**REVIEW**

# Unravelling the functions of biogenic volatiles in boreal and temperate forest ecosystems

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## Abstract

Living trees are the main source of biogenic volatile organic compounds (BVOCs) in forest ecosystems, but substantial emissions originate from leaf and wood litter, the rhizosphere and from microorganisms. This review focuses on temperate and boreal forest ecosystems and the roles of BVOCs in ecosystem function, from the leaf to the forest canopy and from the forest soil to the atmosphere level. Moreover, emphasis is given to the question of how BVOCs will help forests adapt to environmental stress, particularly biotic stress related to climate change. Trees use their vascular system and emissions of BVOCs in internal communication, but emitted BVOCs have extended the communication to tree population and whole community levels and beyond. Future forestry practices should consider the importance of BVOCs in attraction and repulsion of attacking bark beetles, but also take an advantage of herbivore-induced BVOCs to improve the efficiency of natural enemies of herbivores. BVOCs are extensively involved in ecosystem services provided by forests including the positive effects on human health. BVOCs have a key role in ozone formation but also in ozone quenching. Oxidation products form secondary organic aerosols that disperse sunlight deeper into the forest canopy, and affect cloud formation and ultimately the climate. We also discuss the technical side of reliable BVOC sampling of forest trees for future interdisciplinary studies that should bridge the gaps between the forest sciences, health sciences, chemical ecology, conservation biology, tree physiology and atmospheric science.

**Keywords** Biotic interactions · Ecosystem services · Forest–atmosphere interactions · Isoprene · Monoterpenes · Semiochemicals

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## Abbreviations

| | |
|---|---|
| BVOC | Biogenic volatile organic compound(s) |
| DMNT | (*E*)-3,8-dimethyl-1,4,7-nonatriene |
| EFN | Extrafloral nectar |
| EM | Ecosystem management |
| ES | Ecosystem services |
| ET | Ethylene |
| GLV | Green leaf volatile(s) |
| HIPV | Herbivore-induced plant volatiles |
| ICOS | Integrated carbon observation system |
| JA | Jasmonic acid |
| LOX | Lipoxygenase pathway (oxylipin pathway) |
| MeJA | Methyl jasmonate |
| MVA | Mevalonate pathway |
| MEP | 2-*C*-methyl-D-erythritol 4-phosphate pathway |
| MT | Monoterpene |
| $NO_x$ | Nitrogen oxides |
| Pn | Net photosynthesis |
| POA | Primary organic aerosols |

SA         Salicylic acid
SFM        Sustainable forest management
SOA        Secondary organic aerosols
SQT        Sesquiterpene
SHI        Shikimate pathway

## Introduction

Forests occupy one-third of the Earth's land area, and they are one of the major components of the global carbon cycle, providing substantial storage (~ 45%) of terrestrial carbon (Bonan 2008). Boreal conifer forests (Taiga) form the largest terrestrial biome on Earth, covering about one-third ($15 \times 10^8$ ha) (33%) of the total global forested area (Taggart and Cross 2009). Forests are important sinks of atmospheric $CO_2$, representing approximately half of terrestrial net primary production, and at the global scale, larger and older forest trees have a higher carbon accumulation rate than younger trees (Stephenson et al. 2014). In Europe, long-term forest management has reduced the carbon storage not only in living biomass, but also in the coarse woody debris, litter, and soil in managed forests compared with unmanaged forests (Naudts et al. 2016). Globally, deforestation of old wooded areas for agriculture and urbanisation has substantially reduced carbon sequestration and promoted the enrichment of $CO_2$ in the atmosphere (Unger 2014; Alkama and Cescatti 2016).

In addition to $CO_2$ fixation, forests affect global climate by adding atmospheric humidity through evapotranspiration (Bonan 2008) and by emissions of biogenic volatile organic compounds (BVOCs) (Fig. 1). It has been estimated that terrestrial plants re-emit approximately 1–2% of net primary production to the atmosphere as isoprene and monoterpenes (MTs) (Harrison et al. 2013). In some tree species, the proportion of carbon re-emitted as BVOCs can be as high as 8–13% under optimal light and temperature conditions (Kesselmeier et al. 2002; Peñuelas and Staudt 2010). C loss as emitted BVOCs is higher in young (7%) than in older (1.6%) leaves (Ghirardo et al. 2011). However, at the global level the BVOC emission estimates are still highly uncertain and vary significantly. The most commonly used global BVOC model MEGAN 2.1 (Guenther et al. 2012) estimates that isoprene comprises about half of the total global BVOC emission of 1 Pg ($10^{15}$ g), and the rest are other reactive terpenes and other VOCs such as methanol, aldehydes and methyl propanoids. Tropical trees are estimated to be responsible for about 70% and boreal and temperate trees together responsible for 10% of the global annual BVOC emissions (Guenther et al. 2012). Another global emission model, ORCHIDEE (Messina et al. 2016), estimated that the share of the global annual BVOC emissions from boreal and temperate forest is
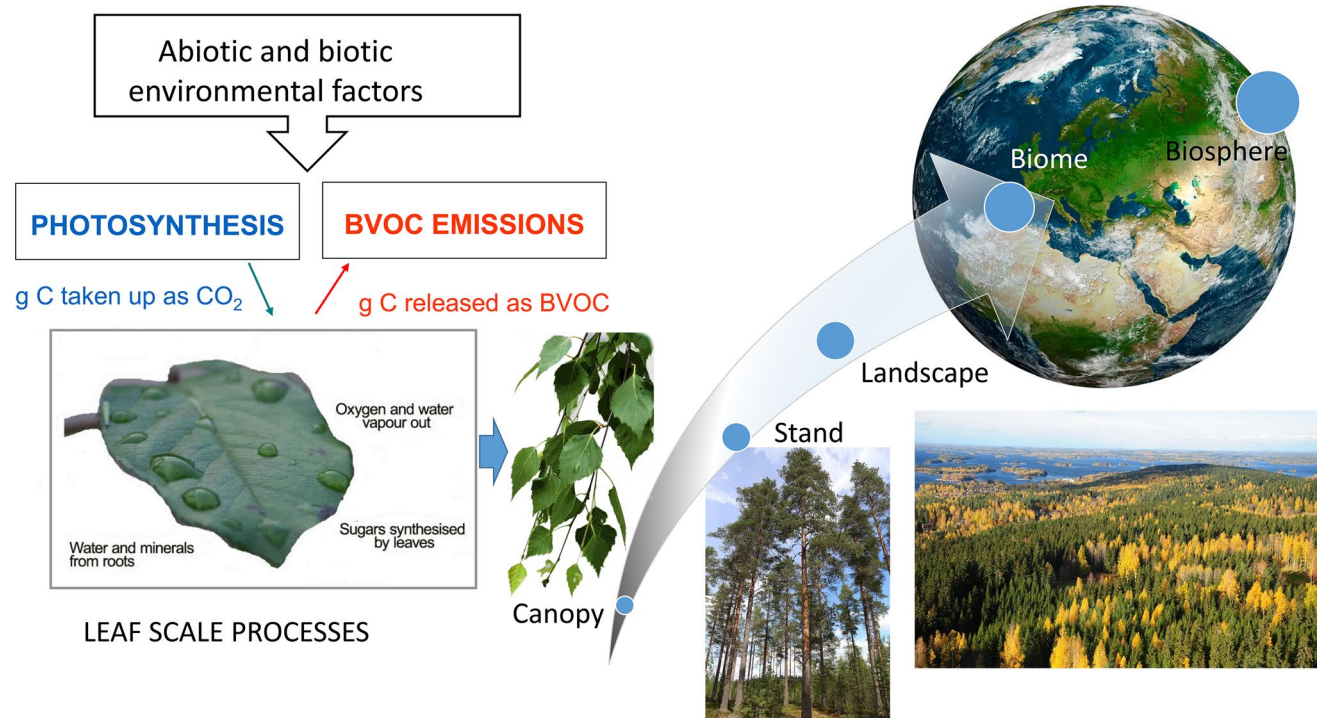


**Fig. 1** The bottom-up approach of basic physiological and ecological processes related to forest BVOC emissions. At different levels, different types of measurements can be taken from leaf level cuvettes to eddy covariance methods at forest stand and landscape levels and satellite remote sensing at the biosphere scale

higher suggesting that MT and sesquiterpene (SQT) emissions from northern regions are particularly underestimated by MEGAN. However, MTs and SQTs are the most reactive BVOCs emitted by the dominating European forest trees (Oderbolz et al. 2013). They readily react with atmospheric oxidants such as ozone, OH and $NO_3$ radicals, which leads to further reactions that form low-volatility vapours (Friedman and Farmer 2018) and SOA (Virtanen et al. 2010) in the forest atmosphere. Biogenic SOA is capable of screening out excess solar radiation and participating in cloud formation (Ehn et al. 2014).

In this review, our focus is on ecological functions and the ecosystem–atmosphere interface of the BVOCs produced by forest trees and other biological sources in forest ecosystems, but also on the ecosystem services (ES) they provide. Climate relevant fluxes of $CO_2$, methane and volatile plant hormones such as ethylene are mostly excluded from this review. Thus, our definition of BVOCs can also be termed biogenic non-methane BVOCs (Kesselmeier and Staudt 1999). We cover whole functional dynamics of BVOCs on ecosystem level from different species interactions in which they participate in forest ecosystems and end with the atmospheric degradation of the compounds and potential functions of their reaction products. We do not cover the various interactions between photosynthesis (Pn) and BVOC synthesis/emissions, because these have been extensively reviewed recently (e.g. Loreto and Schnitzler 2010; Peñuelas and Staudt 2010; Harrison et al. 2013; Fini et al. 2017; Sharkey and Monson 2017). As temperate deciduous forests and boreal conifer forests are the dominating forest biomes in Europe (Naudts et al. 2016), our examples are predominantly from these environments. It should be noted that forest ecosystems can also be a sink of BVOCs (Niinemets et al. 2014) and anthropogenic VOCs (Custodio et al. 2010) and ultra-fine aerosol particles produced from VOCs and drifted from other natural (Holopainen et al. 2017; de Sa et al. 2018) or urban environments (de Sa et al. 2018). On the other hand, photochemical oxidation of anthropogenic VOCs can be even faster in forest ecosystems than in urban environments (Custodio et al. 2010).

