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Isoprene emission by plants in polluted environments

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ABSTRACT

In the past years, anthropogenic activities and climate change have significantly increased exposure of plants to environmental stresses (single or multiple) and pollutants, which negatively affect plant growth, survival, and productivity. Plants may activate an armament of defenses against such environmental stresses. Isoprene, the most abundant biogenic volatile organic compound emitted by plants, is supposed to induce stress tolerance directly, by quenching reactive oxygen species, or indirectly by strengthening photosynthetic membranes and reprogramming expression of genes that are involved in antioxidant defense mechanisms. On the other hand, isoprene is also involved in tropospheric chemistry that contributes to the production of air pollutants when mixing with anthropogenic gases. In this review, we summarized current knowledge about the impact of air and soil pollutants on isoprene emission from plants, focusing on possible feedback and feedforward mechanisms that may affect whole ecosystem functioning and evolution of plant species. Despite limited available information, especially about long-term effects of soil pollutants, it may be speculated that isoprene generally improves fitness of plants challenged by air and soil pollutants, and their interaction with other organisms.

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Isoprene emission; biogenic volatile organic compounds; plant–environment interaction; air pollution; belowground communications; soil pollution

Introduction

Plants are sessile but not passive components of the ecosystems, and they interact with the environment in several ways. Biogenic volatile organic compounds (BVOCs) are gases that are emitted by organisms in all terrestrial and marine ecosystems (Loreto et al. 2014). Plants emit worldwide more than 1 Pg C per year as BVOCs (Guenther et al. 1995, 2012), about half of which is isoprene (Guenther et al. 2006). Leaf BVOCs may be constitutively emitted (generally leaf life-long) or induced by abiotic and biotic stresses (Loreto and Schnitzler 2010). Some constitutive BVOCs may also be induced by stresses (Harrison et al. 2013). More than 1700 BVOCs have been identified, which are emitted by 90 different plant families belonging to both angiosperms and gymnosperms (Knudsen et al. 2006), as well as ferns and mosses (Hanson et al. 1999). As the detection systems get more accurate and high-throughput, the idea that all plants emit BVOCs is becoming realistic. Several roles have been suggested in the protection of plant tissues/cellular integrity, in the interaction between plants and other organisms, both attractants and repellents, as well as in the allopatric interaction (Puig et al. 2018; Lazazzara et al. 2022).

Synthesis of most significant BVOCs occurs through three pathways: the lipoxygenase (LOX), the shikimic acid, and the terpenoid pathways (Pichersky and Gershenzon 2002).

Terpenoids or isoprenoids are the largest group of specialized plant metabolites and derive from two precursors: isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP) (McGarvey and Croteau 1995). Among terpenoids, isoprene (C5H8) is the simplest and most volatile BVOC. Isoprene is formed by the chloroplastic methyl erythritol 4-phosphate (MEP) pathway through isoprene synthase (IspS), which catalyzes the removal of pyrophosphate (PPi) from DMAPP. Constitutive, light-dependent emissions of volatile isoprenoids are generally limited to large amounts of isoprene, especially from fast-growing plants (Loreto and Fineschi 2015), and of monoterpenes from some families of trees and bushes (Loreto and Schnitzler 2010). Emission of isoprene is a metabolic cost for plants, but benefits may outweigh the cost, especially under high temperature (Jardine et al. 2012) and oxidative stress (Vickers et al. 2009). Isoprene was thought to quench reactive oxidative species (ROS) such as hydrogen peroxide (H2O2) (Loreto and Velikova 2001), singlet oxygen (1O2) (Affek and Yakir 2002), or reactive nitrogen species (RNS) (Velikova et al. 2005a), and to stabilize chloroplast membranes (Velikova et al. 2011a) facilitating photosynthetic electron transport rate (Pollastri et al. 2019). The antioxidant role of isoprene is now revised, as isoprene induces a significant shift in the transcriptome and metabolome (Monson et al. 2023)
et al. 2021; Dani and Loreto 2022) that improves the ability of plants to tolerate various stresses. The general role of isoprene as a stress protective agent remains unrivaled. Other, stress-induced, BVOCs provide a clearer action as stress relievers (Paré and Tumlinson 1999; Mithöfer and Boland 2012), improving protection against biotic (e.g. herbivores or pathogens attacks) (Dicke and Baldwin 2010), or abiotic stresses (e.g. drought, high temperatures, or oxidative pollutants) (Loreto and Schnitzler 2010).

