et al.*, 2013) and mevalonic acid

pathway (MVA) for volatile sesquiterpenoids (Taveira *et al.*, 2009; Rajabi Memari *et al.*, 2013; Rosenkranz and Schnitzler, 2013) (Figure 1).

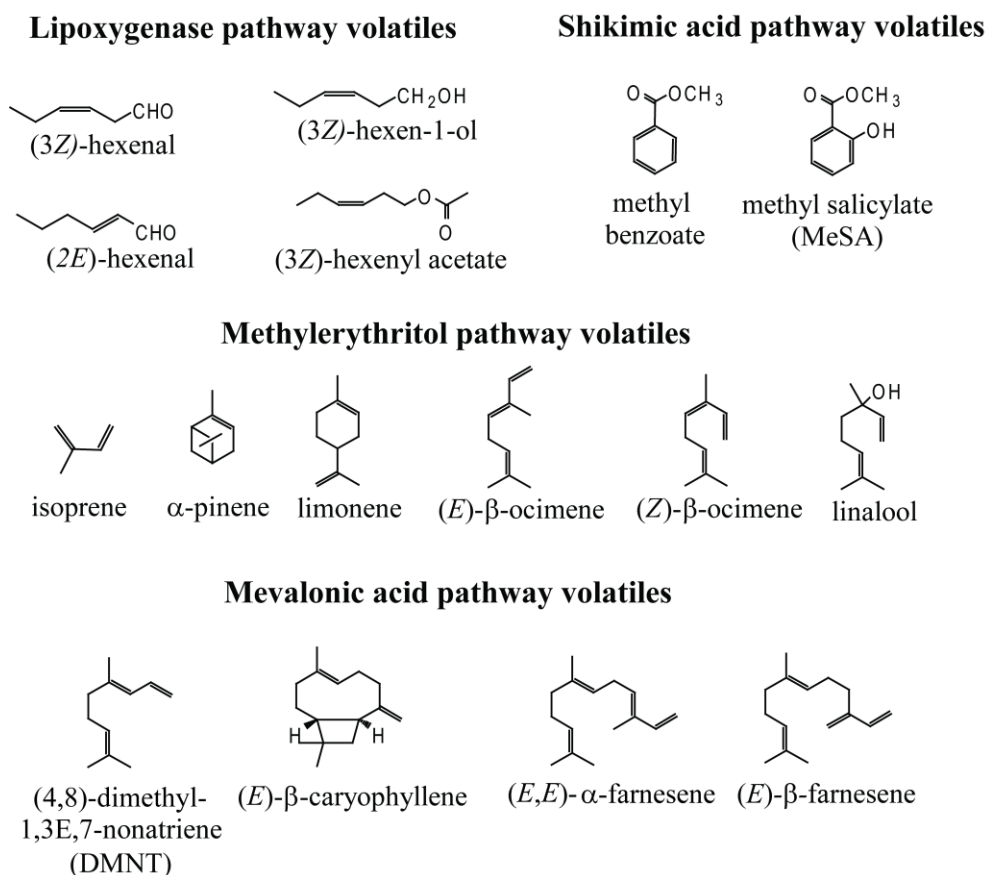


Figure 1. Molecular structures of plant volatiles in the emission of a stressed plant. Fatty acid cleavage products known also as green leaf volatiles (GLV-s) are biosynthesized via lipoxygenase pathway (Hatanaka, 1993), aromatic volatiles such as methyl salicylate (MeSA) are volatile products of shikimic acid pathway (Dudareva *et al.*, 2000), isoprene and monoterpenoids are produced via methylerythritol (MEP) pathway (Pichersky *et al.*, 2006), homoterpene (4,8)-dimethyl-1,3E,7-nonatriene (DMNT) and sesquiterpenes are produced via mevalonic acid (MVA) pathway (Taveira *et al.*, 2009).

Typical stress emissions consist of green leaf volatiles such as (E)-2-hexenal, (Z)-3-hexenol, (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate, volatile mono- and sesquiterpenoids such as linalool, ocimene isomers, farnesene isomers, (E)- β -caryophyllene, methyl jasmonate, methyl salicylate (MeSA), and methanol (Geervliet *et al.*, 1997; Lerdau and Gray, 2003; Holopainen, 2004; Baldwin *et al.*, 2006; Maffei, 2010; Raghava *et al.*, 2010; Copolovici *et al.*, 2011; Spinelli *et al.*, 2011; Copolovici *et al.*, 2012; Pinto-Zevallos *et al.*, 2013). Any stress factor can potentially change the rate of volatile release and alter the bouquet of VOCs and thereby affect the relationships between living organisms (Dicke and Baldwin, 2010; Holopainen and Gershenzon, 2010; Niinemets *et al.*, 2013). For example, leaf damage increases the emission of sesquiterpenes and increases alkaloid content of nectar, and hence,

can alter pollinator preference (Adler et al., 2006; Theis et al., 2009). In addition, (Z)-3-hexenol, which is a signaling volatile of herbivore attack or mechanical wounding, induces the stress reaction in neighboring intact plants (Wei and Kang, 2011). On the other, the bouquet of volatiles can importantly depend on stressed plant species (Llusià et al., 2010a; Llusià et al., 2010b; Holopainen et al., 2013; Llusià et al., 2013) or a stressor (Kännaste et al., 2009, Takabayashi et al., 1991).