## Chemical diversity of BVOCs and their production in plants

BVOCs can be defined as low molecular weight and mostly lipophilic molecules that have high vapour pressure at ambient temperature (Adebesin et al. 2017). Based on their physical properties, BVOCs can be classified as extremely low, low, semi-, intermediate or highly volatile compounds (Finlayson-Pitts 2017). BVOCs represent volatile products from various biochemical pathways (Maffei 2010; Dudareva et al 2013). In addition to plants, the same biochemical pathways

and their volatile end products can be found in forest organisms such as mycorrhiza-forming fungi (Ditengou et al. 2015) and bark beetles (Martin et al. 2003; Gilg et al. 2005).

The major chemical groups of BVOCs emitted by plants (Fig. 2) can be summarised as isoprenoids from two terpene synthesis pathways (the mevalonate pathway (MVA) in the cytosol and the 2-$C$-methyl-D-erythritol 4-phosphate (MEP) pathway) in the plastids, green leaf volatiles (GLVs) from the oxylipin/LOX pathway and aromatic compounds (benzenoids and phenylpropanoids) from the shikimate (SHI) pathway (Maffei 2010; Dudareva et al. 2013). In addition, glucosinolates are a small, but ecologically important group of sulphur-containing compounds in plants of the order Brassicales (Hopkins et al. 2009). Several other highly volatile compounds related to tree physiology, such as acetaldehyde, acetone, acetic acid, formic acid and alcohols ethanol and methanol (Table 1), can also be observed in above forest flux studies (Rantala et al. 2015).

Isoprenoids or terpenoids are constructed from five carbon ($C_5$) isoprene units (terpenes) or their derivatives (terpenoids) (e.g. Wilbon et al. 2013). Terpenes with low carbon content such as isoprene ($C_5$) or MTs ($C_{10}$) are volatile or semi-volatile while compounds with a higher number of carbon atoms such as SQTs ($C_{15}$) are of semi- or low volatility (Mofikoya et al. 2019).

Isoprene or MTs dominate the BVOC emissions of many plant species, and they are globally the most important plant volatiles (Laothawornkitkul et al. 2009). Isoprene emitters are typical in temperate and tropical forests, and MT emitters
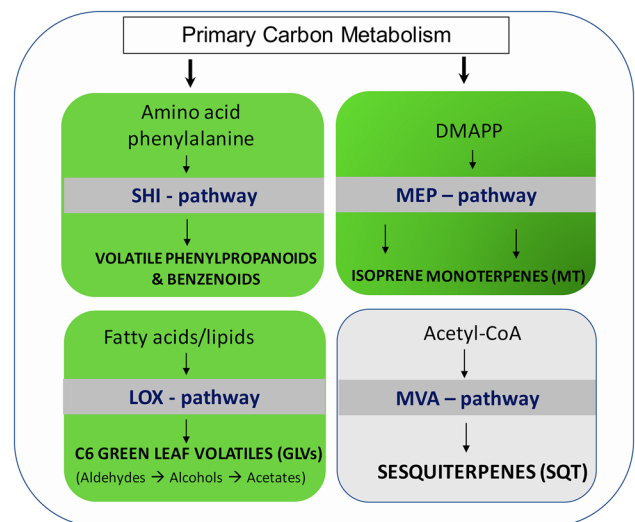
**Fig. 2** Schematic overview of four major secondary metabolite pathways responsible for BVOC production in plants as suggested by Dudareva et al. (2013). *SHI* shikimate pathway; *MEV* mevalonate pathway and *MEP* methylerythritol phosphate. *DMADP* dimethylallyl diphosphate (C5), *GDP* geranyl diphosphate (C10, acyclic MT) and *NDP* neryl diphosphate (C10, cyclic MT), *FDP* farnesyl diphosphate (C15)

**Table 1** Major BVOCs emitted by plants and their synthesis sites in plant cells

| Compound/group | Chemical formula | Molecular structure | Site of synthesis |
|---|---|---|---|
| Isoprene | $C_5H_8$ | | plastids |
| Monoterpenes<br>- α-pinene<br><br>- Linalool (oxygenated) | $C_{10}H_{16}$<br><br>$C_{10}H_{18}O$ | | plastids |
| Homoterpenes<br><br>- (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT) | $C_{11}H_{18}$ | | plastids and cytosol |
| Sesquiterpenes<br><br>- β-caryophyllene | $C_{15}H_{24}$ | | cytosol |
| GLVs, LOX-products, e.g.:<br>- (Z)-3-hexenal<br>- (Z)-3-hexenol<br>- (Z)-3-hexenyl acetate | $C_6H_{10}O$<br>$C_6H_{12}O$<br>$C_8H_{14}O_2$ | | plasmamembranes |
| Phenylpropanoids and benzenoids<br>- Methyl benzoate<br><br>- Methyl salicylate<br><br>- Isoeugenol | $C_8H_8O_2$<br><br>$C_8H_8O_3$<br><br>$C_{10}H_{12}O_2$ | | cytosol |
| Short-chained BVOC: Methanol | $CH_3OH$ | | cell wall |

are typical in coniferous forests (Unger 2014). Methylbutenol (2-methyl-3-buten-2-ol, MBO) is a $C_5$ alcohol mostly emitted by young shoots of pine species, which are known to emit only negligible amounts of isoprene (Aalto et al. 2014). Structurally and bio-synthetically, MBO is related to isoprene (Gray et al. 2003), and its atmospheric behaviour is similar to isoprene.

GLVs form a distinctive smell of damaged green plant tissues. Chemically, they are $C_6$-aldehydes, $C_6$-alcohols and their acetates (Arimura et al. 2017). Emission of these compounds occurs almost instantly after a stress event that causes damage to cellular membranes of plants (Ameye et al. 2018). GLV emissions show a successional trend of compounds with the emission profile changing within a few

minutes of the damage event (Brilli et al. 2011; Maja et al. 2014; Šimpraga et al. 2016).

Volatile aromatic compounds are comprised of benzenoids and phenylpropanoids formed via the shikimate pathway, which is primarily devoted to the synthesis of aromatic amino acids (Misztal et al. 2015; Arimura et al. 2017). Common benzenoids, benzene, xylene and toluene are released to the atmosphere from oil and gasoline used for fuels, but these same compounds are emitted from the foliage, bark and xylem of trees (Misztal et al. 2015; Tiiva et al. 2018). Other common volatile benzenoids released from foliage and flowers of plants are methyl salicylate (MeSA), methyl chavicol, indole and p-cymene (Maffei 2010; Misztal et al. 2015). Typical volatile phenylpropenes are e.g. eugenol,

isoeugenol, methyleugenol, isomethyleugenol, chavicol and methylchavicol (Dudareva et al. 2013).

Biosynthesis of BVOCs takes place either in photosynthetic cells (Fini et al. 2017) or in non-photosynthetic, specialised epidermal cells e.g. in flower petals (Adebesin et al. 2017) and in glandular trichomes (GTs; Fig. 3d) (Tissier et al. 2017; Zager and Lange 2018) or in epithelial cells of conifer resin ducts (Fig. 3a–c) in the xylem, cambium, phloem or needles (Zulak and Bohlmann 2010; Degenhardt et al. 2009).

Evergreens including Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), deciduous beech (*Fagus sylvatica*) and birch (*Betula* spp.) species are MT emitters and cover 75% of the total forest area in Europe (Table 2, Karl et al. 2009). Norway spruce also emits isoprene, although MT emissions are dominant. The predominantly isoprene-emitting deciduous species *Quercus robur* and *Q. petraea* form approximately 5% of European forested area. Other isoprene emitters in boreal/alpine and temperate environments are *Populus* and *Salix* species, while isoprene emitters are more common in warmer climates (Sharkey et al. 2008). All plant organs from flowers to roots can produce and emit BVOCs (Rasmann et al. 2005; Schiestl 2017), but photosynthetic leaves and needles of trees are the most important plant organs when considering the sources of BVOC emission in the forest atmosphere (Karl et al. 2009). In *Populus* sp. branches, a young developing leaf reaches maximum isoprene emission capacity and maximal leaf size at the age of 10–14 days (Sharkey et al. 2008). Coniferous trees are known for their terpene-rich oleoresin composed of non-volatile diterpenes and volatile MTs and SQTs (Sallas et al. 2003; Eller et al. 2013). Conifer oleoresin is stored in resin ducts in the needles, but also in the inner bark (phloem) and the wood (xylem), and from these storage structures, a proportion of the BVOCs is emitted through the bark to the atmosphere (Vanhatalo et al. 2015). Stem MT emission bursts through the bark may occasionally reach 50 ng m$^{-2}$ s$^{-1}$ in spring although they normally stay below 10 ng m$^{-2}$ s$^{-1}$ in *P. sylvestris* (Vanhatalo et al. 2015). Ghimire et al (2016) reported bark MT emissions from intact *P. abies* to be 3 ng m$^{-2}$ s$^{-1}$. When compared to average MT emissions from mature pine needles of 0.34 ng m$^{-2}$ s$^{-1}$ (Ruuskanen et al. 2005), it can be concluded that bark emissions may
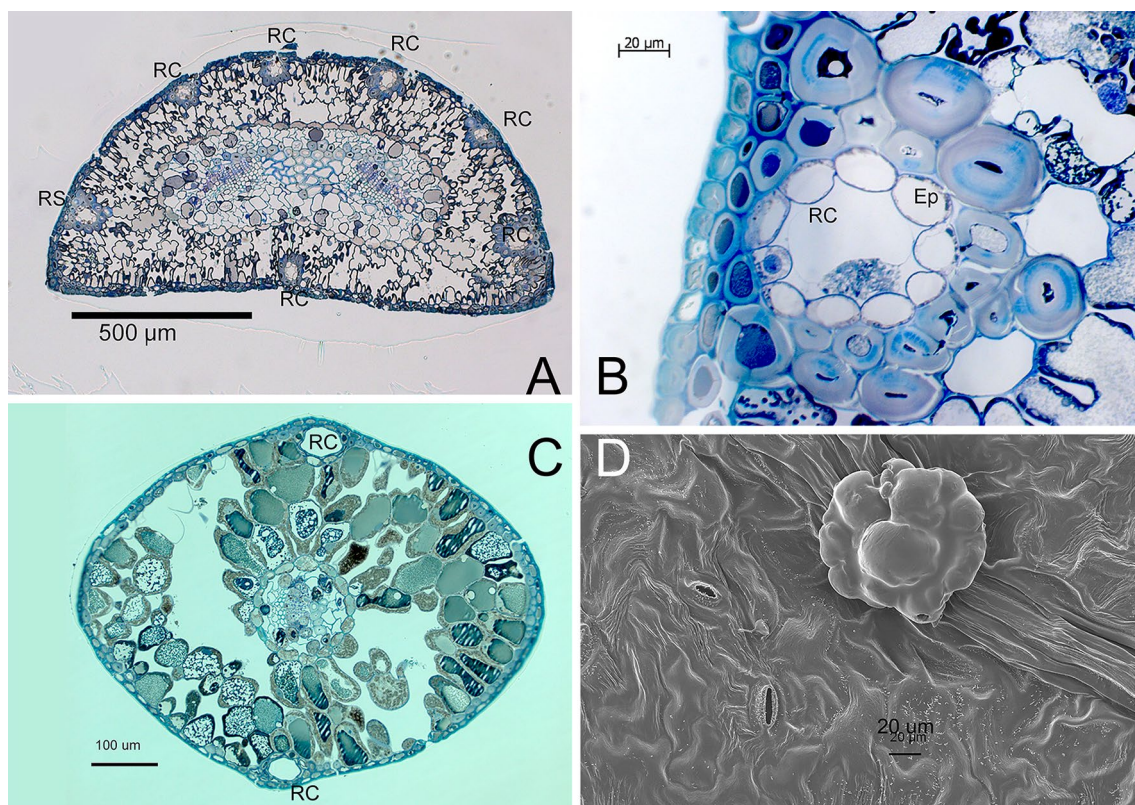