Isoprene plays several roles in atmosphere chemistry, all of which are due to its oxidation (Heald et al. 2009; Archibald et al. 2010). When anthropogenic volatile pollutants such as nitrogen oxides (NO_x) are absent, isoprene further cleanses the atmosphere of ozone. In the presence of NO_x, however, isoprene participates in reactions leading to increased ozone formation (Fehsenfeld et al. 1992) under a well-established stoichiometry (Kanakidou et al. 2005). As the emission of isoprene to the atmosphere is so prevalent, the impact of environmental factors such as light intensity, atmospheric CO_2 concentration, temperature, relative humidity, and nutrient status on isoprene emission has attracted great attention (Loreto and Schnitzler 2010; Harrison et al. 2013). Climate change impact on isoprene emission has been mainly attributed to positive long-term (enzyme-driven) and short-term (substrate-driven) feedback of rising temperature (Lehning et al. 2001; Rennenberg et al. 2006), implying that future emissions of isoprene will also increase (Arnet et al. 2008). This may be counteracted by an often large (and largely unexplained) inhibition of isoprene in rising CO_2 (Rosenstiel et al. 2003; Guidolotti et al. 2011). However, the inhibitory impact of rising CO_2 seems to be lost as the temperature gets higher, and the overall impact of climate change is therefore expected to lead to a heavier load of isoprene in the atmosphere (Sharkey and Monson 2017). We summarized studies on the effects of air and soil pollutants (Tables 1 and 2) on isoprene emission, and possible induction or repression factors.

It may be also hypothesized that, in response to increasing environmental stresses and global warming, a shift of native plants toward species and genotypes able to emit isoprene constitutively or an induced manner will occur (Lerdau 2007), and that pioneer species invading new environments largely benefit from emitting more complex volatile isoprenoids (Lluïa et al. 2010). Here, we focus on reviewing anthropogenic atmospheric and soil pollutants and climate change that could also affect isoprene emission by natural vegetation and thus alter further the load of isoprene in the atmosphere.

**Focus on isoprene and air pollution**

*Isoprene and the chemistry of the troposphere*

Most of the plant BVOCs have relatively short lifetimes in the atmosphere ranging from less than a minute to few hours depending on the atmospheric conditions (Blande et al. 2014). In the case of isoprene, rapid reaction with reactive oxygen and nitrogen species ubiquitous in the atmosphere leads not only to ozone production, but also to the appearance of secondary products of isoprene oxidation. For example, methylvinyln-ketone (MVK), methacrolein (MACR), and 2-methyltetrols like 2-methylthreitol and 2-methylerythritol have been found in the natural aerosol of Amazonia forests characterized by high isoprene emissions (Claeys et al. 2004).

Formaldehyde is also produced by isoprene oxidation and, despite the low yield (<10%), this BVOC has been used as an important proxy of isoprene natural planetary sources by satellite inspection (Palmer et al. 2006). MVK and MACR are markers of isoprene oxidation also in planta and therefore it is possible for these secondary BVOCs to be directly emitted by plants and not only formed by isoprene reactions in the atmosphere (Jardine et al. 2012). Recent results, however, suggest that MVK and MACR might be produced in planta by pathways other than isoprene oxidation (Kai et al. 2012), and that MVK may even be further oxidized to methyl ethyl ketone (MEK), making the pattern of interactions between plant BVOCs and atmospheric chemistry even more complex (Cappellini et al. 2019).

Indeed, ozonolysis (Pinto-Zevallos et al. 2010) results in the formation of many secondary organic aerosols (SOAs) (Seinfeld and Pandis 2006; Laathoworknitkull et al. 2009) with relevant climatic impacts (Claeys et al. 2004; Paulot et al. 2009). Isoprene, monoterpenes, and other terpenoids characterized by high emission rates and high reactivity with the atmospheric oxidants that are present in polluted and urban areas (NO_x, ozone, hydroxyl radical (OH-)), are major contributors of SOA burden (Kanakidou et al. 2005; Goldstein and Galbally 2007). Field studies have shown that under conditions characterized by moderate to high BVOC levels, NO_x predominantly reacts with BVOCs (Brown and Stutz 2012) to produce multifunctional compounds such as organic nitrates (ONs) (Nah et al. 2016; Faxon et al. 2018).

**Impact of atmospheric determinants of climate change on isoprene**

The two main atmospheric constituents affecting isoprene emission are carbon dioxide (CO_2) and ozone (O_3). Anthropogenic CO_2 emission is the most important forcing variable affecting changes in climate since the beginning of the industrial era. Over time, CO_2 concentrations have continued to steadily increase in the atmosphere, reaching 424 ppm in May of 2023 (https://gml.noaa.gov/ccgg/trends/weekly.html). A recent meta-analysis (Feng et al. 2019) summarized decades of experimental data (e.g. Rosenstiel et al. 2003; Possell et al. 2005) showing a largely negative impact of rising CO_2 on isoprene emission, while emission of monoterpenes is substantially unaffected by CO_2. The negative impact of rising CO_2 on isoprene has surprised scientists, as isoprene is almost totally made by photosynthetic carbon (Delwiche and Sharkey 1993; Sharkey et al. 2020), and photosynthesis is stimulated by CO_2 (Long et al. 2004). It has been suggested that the decrease of isoprene emission when CO_2 increases is related: (i) to photorespiration stimulation, and to the consequent reduction of pyruvate available to the MEP pathway (Rosenstiel et al. 2003); or (ii) to competition for phosphoenolpyruvate (PEP) a cytosolic substrate that may support chloroplastic demand (Loreto and Fares 2007); or (iii) to an inhibitory effect on IspS activity (Scholefield et al. 2004). A hypothesis that the CO_2 inhibition is related to a triose phosphate utilization limitation of photosynthesis was recently ruled out (Lantz et al. 2019). Guidolotti et al. (2011) found an inverse relationship between isoprene and intercellular CO_2 concentration (C_i), which holds even at currently ambient CO_2 concentration (>400 ppm). This supports the notion that the CO_2-dependent reduction of
isoprene reflects fine biochemical adjustments. The most recent data indicates that CO$_2$ inhibits the MEP pathway enzyme 4-hydroxy-3-methylbut-2-en-1-yl diphosphate reductase (Sahu et al. 2023). An increase in CO$_2$ may also indirectly stimulate isoprene emission at whole canopy and ecosystem level, because of higher photosynthesis, growth rate, and biomass accumulation (Arneth et al. 2007). However, several lines of evidence indicate that photosynthesis and plant growth/productivity do not always increase linearly with rising in CO$_2$ (Ainsworth and Long 2005).

