Isoprene (C_{5}H_{8}, 2-methyl 1,3-butadiene) is the dominant non-methane volatile organic compound (VOC) emitted by vegetation, comprising nearly half of the estimated biogenic carbon released in the atmosphere as VOCs (Laothawornkitkul et al. 2009). Isoprene emitted by plants is synthesized from the substrate dimethylallyl diphosphate (DMADP) by isoprene synthase (ISPS). Dimethylallyl diphosphate is derived from the 2-C-methyl-d-erythritol 4-phosphate pathway in plastids (Sharkey et al. 2005) where DMADP can also be a substrate for monoterpene synthesis (Bartram et al. 2006). After release to the atmosphere, isoprene, among other terpenes, is a precursor of photochemical smog and tropospheric ozone production (Laothawornkitkul et al. 2009). Oxidation of isoprene in the atmosphere may also lead to secondary organic aerosol formation (Claeys et al. 2004). Both processes have significance for biosphere–atmosphere feedback processes such as light scattering and cloud formation which affect the light environment in forests (Holopainen 2011).

Isoprene-emitting capacity is a highly variable trait. Isoprene is emitted in the highest rate by woody plants (Sharkey et al. 2008), but typically isoprene is emitted by freshwater plants or plants living at the interface between soil and water (Loreto 2002). The subarctic peatland ecosystems dominated by mosses and sedges could be a significant isoprene source at a global scale (Tiva et al. 2007).

In the present-day world, there are several plant families that have isoprene-emitting and non-emitting species (Monson et al. 2013). Plants with an active ISPS gene preferentially emit more isoprene than monoterpenes (Harrison et al. 2013). Isoprene emitters have isoprene as a dominant volatile compound in the emission profile with a typical emission rate >20 nmol m^{-2} s^{-1} (Behnke et al. 2012). Among non-emitters, isoprene emissions are lacking or detectable just at a trace level (emission rate <1 nmol m^{-2} s^{-1}) (Ghirardo et al. 2010). Phylogenetic analysis of 1700 plant species, which have been tested for isoprene emission capacity and having DNA sequencing data (Monson et al. 2013), suggested that during plant evolution isoprene emission capacity may have evolved and been lost multiple times. The requirements for a plant species to evolve high isoprene emission rates are mutations that affect the appearance and expression of ISPS genes, but also those that up-regulate the capacity of leaves to produce DMADP substrate for isoprene synthesis (Sharkey et al. 2005, Monson et al. 2013). To better assess the physiological functions and the adaptive benefit of large isoprene emissions for plants, as well as to solve the puzzling question of why only a few plant species invest carbon in high isoprene emissions, engineered isoprene-emitting or engineered non-emitting isotypes of a plant species are practical tools (Behnke et al. 2007, Laothawornkitkul et al. 2008, Loivamäki et al. 2008, Vickers et al. 2009, Rosenkranz and Schnitzler 2013).

In this issue of Tree Physiology, Behnke et al. (2013) report the response of isoprene-emitting wild-type poplars and isoprene non-emitting transgenic poplars (Populus × canescens (Aiton) Sm.) to multiple stresses separately and in combination, including high-salinity and simulated sunfleck episode treatments. Sunflecks appear in the lower foliage of trees in dense forests (Smith and Berry 2013) with short-term transient exposure to high temperature in combination with high light levels during sunny periods. Behnke et al. (2013) found that salinity stress in combination with sunflecks caused only a marginal reduction in the photosynthesis capacity on non-isoprene-emitting poplar lines. However, under longer-term high-temperature (40 °C) stress, the leaves of non-isoprene-emitting poplar lines collapsed, suggesting that engineered plants with a low isoprene emission potential might not be capable of
resisting high-temperature episodes. These results confirm the earlier observations of reduced thermotolerance of photosynthesis in non-isoprene-emitting poplar (Behnke et al., 2007).

Isoprene is synthesized in plastids, emitted in a light- and temperature-dependent way, and is not stored in leaves. Parts due to these traits, the functions of isoprene in plants are most often associated with resistance against abiotic stresses (Sharkey et al., 2008, Vickers et al., 2009, Loreto and Schnitzler 2010): it is expected that stabilization of thylakoid membranes by isoprene reduces the formation of reactive oxygen species in cells (Harrison et al., 2013). Isoprene emission rates do not show increases in herbivore-damaged trees, contrasting to other terpenoids, and emissions may even be slightly reduced in foliage after herbivore attack (Blande et al., 2007, Brilli et al., 2009). However, studies with isoprene-emitting transgenic plants have shown that isoprene emissions may protect plants by repelling herbivorous insects (Laathaworntikul et al., 2008), whereas non-isoprene-emitting transgenic lines may become more susceptible to herbivorous insects than wild-type lines (Behnke et al., 2011). Current evidence from transgenic isoprene-emitting Arabidopsis suggests that isoprene emissions cannot act as ‘call for help’ cues for parasitoids that attack damaging herbivores (Loivamäki et al., 2008).

An interesting trait of the non-isoprene-emitting *P. × canescens* lines used by Behnke et al. (2013) is the trade-off between isoprene production and other antioxidative systems characterized by elevated levels of antioxidants such as ascorbate, xanthophylls and α-tocopherol (Behnke et al., 2009). Since the ozone quenching and antioxidant properties of these compounds are much higher than those of isoprene, non-isoprene-emitting poplars appeared to be more resistant to ozone and showed less damaged leaf area. First-generation oxidation products of isoprene can be observed from plant leaves (Jardine et al., 2012), suggesting that oxidation may take place already in the leaf. Behnke et al. (2009) were not able to rule out the higher ozone sensitivity of isoprene-emitting *P. × canescens* because of the formation of phytotoxic products of isoprene–ozone reactions within the leaves. Highly reactive isoprenoids produce a multitude of organic compounds in the reactions with ozone, e.g., nearly 1200 compounds detected in the reactions of ozone with the monoterpene limonene (Kundu et al., 2012), many of which have unknown phytotoxic properties. However, it is possible that better ozone tolerance of isoprene non-emitting *P. × canescens* lines is just a pleiotropic effect and should not be generalized yet (Figure 1).

Poplars as fast-growing pioneer trees have great potential in short-rotation biomass production for bioenergy to substitute for fossil fuels. Non-isoprene-emitting poplars are considered to have equal or slightly better yield, may show reduced susceptibility to fungal pathogens, and positive effects on regional climate and air quality, when compared with wild-type poplars (Behnke et al., 2011). Rising temperature is the most significant factor of the current global climatic change to affect vegetation, although CO$_2$ will also have significant effects on vegetation, e.g., by changing C : N ratio of foliage (Penuelas and Staudt 2010). Plants are responding to warming consistently with higher emission rates of isoprenoids, whereas elevated CO$_2$ diminishes isoprenoid emissions in the majority of studies (Penuelas and Staudt 2010), although some recent studies with *Populus* hybrids have given opposite evidence (Sun et al., 2012, 2013). If lower isoprene emissions at elevated CO$_2$ atmospheres will be typical for trees, a lack of isoprene-emitting capacity might not harm plant adaptation to CO$_2$-rich atmospheres (Way et al., 2011). Therefore, the loss of isoprene-emitting capacity (Behnke et al., 2013) could be deleterious for deciduous trees only under the highest temperature extremes where the capacity to emit isoprene will give adaptive benefits.

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**Conflict of interest**

None declared.
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