**Fig. 3** BVOC storage structures on needles and leaves of forest trees. **a** Light microscopy of a section of a *Pinus sylvestris* needle showing seven resin canals (RC) in the outer mesophyll. Resin canals of *P. sylvestris* are continuous. **b** Close-up of one of the resin canals showing the resin excreting epithelial cells (Ep) in the inner surface of resin canal. **c** Section of a *Picea abies* needle having two resin canals in the opposite sides of the needle. Resin canals of *P. abies* are discontinuous. **d** SEM micrograph of *Betula pubescens* spp. *czerepanovii* showing a peltate-type glandular trichome on leaf vein

**Table 2** BVOC emission potential of leaves and needles of selected major European forest tree species including tree coverage of each trees species

| Species | Isoprene | MT | SQT | Stored MTs | % of European forested area |
|---|---|---|---|---|---|
| Evergreens | | | | | |
| *Pinus sylvestris*[a] | 0.1 | 5.0 | 0.1 | Yes | 31.15 |
| *Picea abies*[a] | 1.0 | 2.5 | 0.1 | Yes | 21.36 |
| *Pinus pinaster*[a] | 0.0 | 2.0 | 0.1 | Yes | 2.53 |
| *Quercus ilex* | 0.0 | 43.0 | 0.1 | No | 2.18 |
| *Pinus nigra*[a] | 0.0 | 6.0 | 0.1 | Yes | 1.74 |
| *Abies alba*[a] | 1.0 | 1.5 | 0.1 | Yes | 1.50 |
| Deciduous species | | | | | |
| *Fagus sylvatica* | 0.0 | 21.1 | 0.1 | No | 7.11 |
| *Betula pubescens* | 0.0 | 3.0 | 0.2 | Yes | 4.66 |
| *Quercus robur* | 70.0 | 1.0 | 0.1 | Yes | 2.93 |
| *Betula pendula* | 0.0 | 3.0 | 0.2 | No[b] | 2.32 |
| *Quercus petraea* | 45.0 | 0.3 | 0.1 | Yes | 2.31 |
| *Castanea sativa* | 0.0 | 10.0 | 0.1 | No | 1.08 |
| *Carpinus betulus* | 0.0 | 0.1 | 0.1 | Yes | 0.97 |
| *Larix decidua*[a] | 0.0 | 5.0 | 0.1 | Yes | 0.81 |
| *Populus tremula* | 60 | 0.0 | 0.1 | No | 0.60 |
| *Fraxinus excelsior* | 0.0 | 0.0 | 0.1 | No | 0.60 |
| *Alnus glutinosa* | 0.0 | 1.5 | 0.1 | No | 0.35 |
| *Acer platanoides* | 0.1 | 1.5 | 0.1 | No | 0.34 |
| *Tilia cordata* | 0.0 | 0.0 | 0.1 | No | 0.21 |
| *Alnus incana* | 0.0 | 1.5 | 0.1 | No | 0.19 |
| *Populus* hybrids | 70 | 0.0 | 0.1 | No | 0.18 |
| *Sorbus aucuparia* | 0.0 | 0.0 | 0.1 | No | 0.05 |
| *Salix caprea* | 18.9 | 0.0 | 0.1 | No | 0.04 |
| Exotic species | | | | | |
| *Eucalyptus* sp. | 50.0 | 5.4 | 0.1 | Yes | 0.85 |
| *Robinia pseudoacacia* | 12.0 | 0.1 | 0.1 | Yes | 0.46 |

Data are modified from the data presented by Karl et al. (2009)

*MT* monoterpene, *SQT* sesquiterpene emission potential. *MT* were separated to directly synthesising pool and storage pool (such as glandular hair and resin canal) leaf emissions according to Karl et al. (2009)

[a]Conifer species

[b]Ghirardo et al. (2010)

contribute substantially to the whole tree BVOC emissions from conifers.

Plant roots can be important sources of BVOC emissions in forest ecosystems, but their measurement and quantification are difficult as root systems cannot be separated from the soil microbial network of mycorrhizal fungi and other rhizosphere microbes that also emit BVOCs (Peñuelas et al. 2014; Ditengou et al. 2015). The studies of tree rhizosphere emissions show that terpene storing species like conifers may have significant terpene emissions directly from the rhizosphere area (Lin et al. 2007; Rasheed et al. 2017) and the BVOC composition reflects the emissions from shoots (Ghimire et al. 2013; Tiiva et al. 2019). Deciduous trees and herbaceous plants also have BVOC emissions from the rhizosphere area (Steeghs et al. 2004; Maja et al. 2015). By

analysing the root volatiles of plants, it might be possible to resolve many crosstalk processes underground that are at this point unknown.

The blend of volatile MTs is genotype dependent e.g. in deciduous *Betula pendula* (Maja et al. 2014) and evergreen *Quercus suber* (Loreto et al. 2009), *P. sylvestris* (Bäck et al. 2012) and *Pseudotsuga menziesii* (Joó et al. 2011). Of the major volatiles emitted by conifer trees, MTs are the most variable (Iason et al. 2011). For instance, the MT composition of a *P. sylvestris* stand includes in addition to shoot emissions (Bäck et al. 2012), residue wood (Kivimäenpää et al. 2012; Haapanala et al. 2012) and litter (Kivimäenpää et al. 2018) emissions, which can represent $\alpha$-pinene or $\Delta$-3-carene dominating genotypes with an up to 80% dominance of either of these compounds. This strong genotype

dependence of MT emissions is supported by extracted resin storage samples from needles and wood (Manninen et al. 2002).

# BVOCs in the interactions of forest organisms

The abiotic environment controls plant physiology and the emission of BVOCs from forest plants. Changes in abiotic factors also affect physiology of other forest organisms such as herbivores and their activity, feeding behaviour and distribution (e.g. Robinson et al. 2012; Faelt-Nardmann et al. 2018) and their capacity to induce biotic stress on plants (Holopainen and Gershenzon 2010). Plant BVOC emissions are directly controlled by several abiotic factors including light level and UV radiation, water availability, carbon dioxide ($CO_2$) concentration and phytotoxic tropospheric ozone ($O_3$) (Peñuelas and Staudt 2010). Warming has most consistently resulted in increased MT and SQT emission from plants, while severe drought and elevated $CO_2$ have resulted in reduced BVOC emissions (Holopainen et al. 2018).

## Biotic stress effects on BVOC emissions of forest trees

Biotic stress is caused by herbivores, parasitic plants and microbial plant pathogens. Constitutively emitted BVOCs of plants provide important foraging cues to herbivorous animals and especially for specialist herbivore species, which use volatile cues to locate their specific host plant species among other plants (Finnerty et al. 2017). Herbivore-induced plant volatiles (HIPV) are mostly BVOCs synthesised in plants after feeding damage by a herbivore, although some of the constitutively emitted BVOCs are emitted at higher rates and they are an important part of the herbivore-induced volatile blend (Holopainen and Gershenzon 2010; Aartsma et al. 2017).

## Induction by herbivores

Within HIPV, there are two major classes: (1) GLVs, emitted immediately after wounding (seconds–minutes) and specifically linked to mechanical damage of cell membranes; and (2) compounds that are emitted a few to several hours after infection (MTs, SQTs, homoterpenes, MeSA and methyl jasmonate (MeJA)), indicating induction of specific genes. HIPV emissions from plant foliage are caused by the breakdown of cell membranes under feeding damage and the enzymes secreted by chewing and sucking insects (Ponzio et al. 2013). The main difference between these feeding modes is that feeding by a chewing insect induces jasmonic acid (JA) and ethylene (ET) signalling pathways (Ponzio

et al. 2013; Papazian et al. 2016) and BVOCs regulated by these pathways, while sucking insects like aphids induce the salicylic acid (SA) signalling pathway (Ponzio et al. 2013) and emission of related BVOCs such as MeSA (Kasal-Slavik et al. 2017; Blande et al. 2010b). In general, it has been found that the SA-induced BVOC blend has a lower number of compounds than the JA-induced BVOC blend and SA signalling can downregulate some JA-induced BVOC emissions (Wei et al. 2014).