Moreover, a significant interspecific variability in CO$_2$-responsiveness of isoprene emission was observed and is unexplained. Such variability in the reduction of isoprene emission could be caused by a significant variation in the size and composition of the precursor pools responsible for isoprene emissions (Ninemets et al. 2021). Squire et al. (2014) found that climate change, which includes both rising temperature and CO$_2$, increased isoprene emissions by natural vegetation, and the effect is expected to continue as long as CO$_2$ overfertilizes plants (Squire et al. 2014). Future research should explore the impact of climate change on isoprene emissions and the factors that influence this process.

### Table 1. Air pollutant feedback on isoprene emission and possible induction or repression factors.

<table>
<thead>
<tr>
<th>Plant Material</th>
<th>Air Pollutant</th>
<th>Level</th>
<th>Feedback on isoprene emission</th>
<th>Induction-repression factors</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Populus deltoides</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>+</td>
<td>Increased IspS expression and activity</td>
<td>(Fares et al. 2006)</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>–</td>
<td>Reduced photosynthesis</td>
<td>(Yuan et al. 2016)</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>O$_3$</td>
<td>Canopy level</td>
<td>–</td>
<td>Decrease IspS activity and DMADP content, reduced stomatal conductance</td>
<td>(Li et al. 2023)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>O$_3$</td>
<td>Canopy level</td>
<td>–</td>
<td>Reduced IspS activity and expression</td>
<td>(Calfapietra et al. 2007)</td>
</tr>
<tr>
<td>Populus tremula × tremuloides</td>
<td>O$_3$</td>
<td>Leaf and canopy level</td>
<td>=</td>
<td>Unknown</td>
<td>(Blande et al. 2007)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>O$_3$</td>
<td>Canopy level</td>
<td>=</td>
<td>Reduced DMADP</td>
<td>(Calfapietra et al. 2008)</td>
</tr>
<tr>
<td>Populus nigra</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>–</td>
<td>Decreased photosynthesis</td>
<td>(Fares et al. 2010)</td>
</tr>
<tr>
<td>Populus cathayana</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>–</td>
<td>Decreased photosynthetic parameters</td>
<td>(Yuan et al. 2017b)</td>
</tr>
<tr>
<td>Populus euroamericana</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>–</td>
<td>Decrease plant metabolism, like chlorophyll</td>
<td>(Yuan et al. 2017a)</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>CO$_2$</td>
<td>Leaf and canopy level</td>
<td>=</td>
<td>Pyruvate reduction</td>
<td>(Rosentiel et al. 2003)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Phosphate imbalance and high CO$_2$ substrate availability</td>
<td>(Monson and Fall 1989)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>CO$_2$</td>
<td>Canopy level</td>
<td>=</td>
<td>No trend in IspS activity and gene expression</td>
<td>(Calfapietra et al. 2007)</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>CO$_2$</td>
<td>Canopy level</td>
<td>–</td>
<td>Reduced isoprene fluxes</td>
<td>(Pegoraro et al. 2005)</td>
</tr>
<tr>
<td>Populus alba</td>
<td>CO$_2$</td>
<td>Canopy level</td>
<td>(trend to –)</td>
<td>Competition for the substrate with respiration</td>
<td>(Loreto et al. 2007)</td>
</tr>
<tr>
<td>Populus canescens</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>=</td>
<td>Carbon utilization</td>
<td>(Trowbridge et al. 2012)</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Competition of pyruvate</td>
<td>(Wilkinson et al. 2009)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Competition of pyruvate</td>
<td>(Wilkinson et al. 2009)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Decrease metabolic response</td>
<td>(Sharkey et al. 1991)</td>
</tr>
<tr>
<td>Populus tremula × tremuloides</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>+</td>
<td>Combination of DMADP pool and IspS activity</td>
<td>(Sun et al. 2012)</td>
</tr>
<tr>
<td>Populus tremula × tremuloides</td>
<td>CO$_2$</td>
<td>Canopy level</td>
<td>+</td>
<td>Increase leaf area production</td>
<td>(Sun et al. 2013)</td>
</tr>
<tr>
<td>Populus canadensis</td>
<td>UV-a</td>
<td>Leaf level</td>
<td>+</td>
<td>High photosynthesis</td>
<td>(Pallozzi et al. 2013b)</td>
</tr>
<tr>
<td>Populus canadensis</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>–</td>
<td>Reduced ATP and NADPH</td>
<td>(Pallozzi et al. 2013a)</td>
</tr>
<tr>
<td>Populus canescens</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>–</td>
<td>Metabolome adjustment</td>
<td>(Kaling et al. 2015)</td>
</tr>
<tr>
<td>Populus tremula</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>–</td>