Role of volatile organic compounds in plant-plant-, plant-insect- or plant-insect-environment relationships

The question of why plants emit VOC-s has been posed over and over again, and the role of many volatiles in abiotic stress tolerance, including thermotolerance of photosynthesis and reduced oxidative stress, has been highlighted (Sharkey and Singsaas, 1995; Singsaas et al., 1997; Loreto et al., 1998; Loreto and Velikova, 2001; Velikova et al., 2004; Copolovici et al., 2005; Llusià et al., 2005; Velikova et al., 2005; Vickers et al., 2009; Possell and Loreto, 2013; Sun et al., 2013). Moreover in the 21th century global climate is predicted to change drastically (IPPC, 2007). For example today we know that water availability affects the content and emission of secondary metabolites in plants and different plant species respond to water deficit differently (Kainulainen et al., 1992; Turtola et al., 2003; Peñuelas et al., 2009; Lusebrink et al., 2011; Kännaste et al., 2013). Yet in future in relation to climate change the existence and prolongation of drought may increase the attack of pines of low vitality by the mountain pine beetle *Dendroctonus ponderosae* MPB (Lusebrink et al., 2011).

VOC-s are essential in plant-plant and plant-insect (Baldwin et al., 2002; Duhl et al., 2008; Dicke and Baldwin, 2010; Fatouros et al., 2012; Holopainen et al., 2013; Trowbridge and Stoy, 2013). In plant-herbivore interactions, the volatiles can act as attractants or repellents to herbivores (Laothawornkitkul et al., 2008; Loivamäki et al., 2008). For instance, the monoterpene α -pinene released by wounded Scots pine (*Pinus sylvestris* L.) acts as attractant to large pine weevil (*Hylobius abietis*), and thus, previous damage of a conifer can increase herbivory damage. Yet attraction of *H. abietis* can be reduced by repelling limonene (Nordlander, 1991). Due to the increasing emissions of allylthiocyanate heat stressed *Brassica nigra* plants may become attractive to specialized feeders of Brassicaceae (Figure 2) (Mithen, 2001).

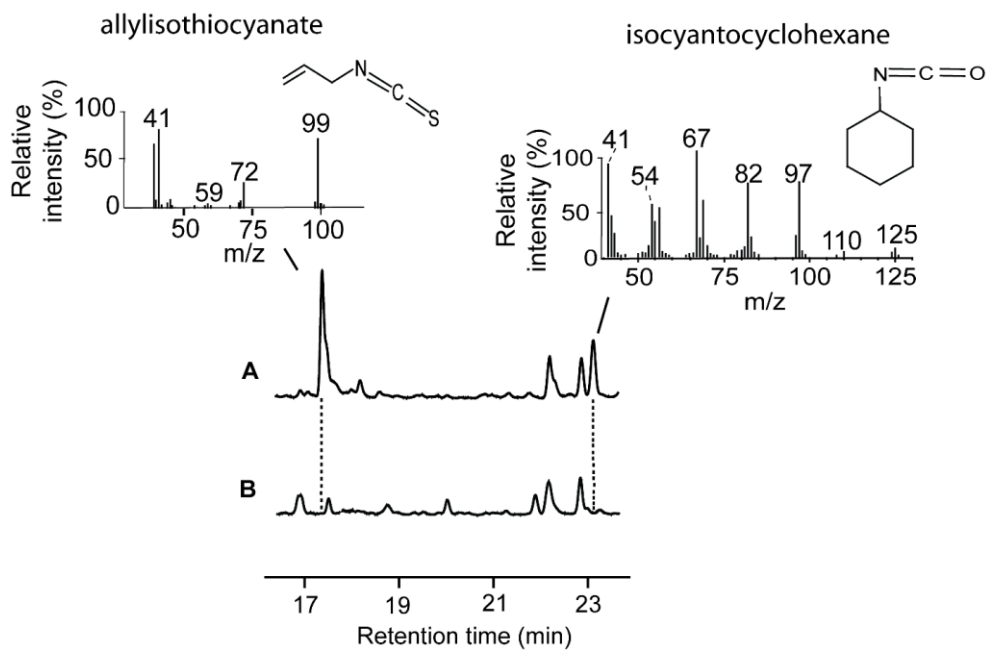


Figure 2. Volatile glucosinolate biodegradation products of *Brassica nigra* released at leaf temperature of 25 °C (A) and 44 °C (B).

For example volatiles emitted from *Tetranychus urticae*-infested lima bean (*Phaseolus lunatus* L.) can activate genes encoding pathogenesis-related proteins and phenylalanine ammonia-lyase in leaves of non-infested neighboring plants', as well GLV-s can serve as signal compounds in plant-plant communication (Arimura et al., 2001; Bate, Rothstein, 1998). This kind of info "sharing" depends on the diffusion and convection of the volatile info between the sender and the receiver plant (Baldwin et al., 2002).

Conclusions

Overall, this information summarized here emphasizes the rich spectrum of stress-triggered volatile emissions and underscores the importance of volatiles in stress responses, stress tolerance and plant interactions with other plants and organisms. While a lot of basic information on plant volatile emissions has accumulated during the last years, we still lack quantitative understanding of how the emission rate scales with the severity of stresses, how far the stress-elicited volatiles travel in the atmosphere and what are the relationships between the strength of the emitted signal and receiver plants' and other receiver organisms' responses. There is encouraging evidence that the strength of the emission signal can be quantitatively related to the severity of both abiotic and biotic stresses (Niinemets et al., 2013) and we argue that future work should be devoted towards filling these important gaps in knowledge.

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