GLV emission from leaves follows feeding activity of chewing herbivores (Maja et al. 2014; Šimpraga et al. 2016) and may stay at a high level when several larvae feed on foliage (Yli-Pirilä et al. 2016). Emission responses of terpenoids (MTs and SQTs) from the foliage of *Betula* spp. had a 3-h delay, before they substantially increasing in response to feeding by Geometrid *Epirrita autumnata* larvae, but MT emissions started to decline earlier than SQT emissions (Yli-Pirilä et al. 2016). Emissions of MeSA are indicative of phloem sap-sucking aphids on both deciduous (Blande et al. 2010a) and evergreen (Pezet et al. 2013) trees. MeSA emission may be related to specific salicylate-inducing proteins found in saliva of aphids, but not in saliva of chewing insects (Cui et al. 2019). MeSA has been shown to have oviposition repellent properties against chewing herbivorous insects (Groux et al. 2014), which may reduce competing herbivores on aphid-infested plants.

Herbivore infestation influences Pn, with trends for decreases in Pn in both herbaceous (Papazian et al. 2016) and woody (Brilli et al. 2009) species. In herbivore-damaged *Populus*, constitutive isoprene emission may become reduced faster than Pn (Brilli et al. 2009). Reduction of Pn and isoprene emission may relate to concurrent induced MT and SQT (Blande et al. 2007) or MT and GLV (Copolovici et al. 2017) emission rates.

BVOC blends induced by herbivores contain typical HIPV compounds in addition to substantial increases in compounds that form the basic constitutive emissions (Niinemets et al. 2013;) such as light- and temperature-dependent isoprene or MTs and SQTs (Fig. 4a, b). A specific type of induced emissions is the release of BVOCs from storage structures e.g. from resin canals (Heijari et al. 2011) or glandular trichomes (Murungi et al. 2016) after damage of these structures. After bark damage by phloem chewing weevils on the stem base of *Pinus* (Heijari et al. 2011) or *Picea* (Miller et al. 2005) seedlings induced linalool emission at shoot tops, indicating systemic de novo production of MTs (Miller et al. 2005). No evidence of increased expression levels of the terpene synthase-encoding genes was detected at feeding damage site of bark (Kovalchuk et al. 2015), although MT emissions from the damaged bark increased substantially (Erbilgin et al. 2003; Heijari et al. 2011; Kovalchuk et al. 2015). This indicates immediate wound sealing by transportation of BVOCs mixed in resin to the feeding
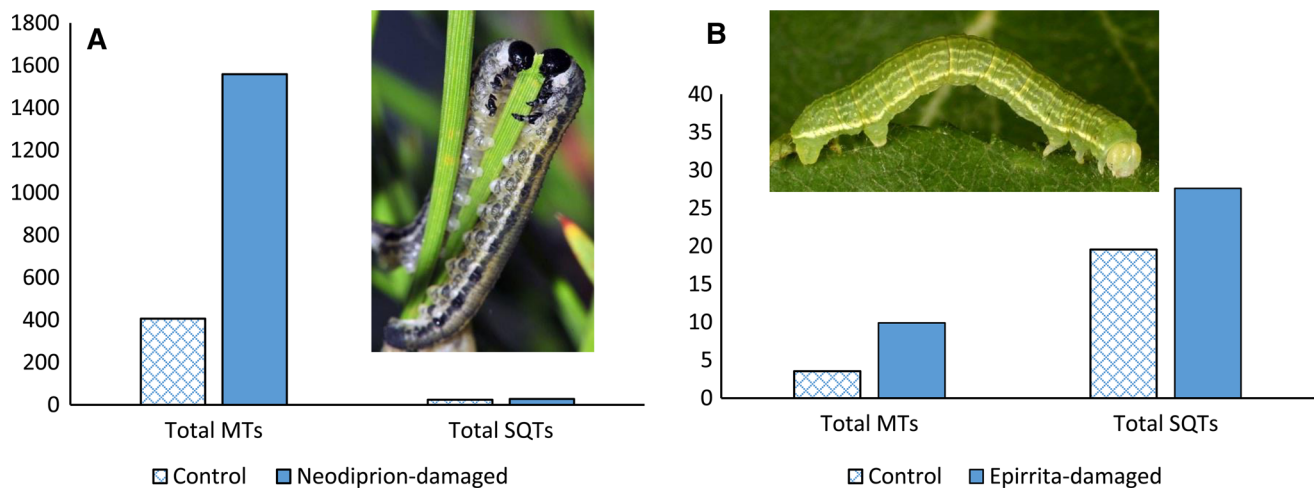
**Fig. 4** Herbivore-induced monoterpene (MT) and sesquiterpene (SQT) emission rates per unit of needle or leaf area (ng $cm^{-2}$ $h^{-1}$) from coniferous and deciduous trees. **a** *Pinus sylvestris.* Control plants and European sawfly (*Neodiprion sertifer)* damaged seedling emission rates (Ghimire et al. unpublished). **b** Control ramets and autumnal moth (*Epirrita autumnata*) damaged mountain birch (*Betula pubescens* ssp. *czerepanovii*) ramets (Mäntylä et al. 2008)

site via resin flow from the storage sites elsewhere in the resin canals (Miller et al. 2005; DeRose et al. 2017).

## Induction by pathogens

Infection or inoculation by plant pathogens (fungi, bacteria or viruses) may increase (Vuorinen et al. 2007; Eberl et al. 2018) or suppress (McCartney et al. 2018) BVOC emissions when compared with healthy control plants or suppress herbivore-induced emission (Eberl et al. 2018). BVOC blends of pathogen infected plants have similar compounds to herbivore-induced blends, and BVOC composition is defined by the type of pathogen (Ponzio et al. 2013). Obligate pathogens are biotrophs that grow on living plant tissue, and they do not kill cells rapidly and in most cases no lytic enzymes are produced, while necrotrophs are non-obligate, kill cells rapidly with cell-wall-breaking enzymes and live on necrotic plant material (Kasal-Slavik et al. 2017). Biotrophs induce the SA pathway similarly to sucking herbivores and necrotrophs induce the JA and ET pathways comparably to induction by chewing herbivores (Ponzio et al. 2013), although biotroph SA pathway/MeSA induction could be minor in the early stages of fungal infection (Vuorinen et al. 2007; Jiang et al. 2016; Kasal-Slavik et al. 2017). Furthermore, it has been found that BVOCs such as the MTs limonene and linalool and MeSA can inhibit germination of fungal spores, but BVOCs from a pathogen resistant cultivar may also induce resistance in otherwise susceptible plant cultivars (Quintana-Rodriguez et al. 2015). Interestingly, hyphae of plant pathogenic fungi can emit similar compounds as the plant, including the MT linalool and several SQTs (Müller et al. 2013). A decrease in isoprene emission is a typical

response to infection by rust fungi in isoprene-emitting trees (Jiang et al. 2016), but so far, our knowledge is too limited to use pathogen-induced BVOC profiles for diagnostic purposes in forest trees.

Evidence of BVOC induction in roots of woody plants by pathogenic fungi is rather limited. However, similar signalling pathways have been found to be activated as by leaf pathogens (De Coninck et al. 2015). The sedge *Carex arenaria* infected with pathogenic *Fusarium* sp. fungi is capable of changing root BVOC profiles to become attractive to antifungal bacteria (Schulz-Bohm et al. 2018). Beneficial fungi growing in forest soil emit BVOCs that may affect harmful and pathogenic microorganisms. For example, isolates of a common forest saprobic fungus, *Trametes versicolor*, suppress the growth of pathogenic *Armillaria* spp. and are capable of emitting nearly 200 different BVOCs (Szwajkowska-Michalek et al. 2018). An isolate emitting the highest concentration of 2-methylbutanal exhibited a greater capacity to inhibit the growth of *Armillaria* spp. (Szwajkowska-Michalek et al. 2018).

## Induction by other plant parasites and symbionts

Infestation by the parasitic plant dodder (*Cuscuta* spp.) induced higher levels of SA across cultivars of evergreen cranberry (*Vaccinium* sp.), but did not affect host BVOC composition (Tjiurutue et al. 2016). Parasitic mistletoe (*Viscum* spp.) plant on *Pinus nigra* did not acquire pine terpenes from the host plant, but the severity of attack was associated with increases of some MTs and significant reduction of SQTs and diterpenes in host needles (Lázaro-González et al. 2018). Inoculation of pine stem with the pine wilt nematode

*Bursaphelenchus xylophilus* did not change BVOC composition of *Pinus* spp., but wounding itself induced SQT and diterpene production (Rodrigues et al. 2017), while the *α*-pinene synthase gene in inoculated pine shoot cultures was upregulated in *Pinus pinea*, but not in *Pinus pinastri* (Trindade et al. 2016).

Endophytic fungi live in plant leaf tissues asymptomatically, are mutualists and give protection against herbivores and pathogens. Young leaves of the deciduous trees are re-infected annually by endophyte spores (Helander et al. 2006). An endophytic fungus *Urnula* sp. that infects fern trees can produce over 150 BVOCs including the SQT *α*-farnesene, when cultured on agar (Strobel et al. 2017). These volatiles inhibited growth of several pathogenic fungi including *Botrytis cinerea*, *Ceratocystis ulmi*, *Pythium ultimum*, *Fusarium solani*. In future BVOC studies, it will be important to estimate how much of the tree foliage BVOC emissions are actually synthesised by endophytic fungi and how much by the host plant. In grasses, endophytes inhibited aphid population growth and in one grass species endophyte infection imposed stronger differences in BVOC profiles than herbivore damage (Li et al. 2014).

## Talking trees and plant–plant communication

In the 1980s, ecologists became interested in the "talking trees" phenomenon (Baldwin and Schultz 1983) showing communication between trees (Haukioja et al. 1985). A chamber experiment (Baldwin and Schultz 1983) and field experiments (Rhoades 1983; Haukioja et al. 1985) demonstrated that neighbours of defoliated tree saplings showed increased resistance against herbivores. It was considered that damaged trees were "talking" to their neighbours about the threat of herbivores (Baldwin and Schultz 1983). Herbivore-induced BVOCs were found to attract natural enemies of herbivores in laboratory conditions, and leaves of neighbouring healthy plants also became attractive (Takabayashi et al. 1991). The BVOCs induced by feeding of spider mites on lima bean induced the expression of at least five different defence genes in healthy lima bean (Arimura et al. 2000) and induced secretion of extrafloral nectar (EFN) by healthy plants (Heil, 2008; Blande et al. 2010a). A meta-analysis by Karban et al. (2014) indicated that 40 out of 48 studies gave evidence of plant–plant communication with herbivore-induced BVOCs and improved herbivore resistance in signal-receiving plants, but only six woody plant species were studied.