<td>Metabolome adjustment</td>
<td>(Kaling et al. 2015)</td>
</tr>
<tr>
<td>Quercus pubescens</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>– (after recovery)</td>
<td>Inhibition of photosynthetic intermediates (long term)</td>
<td>(Velikova et al. 2005b)</td>
</tr>
<tr>
<td>Quercus mongolica</td>
<td>O$_3$</td>
<td>Canopy level</td>
<td>–</td>
<td>Decrease IspS activity and DMADP content, reduced stomatal conductance</td>
<td>(Li et al. 2023)</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Low ATP levels</td>
<td>(Loreto and Sharkey 1990)</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>+</td>
<td>Increase Metabolic response</td>
<td>(Sharkey et al. 1991)</td>
</tr>
<tr>
<td>Quercus rubus</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>+</td>
<td>Response to energy /power excess</td>
<td>(Tognetti et al. 1998)</td>
</tr>
<tr>
<td>Quercus gambelli</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>+</td>
<td>Increased leaf area</td>
<td>(Harley et al. 1996)</td>
</tr>
<tr>
<td>Salix matsudana</td>
<td>O$_3$</td>
<td>Canopy level</td>
<td>–</td>
<td>Decrease IspS activity and DMADP content, reduced stomatal conductance</td>
<td>(Li et al. 2023)</td>
</tr>
<tr>
<td>Sphagnum papillosum</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>=</td>
<td>Warm weather</td>
<td>(Tiiva et al. 2007b)</td>
</tr>
<tr>
<td>Picea abies</td>
<td>O$_3$</td>
<td>Canopy level</td>
<td>=</td>
<td>Stimulation of monoterpene rather than isoprene</td>
<td>(Yu and Blande 2021)</td>
</tr>
<tr>
<td>Picea abies</td>
<td>O$_3$</td>
<td>Canopy level/ intracellular</td>
<td>–</td>
<td>Stomatal conductance</td>
<td>(Yu and Blande 2022)</td>
</tr>
<tr>
<td>Phragmites australis</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>+</td>
<td>Oxidative stress</td>
<td>(Velikova et al. 2005a)</td>
</tr>
<tr>
<td>Phragmites australis</td>
<td>CO$_2$</td>
<td>Canopy level</td>
<td>–</td>
<td>Nitrogen reduction</td>
<td>(Schollefeld et al. 2004)</td>
</tr>
<tr>
<td>Acacia nigrescens</td>
<td>CO$_2$</td>
<td>Canopy and Leaf level</td>
<td>–</td>
<td>Reduced DMADP and IspS activity</td>
<td>(Posell and Hewitt 2011)</td>
</tr>
<tr>
<td>Eucalyptus globulus</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Competition of pyruvate</td>
<td>(Wilkinson et al. 2009)</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>CO$_2$</td>
<td>Leaf level</td>
<td>–</td>
<td>Competition of pyruvate</td>
<td>(Wilkinson et al. 2009)</td>
</tr>
<tr>
<td>Ginkgo biloba</td>
<td>O$_3$</td>
<td>Leaf level</td>
<td>+</td>
<td>Season variability</td>
<td>(Li et al. 2009)</td>
</tr>
<tr>
<td>Ginkgo biloba</td>
<td>CO$_2$</td>
<td>Branch level</td>
<td>+</td>
<td>Induced (Response to stress)</td>
<td>(Li et al. 2009)</td>
</tr>
<tr>
<td>Subarctic fen (mostly Warnstorfa exannulata)</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>=</td>
<td>No change in Net ecosystem CO$_2$ exchange (NNE)</td>
<td>(Faubert et al. 2010)</td>
</tr>
<tr>
<td>Subarctic fen (mostly Warnstorfa exannulata)</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>+</td>
<td>Changes in C assimilation</td>
<td>(Tiiva et al. 2007a)</td>
</tr>
<tr>
<td>Mucuna pruriens</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>=</td>
<td>No change leaf area</td>
<td>(Harley et al. 1996)</td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>UV-b</td>
<td>Leaf level</td>
<td>=</td>
<td>Lack of physiological flexibility</td>
<td>(Centritto et al. 2014)</td>
</tr>
</tbody>
</table>

Positive or negative feedback (+/−) refers to the direct effects of pollutants on the isoprene emission capacity while = indicates no change.
increase of isoprene emission by natural vegetation is expected when accounting for rising temperature only (Sanderson et al. 2003; Lathière et al. 2005; Wu et al. 2012). By modeling temperature and CO₂ interaction (which includes direct and indirect CO₂ effects) indeed it is confirmed that isoprene emissions will be stimulated over the twenty-first century (Arneth et al. 2007; Heald et al. 2009). A framework modeling study based on a scenario where the effect of climate and natural vegetation changes (driven by the rising of temperature and by the expansion of broadleaf forests respectively) co-occur, suggests an increase of isoprene emission by ~42% by 2050, which drops to ~4% if CO₂ inhibition of isoprene emission is also included (Tai et al. 2013). However, the CO₂ suppression is temperature-dependent and almost non-existent at 35°C (Sahu et al. 2023). Table 1 shows the contrasting effects of CO₂ on isoprene, indicating that further studies are needed to determine the potential effect of high CO₂ levels in the long term.