Trees are modular organisms, and not all parts have vascular connection to each other. Frost et al. (2007) showed that BVOCs can act as external signals in within-plant communication (intraspecific signals) that potentially carry information to distant parts of the plant and aid herbivore defence. A follow-up study (Frost et al. 2008) showed that one of the GLV compounds induced after mechanical and feeding damage, cis-3-hexenyl acetate, can prime transcripts of genes that mediate oxylipin signalling and prime the release of terpene volatiles. Therefore, it is possible that plants in plant–plant communication just "eavesdrop" on these signals that are aimed for internal communication but result in similar responses in neighbouring plants of the same species (intraspecific signals) (Marković et al. 2019), or other species (interspecific signals) (Frost et al. 2008). Furthermore, BVOCs are not the only medium for plants to signal between each other. The ratio of red and far-red light (R/FR) is different in light reflected from photosynthesising plant leaves, when compared to direct sun light. Plants sense neighbouring plants with the help of this ratio in reflected light using a phytochrome photoreceptor, and they can modify their growth shape before the actual shading effect by neighbours (Ballaré and Pierik 2017). Emissions of the volatile plant hormone ethylene are largely increased under low R/FR light, and in shaded conditions, this may also lead to downregulation of herbivore-induced terpene synthesis and emissions (Ballaré and Pierik 2017).

## Sensing of BVOC signals

The enormous diversity of plant volatiles and their combination in BVOC plumes emitted by plants (Junker et al. 2018) provide a challenge for individual insects to find the cues of their specific host plant (Kessler and Kalske 2018). This is partly solved in the insect olfactory system which employs strategies of combinatorial coding to process general odours as well as labelled lines for specific compounds from their host that need an immediate response (Haverkamp et al. 2018). The capacity to sense the BVOC signals from their specific host plant is important for forest herbivores such as bark beetles (Progar et al 2014) and their enemies (Peng et al. 2017). The perception of BVOCs by an insect antenna takes place on odour-perceiving sensilla hairs. A BVOC molecule enters the sensilla through cuticular pores. In the sensilla, lymph odour-binding proteins transport the BVOC molecule to the chemosensory receptor proteins on the dendrite of the olfactory receptor neuron, which transmits information further to the brains (Peng et al. 2017). There are two types of olfactory sensory receptors; a broadly tuned receptor detects several dozen different compounds, and highly selective receptors are tuned to odours of outstanding ecological relevance (Haverkamp et al. 2018). In the atmosphere, elevated $O_3$ may rapidly reduce BVOC signals (Blande et al. 2014; Farre-Armengol et al. 2016) while at elevated $CO_2$ herbivores may become more sensitive to plant BVOCs improving their orientation and performance (Dai et al. 2018). Plants reduce their isoprene emissions in response to elevated $CO_2$ (Peñuelas and Staudt 2010), which suggests that isoprene may less disturb the attraction of some

specialist parasitic wasps towards herbivore-induced BVOCs (Loivamäki et al. 2008).

It is well known that BVOCs play roles in volatile plant–plant signalling and plants can take advantage of these signals in intelligent ways (Trewavas 2017). However, the mechanisms of how signal-receiving plants are sensing these signals are not known. Trewavas (2017) suggested that since plants synthesise many BVOCs, they do have enzymes to produce the chemical, so they have the potential with slight modification of producing a similar protein for sensing them. For perception of BVOC molecules on receiver plant leaf surfaces, Arimura and Pearse (2017) proposed that the mechanism might involve similar perception of BVOC molecules on receiver plant leaf surfaces as proposed for active transport of BVOCs in emissions (Widhalm et al. 2015). The perception may include specific odour-binding transport proteins (specific type of lipid transfer proteins) to transport BVOC molecules to the potential receptor proteins in plant cells. Plants primed with a BVOC stimulus from damaged plants show faster and stronger defence responses after herbivore attack than non-primed plants, and this leads to lower performance of herbivores (Blande et al. 2010a, b; Douma et al. 2017). The energetic costs of priming are relatively low (Douma et al. 2017) compared to active induced defences which include substantial carbon allocation to chemical and structural defences (Stenberg et al. 2015).

## BVOCs of rhizosphere, litter and understory

Forest structure can be divided into three different layers: the forest floor, the understory and the canopy, and all of these act as sources of BVOCs. In forest stands, the canopy layer of living trees has a substantial volume and leaf area and it acts as the most important emission source for BVOCs (Zhou et al. 2017), but can also act as a sink when atmospheric BVOCs such as MTs are taken up through stomata (Niinemets et al. 2014) or when reaction products of rapidly reactive BVOCs such as SQTs are deposited on foliage (Zhou et al. 2017). In addition to green foliage, wood, phloem and bark of trunk and branches of living trees act as important pools of stored BVOCs such as oleoresin MTs in conifer forests (Taipale et al. 2011; Ghimire et al. 2016). Furthermore, some plant species such as woody shrubs (Himanen et al. 2010; Mofikoya et al. 2018) growing in the understory can act as significant emission sources. On the forest floor, important BVOC emission sources include leaf, needle and wood litter (Holopainen et al. 2010; Mäki et al. 2017; Kivimäenpää et al. 2018) and the root systems of living (Lin et al. 2007; Rasheed et al. 2017) and dead trees (Haapanala et al. 2012; Kivimäenpää et al. 2012). BVOC synthesis and emissions by soil microbes in temperate and

boreal forests still need similar assessment as in tropical forests (Bourtsoukidis et al. 2018).

Plant roots secrete or emit a vast array of compounds into the rhizosphere including non-volatile exudates, such as organic acids, but also BVOCs (Steeghs et al. 2004; Lin et al. 2007; Rasheed et al. 2017; Tiiva et al. 2019). Root MTs may have inhibiting effect on the activity of methanotrophic bacteria (Maurer et al. 2008) or other soil microbes (Adamczyk et al. 2015); in contrast, they may also become mineralised by microbiota (Maurer et al. 2008). MTs emitted within the soil profile, either by roots or by decaying biomass, may enhance the biodegradation of various organic pollutants (Rhodes et al., 2007). Lin et al. (2007) measured root content of volatile isoprenoids (specifically MTs) of *Pinus* sp. in field conditions and MT diffusion in the soil. They found significantly decreasing emission rates of MTs with increasing distance from the mature tree trunks. MTs can have relatively high concentrations in conifer root tissues while emissions are rather low (Lin et al. 2007). Reason for this could be that MTs are reactive, rapidly degrade in the air (Faiola et al. 2018), adsorb on various surfaces (Schaub et al. 2010) or diffuse in soil water (Hiltpold and Turlings 2008). Therefore, a considerable proportion of volatile isoprenoids existing in the rhizosphere may not diffuse from the soil to the atmosphere (Lin et al. 2007).

MTs and SQTs released from insect-damaged roots attract entomopathogenic nematodes in the rhizosphere (Rasmann et al. 2005), and the diffusion of these BVOCs takes place through the gaseous rather than the aqueous phase of soil pores, as they diffuse faster and further at low moisture level (Hiltpold and Turlings, 2008). So far, the role of phytogenic VOCs in defence of forest tree roots against biotic stressors is not well known. Root-associated microbes are involved actively in function of roots (De Coninck et al. 2015), and they are capable of emitting BVOCs. Fungal symbionts use their BVOCs to induce mycorrhiza formation (Ditengou et al. 2015), and rhizobacteria of several bacterial genera use their BVOCs to protect roots against fungal pathogens (Mendez-Bravo et al. 2018). Ectomycorrhiza formation may activate jasmonic acid signalling, alter BVOC profiles and reduce herbivory in foliage of *Populus × canescens* (Kaling et al. 2018). MTs released from tree leaf litter may also have important allelopathic effects in soil e.g. by inhibiting germination and growth of competing herbaceous understory species (Silva et al. 2017).

Recent progress in studying soil microbes in tropical forests (Bourtsoukidis et al. 2018) suggests that they can have a more important role in soil BVOC, especially SQT emissions, than in temperate and boreal soil. Bourtsoukidis et al. (2018) showed that the highest emission rates are from the upper 0–5 cm of the organic soil layer and that these emissions were linked to bacterial and fungal activity by measurement of rRNA transcript abundances. Peñuelas

et al. (2014) reported that soil bacterial VOC profiles are rich in alkenes, alcohols, ketones and terpenes and that fungal VOCs are dominated by alcohols, benzenoids, aldehydes and ketones. Tiiva et al. (2019) suggested that the BVOC blend of the *P. sylvestris* rhizosphere, which is dominated by 1,3- and 1,4-dimethylbenzene (benzenoids), decanal (aldehyde) and phenol, more closely matches typical fungal BVOC profiles than bacterial BVOC profiles or the pine BVOC composition supporting the results of Peñuelas et al. (2014). Analysis of BVOC emissions by boreal wild mushrooms (fungal basidiocarps) also supported these results as unsaturated C6–C10 alcohols and aldehydes (Aisala et al. 2018) and ketones and alcohols (Zhang et al. 2018a) dominated, although some MTs such as limonene (Aisala et al. 2018) and linalool (Zhang et al. 2018a, b) were observed.