The other gas that has received large attention for its feedback on isoprene is ozone. While generally, CO₂ improves plant growth (Long et al. 2004), ozone is a serious environmental stress that causes heavy damage to photosynthesis. Indeed, when ozone enters the leaf, it is degraded to other components, damages photosynthetic apparatus with detrimental effects on growth rate and biomass production, and accelerates leaf senescence (Ashmore 2005; Fares et al. 2006; Wittig et al. 2009). Meta-analysis data analysis shows that isoprene and photosynthesis are reduced to similar extent (10%) by high O₃ exposure (Feng et al. 2019). However, isoprene emission is significantly increased by exposure of leaves to high UV-b (Harley et al. 1996; Tiiva et al. 2007a) and UV-a (Pallozzi et al. 2013b) radiation, which is a requisite for O₃ formation in the atmosphere. Thus, the overall impact of air pollution on isoprene emission needs additional field testing where all factors dynamically interact together.

We speculate that both effects of climate change and environmental stress could lead to an increase of isoprene-emitting species in polluted environments in response to the negative effects (e.g. oxidative stress) resulting from increased air and soil contaminants.

Figure 1 summarizes the interaction between plant isoprene emissions and atmospheric pollutants in cities and industrial areas, which may have two effects: on one hand this interaction may increase the O₃ load and high O₃ episodes may exacerbate environmental stresses; on the other hand, this same interaction may favor evolution of a vegetation that is resistant to O₃ pollution and associated oxidative stresses. As isoprene is involved in generic

<table>
<thead>
<tr>
<th>Plant Material</th>
<th>Soil pollutant</th>
<th>Level</th>
<th>Feedback on isoprene emission</th>
<th>Induction-repression factors</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Populus nigra</td>
<td>Ni(NO₃)₂</td>
<td>Leaf level</td>
<td>+</td>
<td>Increase photosynthetic carbon budget</td>
<td>(Velikova et al. 2011b)</td>
</tr>
<tr>
<td>Populus cathayana</td>
<td>N</td>
<td>Leaf level</td>
<td>+</td>
<td>More carbon allocation for isoprene</td>
<td>(Yuan et al. 2017b)</td>
</tr>
<tr>
<td>Populus canescens</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>=</td>
<td>Higher cytosolic DMADP contrasts the reduced chloroplastic DMADP</td>
<td>(Behnke et al. 2013)</td>
</tr>
<tr>
<td>Populus euphratica</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>=</td>
<td>Higher cytosolic DMADP contrasts the reduced chloroplastic DMADP</td>
<td>(Behnke et al. 2013)</td>
</tr>
<tr>
<td>Populus canescens</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>=</td>
<td>No trend in isoprene enzyme activity</td>
<td>(Teuber et al. 2008)</td>
</tr>
<tr>
<td>Tetradia riparia</td>
<td>ZnSO₄</td>
<td>Leaf level</td>
<td>+</td>
<td>Adaptive response</td>
<td>(Bibbiani et al. 2018)</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>N</td>
<td>Leaf level</td>
<td>+</td>
<td>Higher Leaf N and IspS activity</td>
<td>(Litvak et al. 1996)</td>
</tr>
<tr>
<td>Phragmites australis</td>
<td>P</td>
<td>Leaf level</td>
<td>−</td>
<td>Unknown</td>
<td>(Fares et al. 2008)</td>
</tr>
<tr>
<td>Arundo donax</td>
<td>P</td>
<td>Leaf level</td>
<td>−</td>
<td>Competition for Pi-rich intermediates or feedback inhibition induced by accumulation of starch</td>
<td>(Cocozza et al. 2019)</td>
</tr>
<tr>
<td>Arundo donax</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>=</td>
<td>Competition for Pi-rich intermediates or feedback inhibition induced by accumulation of starch</td>
<td>(Cocozza et al. 2019)</td>
</tr>
<tr>
<td>Arundo Donax</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>+</td>
<td>Fueled by extra-chloroplastic carbon source</td>
<td>(Cocozza et al. 2020)</td>
</tr>
<tr>
<td>Arundo Donax</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>=</td>
<td>Possible activation of secondary metabolism for feeding isoprene pathway</td>
<td>(Pollastri et al. 2018)</td>
</tr>
<tr>
<td>Eucalyptus globulus</td>
<td>NaCl</td>
<td>Leaf level</td>
<td>=</td>
<td>IspS activation stable</td>
<td>(Loreto and Defne 2000)</td>
</tr>
</tbody>
</table>

Positive or negative feedback (+/−) refers to the direct effects of pollutants on the isoprene emission capacity while = indicates no change.
antioxidant protection (Loreto and Schnitzler 2010) this may lead to higher isoprene emission by both native and alien (invasive) species (Lerdau 2007). The two effects may feedback on each other, and the loop may cause unpredictable consequences. Llusia et al. (2010) suggested that protection against multiple environmental stress conferred by high capacity to emit terpenoids accounted for the success of invasive plant species in Hawaii. Similarly, establishment and proliferation of Artemisia vulgaris in a new habitat seems to be related to its capacity to emit BVOCs (Barney et al. 2005). On the other hand, it is also conceivable that human-driven land use change, by replacing natural vegetation with agricultural crops, has selected against high isoprene emitters (Loreto and Fineschi 2015). Changes in natural vegetation (reduction of isoprene-emitting species) could affect air quality (Tai et al. 2013; Hantson et al. 2017). Clearly, understanding the future effects of climate change on isoprene emission is a very complex task, because of the wide range of multiple and concomitant environmental factors that could have synergistic or antagonistic effects.

The future rising of environmental stresses other than O₃ pollution but still related to anthropogenic processes and known to trigger oxidative stresses may also lead to a positive feedback for isoprene (both constitutive and induced, Figure 1) and other BVOCs biosynthesis and emission, acting as a plant-defense-system in response to climate change and warming (Penuelas and Llusia 2003). For example, field measurements showed that white oak tree canopies have higher isoprene emission rates when exposed to more sunlight, reduced water availability, and high temperature (Sharkey et al. 1996). Interestingly, these plants did not show any anomalies in their growth and an increased thermotolerance (Singsaas et al. 1997) and it is suggested that the quenching of ROS by isoprene could be an effective way to reduce the negative effects of oxidative stress compounds (Velikova et al. 2005a).

Besides CO₂ and O₃, aerosols may also affect isoprene emission. Indeed, varying in size and composition (McMurry 2000) natural and anthropogenic aerosols are of particular interest as they act as condensation nuclei of particles (Novakov and Penner 1993) and absorb solar radiation (Andreae and Crutzen 1997). We have already considered that isoprene and more complex volatile terpenoids play a direct or indirect role in the formation of ozone and SOA (see above). While monoterpenes are well-known aerosol precursors, directly, or after ozonolysis (Joutsensaari et al. 2005), the impact of isoprene on aerosol has been more controversial. Early studies showing that isoprene may contribute to SOA formation (Claeys et al. 2004) have received experimental validation (Claeys and Maenhaut 2021), but large emissions by isoprene in forests have been also shown to inhibit particle formation (Kiendler-Scharr et al. 2009), and to suppress the formation of anthropogenic SOA (Li et al. 2022).

Aerosols may also feedback on isoprene emission, for example by dimming light available to photosynthesis. An earth system model study showed that the global land isoprene emission is weakly sensitive (−1% to 2%) to aerosol pollution (Strada and Unger 2016). However, at the regional scale, anthropogenic aerosol pollution led to a reduction (−2 to −12%) in annual average isoprene emission over Europe and China (Strada and Unger 2016). Thus, the impact of aerosol on isoprene emission seems to be variable and needs to be studied further and on different ecosystems.

Figure 1. Dynamic of plant isoprene emission and settlement of alien isoprene-emitting species induced by anthropogenic processes determining environmental stresses or by climate change. Positive or negative feedback (+/−) refers to the direct effects of pollutants on the isoprene emission capacity. ↑ represents the direct effects of anthropogenic processes and climate change on the increasing of air and soil determinants and settlement of new isoprene emitter species. Figure was created with BioRender.com.
Focus on isoprene and soil pollution

Soils may also contribute to the exchange of BVOCs, as sinks or sources, depending on the very diverse soil composition in terms of microorganisms, flora, and fauna, thus expanding functional considerations on trophic interactions between aboveground and belowground plant compartments (Penuelas et al. 2014). While the complex relationships between isoprene and atmospheric pollution have been largely investigated, much less is known about the impact of soil pollution on isoprene. It could be speculated that isoprene antioxidant action also improves resistance to soil pollution.

‘Soil pollution’ refers to the presence of a chemical or substance out of place and/or present at a higher-than-normal concentration that has adverse effects on any non-targeted organism (FAO and ITPS 2015). Soil pollution acts as an abiotic stress on plants. It triggers ROS production, leading to adaptive plant responses including the improvement of the primary antioxidant redox system and the increase of the biosynthesis of secondary metabolites (Ferrer et al. 2018). Except natural areas with specific geological conditions, the major soil pollutants are related to anthropogenic (industrial) activities that release different kinds of pollutants, from complex hydrocarbons released by oil industries to very simple chemical elements such as heavy metals released as byproducts of several processes or nutrient elements such as nitrates from excess fertilization or phosphates from commercial cleaning industries. Table 2 shows studies focused on the feedback of soil pollutants on isoprene emission and the potential suppression and induction factors.