Nest mounds of *Formica* sp. wood ants can constitute significant aggregations of conifer needle litter and fungal hyphae, thus being potential BVOC sources. Analysis of BVOC emissions of nest mounds revealed that emissions are rich in MTs, particularly α-pinene, β-pinene and limonene with lower quantities of longifolene, myrcene, sabinene, camphor and camphene (Sorvari and Hartikainen, unpublished). However, ant workers are important emitters of formic acid, which is also a product of atmospheric MT–OH reactions (Friedman and Farmer 2018). Ants spray formic acid as a defence chemical when disturbed, and inside their nest, ant workers mix it with conifer resin to increase the antifungal effects of resin against entomopathogenic fungi (Brütsch et al. 2017). In addition to nest mound emissions, ants produce alarm pheromones and trail pheromones. Alarm pheromones are typically short chained compounds with one to 16 carbons that make those compounds highly volatile, such as 2-heptanone, 4-methyl-3-heptanone, citronellal, tridecane and undecane (Lenz et al. 2013). Trail pheromones are often aromatic amines (e.g. pyrazines), SQTs (e.g. farnesenes), carboxyl acids, aldehydes, acetate esters or ketones (Cerda et al. 2014).

## Role of forests in BVOC-based biosphere–atmosphere feedbacks

### BVOC reactions in the atmosphere

In principle, organic C released to the atmosphere as BVOCs is continually subject to reactions in the gas and particle phases throughout its atmospheric lifetime. Finally, the reaction products are lost as the deposition of organic particles on various surfaces (Blande et al. 2014; Holopainen et al. 2017) or become oxidised to small-molecular gases such as CO or $CO_2$ (Kroll and Seinfeld 2008). Friedman and Farmer (2018) summarised the role of MT BVOCs in atmospheric reactions in the following three processes: (1)

BVOCs acting as parent hydrocarbons for the formation of SOA in reactions with ozone ($O_3$) (Joutsensaari et al. 2015; Zhao et al. 2017; Berndt et al. 2018), hydroxyl radical (OH) (Berndt et al. 2018; Friedman and Farmer 2018) or nitrate ($NO_3$) radical (Hellen et al. 2018), (2) BVOCs that react with hydroxyl (OH) radicals to form peroxy radicals ($RO_2$) (Zhao et al. 2015), which participate in photochemical tropospheric $O_3$ production (Berndt et al. 2018; Friedman and Farmer 2018) and (3) BVOCs that react with $O_3$ at night to produce OH radicals (Lee et al. 2016).

Formation of phytotoxic ozone begins with the photochemical oxidation of nitric oxide (NO) to nitrogen dioxide ($NO_2$) under sunlight in the atmosphere (Atkinson and Arey 2003) and is followed by reactions with anthropogenic VOCs and BVOCs (Pinto et al. 2010; Hellen et al. 2018). Formation of $O_3$ is often highest in downwind rural or forested areas outside metropolitan areas, where NOx react with local BVOCs (Jeon et al. 2014). Reactions of newly formed $O_3$ with the BVOC molecules that have double bonds (Atkinson and Arey 2003) also lead to formation of reactive OH radicals (Berndt et al. 2018; Friedman and Farmer 2018). In addition to $O_3$, many BVOCs are very reactive with hydroxyl radicals (OH) or nitrate ($NO_3$) radicals leading to formation of SOA (Atkinson and Arey 2003). As OH radicals are the main sink of the greenhouse gas methane in the atmosphere, competing BVOCs prolong the lifetime of methane and enhance climate warming (Kaplan et al. 2006; Laothawornkitkul et al. 2009). On the contrary, biogenic SOA is capable of screening out excess solar radiation and participating in cloud formation (Ehn et al. 2014) mitigating climate warming. Extremely high variability in the atmospheric reactivity of individual BVOCs may affect reactivity of the local BVOC blend. For example, the atmospheric lifetimes of the SQTs β-caryophyllene and longifolene with $O_3$ are 2 min and > 33 d, respectively (Atkinson and Arey 2003).

## Secondary organic aerosols and their effects

Blue haze over forested areas (Went 1960) is one of the first observations indicating that organic volatiles released from trees in the air might be involved in several chemical reactions in the atmosphere including $O_3$ formation and the aerosol nucleation (Kulmala et al. 2013) or BVOC condensation over seed particles such as sulphur-rich particles (Tröstl et al. 2016). Recently, Kirkby et al. (2016) have shown that galactic cosmic radiation is enough to induce nucleation of pure BVOCs leading to formation of SOA. Therefore, higher BVOC emission from forests may promote radiative forcing by cloud condensation nuclei (CCN) and cloud formation (Joutsensaari et al. 2015; Zhao et al. 2017) leading to screening of excess solar radiation for the vegetation even in pristine pollution-free environments. SOA absorbs light in the short visible and near-UV region radiation wavelengths

(Saleh et al. 2013) while primary organic aerosols (POA) and black carbon released e.g. from forest fires and biomass burning more efficiently absorb thermal radiation in the atmosphere and darken e.g. arctic snow and thus are associated with global warming (IPCC 2014).

Biosphere–atmosphere interactions are dynamic, interacting through a series of feedback loops. Better understanding of these loops can improve forecasts of climate and vegetation resilience. Variability in terrestrial vegetation growth and phenology can modulate fluxes of water and energy to the atmosphere (Sheil 2018), thus affecting the climatic conditions that regulate vegetation dynamics. The BVOCs from natural vegetation may significantly affect cloud formation (Joutsensaari et al. 2015; Zhao et al. 2017) and precipitation in different vegetation regions.

## BVOCs and forest management

### Timber felling effects on BVOC emissions

Thinning of young densely growing conifer forest is needed to reduce stand density and to support the further growth of trees. Mechanical damage during thinning activities leads to emissions of BVOCs, mostly resin-stored MTs from cut trees, their branch residues, stumps and finally the logs, if they are stored in the forests (Räisänen et al. 2008b). Commercial thinning increased MT flux to the atmosphere by tenfold at 6 m above a stand of ponderosa pine (*Pinus ponderosa* L.) (Schade and Goldstein 2003). Approximately twofold–threefold increase in aerial MT concentrations after thinning and nearly fourfold increases after clear-cutting of *P. sylvestris* were found, when compared to MT emissions of an intact pine stand (Räisänen et al. 2008a, b).

Clear felling of forest leaves the tree stumps as residue wood, which still has a living root system. This may end up in a flow of resin from the root system to the stump surface for wound healing and substantial BVOC emissions from fresh and drying resin. Kivimäenpää et al. (2012) reported MT emissions from the *P. sylvestris* stump cut-surface area to be 27–1582 mg m$^{-2}$ h$^{-1}$ when measured within 2–3 h after tree cutting and 2–79 mg m$^{-2}$ h$^{-1}$ after 50 days. Haapanala et al. (2012) found in longer-term monitoring the average MT emissions from pine stump surfaces to be 25 mg m$^{-2}$ h$^{-1}$. Kivimäenpää et al. (2012) estimated that the daily MT emission rates from fresh stumps of a clear-felled *P. sylvestris* stand with a density of 2000 trees per ha could be 100–710 g ha$^{-1}$ d$^{-1}$ in a 40-year-old stand and 137–970 g ha$^{-1}$ d$^{-1}$ in a 60-year-old stand. Haapanala et al. (2012) evaluated that BVOC emission from annually cut Scots pine forests (including stumps, branches and needle litter) in Finland would be in the order of 15 kilotonnes per year, which is approximately 10% of the estimated annual

MT release (114 ktn) from intact *P. sylvestris* forests in Finland (Tarvainen et al. 2007).

## Applications in forest protection against pests and diseases

Studies with some key forest pest species have shown that BVOCs have an important role in controlling pest behaviour and as determinants of pest resistance of forest trees. Pine and spruce plantations in Europe are under continuous threat by large pine weevil (*Hylobius abietis*) adults, which feed on seedling bark phloem and cause death of seedlings. Adult weevils are controlled with insecticides in plantations (Luoranen et al. 2017), but efforts have been made to develop pesticide-free control methods of *H. abietis.* These include traditional biological control of *H. abietis* larvae with entomopathogenic nematodes in larval feeding sites in rotten conifer stumps (Kapranas et al. 2017). In order to control adult weevils, breeding for resistance (Zas et al. 2017), release of repellent BVOCs from dispensers (Lundborg et al. 2016b) and treatment with repellent plant extracts (Egigu et al. 2011) have been applied. Spraying of natural elicitors such as methyl jasmonate (MeJA), which controls resin acid and MT production, has reduced *H. abietis* damage intensity in seedlings (Heijari et al. 2005; Zas et al. 2014; Lundborg et al. 2016a, b). Timing of the elicitor treatments is crucial, because too early treatment in the spring may lead to serious growth disturbances of current-year shoot development (Heijari et al. 2005). Increased ratio of MTs $\beta$-pinene/$\alpha$-pinene in the phloem of elicitor-treated seedlings reduced *H. abietis* damage (Lundborg et al. 2016a). When additional MTs $\beta$-pinene, $\Delta$-3-carene, bornyl acetate and 1,8-cineole were released from a dispenser in addition to natural pine odour, reduced catches of *H. abietis* were found (Lundborg et al. 2016b).

BVOCs such as the MT $\alpha$-pinene released from conifer resin are important orientation cues for bark beetles to locate suitable host tree species. Females of the bark beetle *Dendroctonus ponderosae* (mountain pine beetle) accumulate MT esters verbenyl oleate and verbenyl palmitate during their larval development and possibly use these compounds as precursors for verbenol, which they release as an aggregation pheromone to coordinate mass attack of individual trees (Chiu et al. 2018). Verbenone, another $\alpha$-pinene derivative, is an anti-aggregation hormone emitted by females if population density is too high. Thus, verbenone is a repellent of bark beetles (Rappaport et al. 2001; Ranger et al. 2013; Progar et al. 2014) and formulations of verbenone are commercially available for use in the western USA (Progar et al. 2014). However, under solar radiation this compound can be photoisomerised to chrysanthenone, a compound that acts as an attractant for females of xylem feeding cerambycid beetles (Zhang et al. 2015).

Ascomycete fungi that live on conifer bark and might be mutualists of conifer bark beetles are known to produce BVOCs that have attractant and repellent effects (Kandasamy et al. 2016). The BVOCs of these fungi have potential to act together with bark beetle pheromones to improve the efficiency of pheromone traps in bark beetle monitoring. On the other hand, dispensers with these fungal BVOCs and oxygenated MTs might be used for repelling beetles from potentially attacking sensitive stands e.g. in wind fall areas (Kandasamy et al. 2016; Seybold et al. 2018). These examples show potential, but also some of the difficulties in using BVOCs in pest control in forest ecosystem. There needs to be better knowledge of how a specific BVOC and its enantiomers (chemical isomers) affect various target and non-target organisms and what are the synergistic effects together with other BVOCs (Lundborg et al. 2016b, Seybold et al. 2018).

Many BVOCs, particularly MTs in higher concentrations, are directly toxic to plant pathogenic fungal populations and may prevent germination of fungal spores in addition to their capacity to induce pathogen resistance in infested plants and provide associational resistance in neighbouring plants (Quintana-Rodriguez et al. 2015). In *P. abies* trees MeJA elicitor treatment increased the accumulation of terpenoid resin components and gave protection against infection by *Ceratocystis polonica*, a bark beetle-associated fungus (Zeneli et al. 2016). Chitosan, a polysaccharide elicitor made of fungal and crustacean chitin, has several modes of action including activation of several signalling pathways such as the octadecanoic pathway and thus affects GLV emissions and jasmonic acid content in plants (El Hadrami et al. 2010). In forest nurseries, chitosan treatment has given protection against pine pathogens (Aleksandrowicz-Trzcinska et al. 2015) while in a 15-year-old *Pinus taeda* stand, chitosan treatment increased the oleoresin production of bark but did not suppress lesion growth of bluestain fungi or intensity of bark beetle attack (Klepzig and Strom 2011). Plant elicitors that activate plant chemical defence (Holopainen et al. 2009) may significantly reduce the use of insecticides in nurseries and forest plantations (Luoranen et al. 2017).

In modern forest management, pest-centric pest management strategies are gradually being replaced by more holistic community-based strategies called sustainable forest management (SFM) or ecosystem management (EM) (Alfaro and Langor 2016). According to Alfaro and Langor (2016), the principles of SFM and EM strategies require consideration of the fact that all species contribute to ecosystem structure and function and buffering against pest outbreaks is often done in ways that are poorly understood and cannot be adequately measured. In agroecosystems, manipulation of the tritrophic effects (attraction of a pest insect's natural enemies) with induced BVOCs is under development (Heil 2008; Stenberg et al. 2015), but highly diverse forest ecosystems are more

challenging in this task. In forest ecosystems, BVOCs are important in chemical defence of trees, community level signalling, associational pest resistance and in abiotic and biotic stress control of forest trees and thus integrates the means of EM (Iason et al. 2018). In natural forest settings, herbivore-induced BVOCs are known to attract insect-feeding birds, e.g. to a moth-damaged *Betula* spp. (Mäntylä et al. 2008). However, we do not yet know enough about how BVOCs affect parasitoids and predator insects in forest ecosystem or the intricacies of the process. For example, on *P. sylvestris*, a specialist egg parasitoid wasp of the pine sawfly did not innately show a positive response to oviposition-induced BVOCs, but instead wasps need to learn them (Mumm et al. 2005). Furthermore, these egg parasitoids did not show any response to BVOCs induced by the larval feeding of the host sawfly species (Mumm et al. 2005). Therefore, better knowledge of BVOC functions in forest ecosystems is essential for improved forest EM in future.

## BVOC sampling in forest sites

In addition to remote sensing (Foster et al. 2014) and atmospheric monitoring stations (Kulmala et al. 2013), direct BVOC sampling from trees e.g. in remote forest sites with pathogen or insect outbreaks, is necessary to understand the effects of stress on BVOC emissions. For estimates of BVOC emission rates per unit of plant leaf area or dry weight, reliable sampling enclosures (Ortega et al. 2008) and analysis methods (Materić et al. 2015; Niinemets et al. 2010) are needed. Flux measurements depend on dynamic sampling where BVOC mixing ratios in an air flow can be quantitated (Tholl et al. 2006; Ortega et al. 2008; Materić et al. 2015), whereas qualitative analyses, e.g. the BVOC composition of floral scent, can be conducted with a static system by enclosing an adsorbent fibre and a flower in the same enclosure (Tholl et al. 2006). Simultaneous measurement of environmental data (light, temperature, humidity) over the period of sample collection is needed for emission calculations and temperature standardisation (Ortega et al. 2008).

Enclosure materials should be transparent and inert to BVOCs (Tholl et al. 2006;), such as some leaf Pn cuvettes (Fig. 5a). enclosures made of glass (Fig. 5b) or PTFE (polyetrafluoroethylene, Teflon) film (Fig. 5c), or bags made of PTFE (Ortega et al. 2008) or pre-heated polyethylene terephthalate (PET) (Stewart-Jones and Poppy 2006; Fig. 5d). If using leaf, branch or photosynthesis cuvettes made of acrylic, or another less inert material, they should be preferably coated inside with PTFE film for BVOC sampling (Aalto et al. 2015; Fig. 5a). Air removed for sampling is replaced with clean air pumped through PTFE tubing with dust and activated charcoal filters and $MnO_2$ as an ozone scrubber (Joó et al. 2011; Ortega et al. 2008; Fig. 5d).
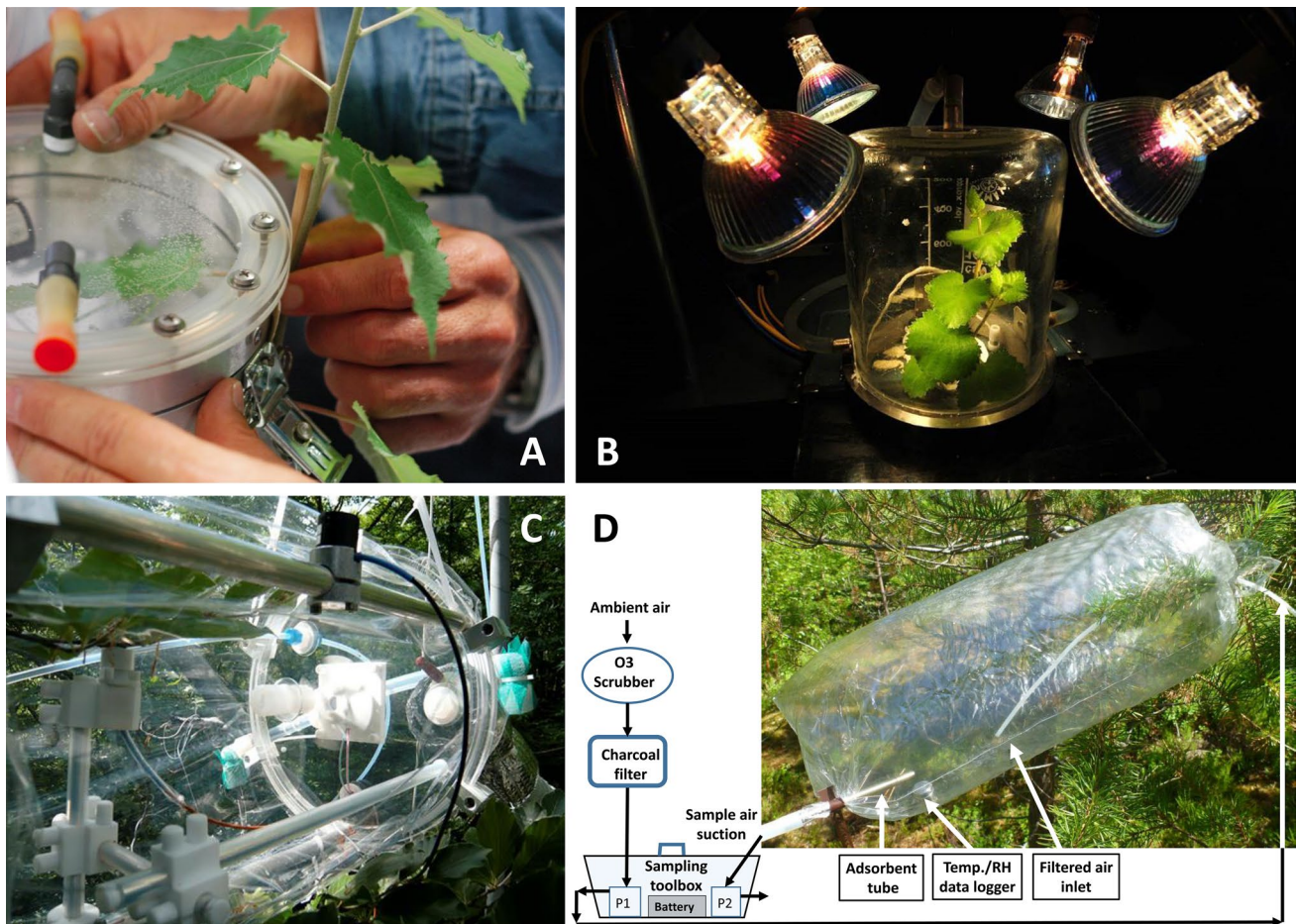
Fig. 5 BVOC sampling from tree leaves. **a** Outdoor leaf cuvette, **b** indoor cooled shoot cuvette for online PTR–MS sampling in the laboratory, **c** outdoor branch cuvette for photosynthesis measurements and BVOC sampling in the field. Cuvette is made of Teflon film, and all inner parts are made of Teflon from inside and supportive steel out-side. **d** A branch enclosure made of a PET cooking bag for sampling of BVOCs in remote forest sites. Temperature and relative humidity are monitored with small dataloggers inside and outside of the enclosure

Materić et al. (2015) list two main categories of BVOC sampling and analysis; (1) gas chromatography–mass spectrometry (GC–MS) for online or offline sampling and (2) fast online MS techniques with soft chemical ionisation, such as proton transfer reaction–mass spectrometry (PTR–MS). Online sampling needs heavy instrumentation at the sampling site but allows continuous monitoring of emissions with high time resolution. Offline GC–MS sampling is based on suction of dynamic BVOC samples through adsorbent-filled glass or steel tubes (Fig. 5d) and tight closing of tubes for storage and later desorption and GC–MS analysis in the laboratory (Tholl et al. 2006). The suggested porous adsorbent polymers for volatile and semi-volatile $C_6$–$C_{30}$ compounds are e.g. Tenax TA, while for highly volatile $C_2$–$C_{12}$ compounds Carbopack, Carbosieve and Carbotrap products are more effective (Tholl et al. 2006; Ho et al. 2018). A combination of different sorbent types in sample tubes allows a better yield of both high- and less volatile molecules (Ho

et al. 2018). Moreover, the choice of adsorbent mesh size, surface area and temperature limit must be adequately made. Sample loss via breakthrough is minimised with low flow rates such as 50 ml $min^{-1}$ (Ho et al. 2018), but for optimisation of BVOC yield per unit of sampling time, flow rates of 100–200 ml $min^{-1}$ are often used (Joó et al. 2011; Maja et al. 2015; Carriero et al. 2016).