Heavy metal soil pollution is a problem of major importance for plant productivity and survival (Foy et al. 1978; Salt et al. 1998; Fargašová and Molnáróva 2010). There are several cases in which the effect of heavy metal pollution on BVOC emissions has been investigated. Velikova et al. (2011b) suggested that heavy metal (Ni) pollution increases both constitutive (isoprene) and induced (monoterpenes and sesquiterpenes) isoprenoid emissions. Indeed, other reports indicate that high doses of copper could induce emission of BVOCs (Obara et al. 2002; Mithöfer et al. 2004) of which characterize the interplay between plants and herbivores (Winter et al. 2012). Soil cadmium stress seems to increase total leaf VOC emission (Lin et al. 2022), and induces an upregulation of IspS over time (Li et al. 2017).

Moreover, in unstressed leaves, it was found that isoprene enhanced the expression of defense-related genes that may be involved in resistance against heavy metal stress (Zuo et al. 2019). For example, in unstressed transgenic models (Arabidopsis and tobacco) and in non-emitting lines fumigated with isoprene, tolerance genes for heavy metal detoxification (MRPs and HIPPP32) were upregulated, together with tolerance genes for other soil stresses like salinity (like CIPK20, NCED3) and drought (NCED5, ATAF1) (Zuo et al. 2019). This transcriptome upregulation of stress-tolerance genes could lead to increased resistance of emitting species when interacting with challenging environments.

The impact of nutrients on isoprene emission has received even wider coverage. Nutrient excess is often a consequence of pollution and over-fertilization, and finally eutrophication (Shortall 2013). Nitrates seem to generally elicit production and emission of isoprene, possibly making more N available for isoprene synthase biosynthesis (Litvak et al. 1996; Fernández-Martínez et al. 2018). On the other hand, excess of phosphorus in soils has a clear inhibitory effect on isoprene emission, assessed in different experiments (Fares et al. 2008; Cocozza et al. 2019; Cocozza et al. 2020) but never explained physiologically. Intuitively, high phosphorus should be beneficial for the synthesis of a molecule that requires large inputs of phosphorylated substrates of isoprene, like adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH) (Sharkey and Yeh 2001). High phosphorus also stimulates photosynthesis which supplies carbon for isoprene synthesis. However, uncoupling of isoprene synthesis and photosynthesis is often observed, for example under elevated CO2 (cfr. see above), or under water and salt stress (Loreto and Schnitzler 2010). It was proposed that competition with mitochondrial respiration for pyruvate or phosphoenolpyruvate is responsible for the inhibition of isoprene emission under high phosphorous nutrition (Fares et al. 2008), similar to what may occur under elevated CO2 (Rosenstiel et al. 2003), although we think that all pyruvate for isoprene synthesis comes from the Calvin-Benson cycle (Sharkey et al. 2020).

While different nutrients may have opposite effects on isoprene emission, a reduction of the intensity of emitted BVOCs in plants cultivated under high level of fertilization seems to be a convergent result (Fernández-Martínez et al. 2018), which may also explain why storage of BVOCs into reservoirs is a lost trait in recently evolved angiosperm crops. Evolution against emission of BVOCs may have an important trade-off in terms of improved plant productivity in the absence of stress, but losing the capacity to synthesize and emit BVOCs may not pay off when plants must defend themselves from abiotic stresses or must communicate with other organisms. We hypothesize that native and pioneer plants of polluted areas emit more isoprene (constitutive and induced) and speculate that the capacity to produce large amounts of isoprene may confer an adaptive advantage in a rapidly changing climate characterized by more frequent extreme events and pollution episodes.

Water and salt are important components of soils. Isoprene synthesis and emission continues even under drought or high salinity, despite concurrent photosynthesis inhibition (Brill et al. 2007). The massive literature covering the impact of these stresses on isoprene has been reviewed (e.g. Loreto and Schnitzler 2010; Loreto et al. 2014; Monson et al. 2021) and the topic is beyond the scope of this work aiming at reviewing only impacts of soil pollutants. However, we redirect the readers to cited references for a more complete understanding of the impact of water and salt on BVOCs, and particularly on isoprene.

Soil structure and composition influence the development and morphology of the root system. The root is the anchorage system of plants and is critical for the uptake of nutrients required for plant growth and physiology, including the isoprene pathway. If for the aboveground part of plants (leaves) there is much scientific evidence on the effects and activities of in situ emission of isoprene, less well studied is whether belowground heterotrophic tissues (roots) can also emit isoprene, and if roots are also influenced when plants acquire or enhance their capacity to emit isoprene. Although isoprene is mainly emitted from leaves, there is evidence that the root systems of poplar (Ghirardo et al. 2011) and transgenic Arabidopsis (Loivamäki et al. 2007; Miloradovic van Doorn et al. 2020) emit a
small amount of isoprene. It was shown that the constitutive promoter of isoprene synthase (PcIspS) is present and active in specific regions of roots (Cinege et al. 2009; Miloradovic van Doorn et al. 2020).

There are reports of isoprene affecting root development. Miloradovic van Doorn et al. (2020) recently proposed a ROS-related role of isoprene in roots, showing an altered lateral root development and differences in ROS accumulation in roots. ROS are known to be involved in many pathways, especially under a challenging environment, being signals able to activate defenses responses also coordinating the developmental processes with environmental conditions (Locato et al. 2018). An interplay between ROS and hormones, in particular auxin, ethylene, and abscisic acid has also been reported (Xia et al. 2015). Isoprene also seems to interfere with many hormones, especially those sharing the same MEP pathway (cytokinins and abscisic acid, Barta and Loreto 2006; Dani et al. 2022) but possibly also with auxins (Dani and Loreto 2022). The effect of these interactions on roots is unknown, but a possible scheme of signaling function of internal isoprene in roots in relation with ROS was proposed (Miloradovic van Doorn et al. 2020). ROS signaling affects hormonal networks and signaling processes that regulate response to environmental drivers (Mittler 2017). It was proposed that isoprene could adjust ROS by quenching (direct) or changing gene expression (indirect) and so regulate all ROS-related pathways, including those involving phyto-hormones. Even if the molecular mechanism of this interplay is still relatively unknown, it could influence the growth of the root system, in particular the development of lateral roots (Miloradovic van Doorn et al. 2020). Isoprene also affects the root proteome and many of the proteins affected are involved in redox and stress responses (Miloradovic van Doorn et al. 2020). Soil pollutants directly affect root development and the determinants of root system architecture (Lombardi et al. 2021) and this might also contribute to change BVOC emission by aboveground and belowground plant organs (Figures 1 and 2), in turn altering plant capacity to cope with pollution and environmental constraints (e.g. drought stress).

Finally, root volatiles often are key elements of plant-plant communication and of interactions of plants with soil microbiome (Figure 2), with positive consequences on priming defensive responses, facilitating root nutrient uptake, or counteracting the negative effects of pollutants. For example, BVOCs emitted from roots may facilitate interactions with arbuscular mycorrhizal fungi, expanding their beneficial functions, from improving resistance to soil stresses to enhancing nutrient availability (Asensio et al. 2012). However, whether these same functions may be attributed to isoprene is unclear. We hypothesize that this beneficial interaction (BVOCs-soil microbiome) could lead to better plant tolerance to soil stress and have positive feedback on plant biomass (Figure 2). In leaves, isoprene does not seem to be a messenger able to be captured by receptors and induce priming in receiving plants (Giordano et al. 2021), but it seems to influence insect feeding (Laonthawornkitkul et al. 2008; Loivamäki et al. 2008). This may very well be the case in roots as well, where the emission of isoprene by plants is also elusive, and possibly tiny.

Soil constraints increase ROS formation, and it was shown that ROS, and ROS scavenging enzymes, play crucial roles in early-stage root-mycorrhiza interaction (Baptista et al. 2007; Nanda et al. 2010; Ditengou et al. 2015). Several studies have shown that the intensity of ROS burst is important for root-microbes (mutualistic or pathogen) interaction and contact (Baptista et al. 2007; Nanda et al. 2010), and plant redox balance could be fundamental to differentiate between the various microbes. ROS adjustment by isoprene (direct or indirect) could be crucial for regulating root redox balance, and root isoprene emission could facilitate the interaction and communication with soil microbiome.
(Figure 2). It is known that volatiles are a signal for above-ground plant communication (Ninkovic et al. 2021). Whereas the role of isoprene as a message allowing such communication, both above and below ground, is still unclear, other root BVOCs have been extensively studied and are known to effectively elicit belowground communication (Schenkel et al. 2015; Abbas et al. 2022). If BVOCs are stimulated by soil pollution this may favor belowground plant–plant communication, perhaps priming the defensive system of plants and improving plant resistance to soil pollution and other soil-borne stresses (Figure 2).

Conclusion and future directions

Over the past years, isoprene emission has been well studied for its effects on atmospheric pollution and on plant defense, but the reciprocal impact of isoprene, soil, and atmospheric pollutants is more elusive and complicated, especially when considering that direct measurements of isoprene emission are missing (in soils) and that long-term responses at whole plant and community level have not been extensively investigated yet (both in soils and air).

Future studies should evaluate the long-term effect of pollutants, including evolutionary impacts on the composition of natural and semi-natural forests around cities and industrial areas where anthropogenic pollution may be persistent over time. This would allow a better evaluation on how policies of re-forestation and afforestation of these areas may impact on air quality, also considering climate change pressures, which may lead to regional expansion of broadleaf forests, the main emitters of isoprene, and in boreal areas (Wu et al. 2012). Tables 1 and 2 highlight the contrasting effects of air and soil pollutants on isoprene and show how many studies focus on isoprene emission at foliar level. Future studies are needed at whole plant level especially for the potential long-term effect. Soil pollution impacts on isoprene are largely uninvestigated, and the impact of soil microorganisms on isoprene emission by plants is also largely unknown, although preliminary experiments indicate that beneficial microorganisms such as mycorrhiza (Pollastri et al. 2018) and plant growth-promoting rhizobacteria (Brunetti et al. 2021) may stimulate isoprene emission.

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