Fast real-time PTR–MS (Materić et al. 2015; Šimpraga et al. 2011) and PTR–time of flight–MS technology (Kaser et al. 2013; Maja et al. 2014) have become prevalent techniques in laboratories and forest atmosphere monitoring stations, where measuring towers allow microclimatic, BVOC and ecophysiological data collection from air and foliage at different heights of the tree canopy (Šimpraga et al. 2011, 2013; Aalto et al. 2014, 2015). The advantages are high time resolution and high sensitivity for detection of rapid changes in BVOC emissions caused by plant growth (Brilli et al. 2016) or mechanical (Brilli et al. 2011; Kaser et al. 2013),

fire-induced (Brilli et al. 2014) or herbivore-induced damage (Schaub et al. 2010; Maja et al. 2014). A disadvantage of PTR–MS is that separation of molecules with the same molecular mass, such as various MT or SQT compounds, is not possible. This disadvantage is particularly significant to studies that require a detailed qualitative and quantitative analysis of volatile blends, such as those induced by herbivores (Maja et al. 2014) or blends used to identify the pest species (Sun et al. 2019). Finally, there is no single method that meets all requirements for determining the whole set of BVOCs emitted by living plants and at the same time minimising any disturbance (Tholl et al. 2006).

## Ecosystem services provided by BVOCs

Ecosystem services (ES) are all the benefits that humans receive from functional ecosystems. ES can be divided (Fig. 6) into provisioning, regulating and cultural services (Locatelli et al. 2017). Provisioning services cover food, cellulose and timber products, but also BVOCs that can be distilled for perfumes, flavourings, pharmaceuticals, turpentine oil, biodiesel, pest protection agents and after polymerisation as alternative organic feedstocks for green plastics and composites (Wilbon et al. 2013). Bioenergy sources of forests such as residual wood (Thiffault et al. 2015) or distilled wood extracts, including common BVOCs such as MTs in pine oil (Vallinayagam et al. 2014), are considered important provisioning ES in future forests.

Regulating services include ecosystem function including pollination services (Fig. 6), soil processes, hydrological cycles and water filtration and e.g. atmospheric $CO_2$ sequestration into living biomass and soil carbon (Locatelli et al. 2017). Stored BVOCs such as the MT pools in dead wood (Turtola et al. 2002) and needle litter (Kainulainen et al. 2003) can be important parts of carbon sequestration in the soil. Clean air is an important ES and BVOCs of forest trees

provide that by removing e.g. ozone in forest air (Niinemets 2018) and urban air (Grote et al. 2016). However, urban and periurban forests may also provide some disservices in polluted urban air, when their BVOCs participate in urban $O_3$ formation (Grote et al. 2016). In the forest atmosphere, BVOC reactions with $O_3$ and other reactive gases resulting in SOA formation may lead to improved light dispersion in the forest canopy (Niinemets 2018; Rap et al. 2018), the decreased urban heat island effect (Jin et al. 2010), processes supporting cloud formation (Joutsensaari et al. 2015; Zhao et al. 2017) and eventually to increased precipitation (Sheil and Murdiyarso 2009). The biological regulation includes pollination services, which are strongly dependent on flower BVOCs (Adebesin et al. 2017). Plants utilise BVOC-based communication between plants and between plants and other organisms. At the ecosystem scale, these BVOC signals provide many ESs, which maintain ecosystem resilience and prevent e.g. insect outbreaks in forests (Niinemets 2018). High vegetation diversity in forest ecosystems increases the level of ES, and more ES are found in forests with more tree species (Gamfeldt et al. 2013). Niinemets (2018) concluded that in future assessment of the regulatory services of forests under climate change, BVOCs at the vegetation–atmosphere interface should be a high-priority research target.

The third type of ES, cultural services of forest ecosystems includes recreation services and spiritual services including health effects (Locatelli et al. 2017). Visits to urban forests have been shown to reduce blood pressure and heart rate in women and are thus associated with beneficial short-term changes in cardiovascular risk factors (Lanki et al. 2017). This has been explained by psychological stress relief such as reduced air pollution and noise exposure. However, sensing the smell of common forest BVOCs may also have a role in stress relief. MTs such as $\alpha$-pinene and limonene are associated with the scent of clean or "fresh air" and are often used air fresheners for indoor air in households (Liu et al. 2007). Tsunetsugu et al. (2009) analysed Japanese studies of "forest bathing" ("Shinrin-yoku") and found that sensing of a weak smell of $\alpha$-pinene, a major conifer forest BVOC, induces a relaxed physiological state in humans, whereas a relatively strong smell of $\alpha$-pinene, such as the one released after intensive logging of conifers, induces a stress state in the human body.

Historically, the positive health effects of BVOCs of forest trees (Eylers 2014) or BVOC reaction products such as ozone (Grose 2011) have been the major reason why sanatoria for tuberculosis patients were established since the early 1900s in remote forest sites particularly in MT-rich conifer (Eylers 2014) and eucalyptus (Le Get 2018) forests. Roof terrain of a sanatorium, immediately above the treetops, was used for sunbathing and breathing the forest air by patients (Fig. 7a, b). It has also been argued that most of the positive effects of sunbathing treatments were rather from the

**Fig. 6** Classification of ecosystem services provided by BVOCs in forest ecosystems

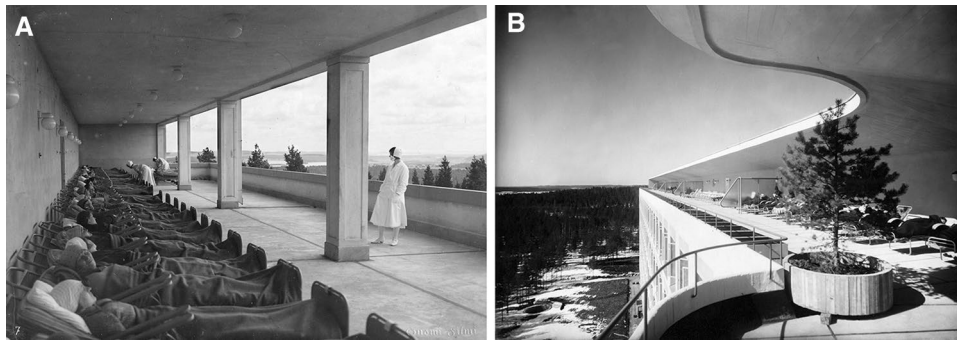| Provisioning | Regulatory | Cultural |
|---|---|---|
| • Pharmaceuticals | • Pollination guides | • Sensation of forests (forest bathing) |
| • Perfumes | • Ozone removal | • Stress relief |
| • Spices | • BVOC signals in ecosystem resilience | • Indirect health effects |
| • Fragrances | • Secondary aerosols formation | |
| • Wood odour quality | • Cloud formation | |
| • Turpentine oil | | |
| • Biodiesel | | |
| • Pesticides | | |

*Ecosystem services by forest BVOCS*

**Fig. 7** Health-related ecosystem services of conifer BVOCs for tuberculosis patients in sanatoriums. **a** The roof terrain for sunbathing at forest canopy top level in Tarinaharju Sanatorium, Siilinjärvi, Finland. Photograph from the film Ne 45000 by Erkki Karu, 1933. Courtesy of © KAVI/Suomi-Filmi Oy, **b** Paimio Sanatorium in Pai- mio, Finland, was designed by architect Alvar Aalto and completed in 1933. Sanatorium was established in a younger pine forest, and the roof terrain was equipped with planter boxes to grow pine saplings in order to improve the BVOC exposure of patients. Photograph by Gustaf Welin 1933. Courtesy of Alvar Aalto Museum

improved vitamin D availability for patients than from the BVOC rich air (Eylers 2014). During the 1940s, the discovery of streptomycin as an important cure for tuberculosis led to the closure of sanatoria (Eylers 2014), albeit recently it has been shown that MTs improve efficiency of antibiotics against drug-resistant *Mycobacterium tuberculosis* strains (Sieniawska et al. 2018).

BVOCs have multiple functions in forests and forest ecosystems, and it is obvious that they act in all three main types of ES. In agroecosystems, ecostacking (Hokkanen 2017) is a concept that combines in a synergistic manner the ES of functional biodiversity from biological and biogeochemical to socio-economic levels for sustainable plant production systems. Multifunctionality of BVOCs in forest ecosystems will give these chemicals important roles as physico-chemical tools to guide the ecostacking of ES of forest ecosystems for sustainable forestry to maintain regulating and cultural services, but at the same time allow improvement of the provisioning services gained from forests.

## Climate change, BVOCs and future forests

Global food security for the fast-growing human population requires an increasing need for land area to be used for agricultural production, which has led to a decrease in the global total forest area (Payn et al. 2015). However, at the same time the area of plantation forests has increased, particularly in temperate forests, and nearly 20% of all plantations have been with introduced species (Payn et al. 2015). Another threat for current forests is global climate change which changes the abiotic growing conditions for local tree species and promotes spreading of introduced pests and pathogens (Couture and Lindroth 2012; Seidl et al. 2018). This could be an addition to the increased biotic stress from native pest species (Ghimire et al. 2017; Nordlander et al.

2017) on forest trees in changed environmental conditions. BVOCs of forest trees are highly responsive to the abiotic (Peñuelas and Staudt 2010; Kivimäenpää et al. 2013) and biotic (Kivimäenpää et al. 2016; Ghimire et al. 2017) stresses related to climate change. Changes in BVOC emission profiles can predict survival of forest species and their further adaptation potential. For example, high isoprene emitters such as *Salix* and *Populus* have adapted to high soil humidity, while MT emitters are more common in xeric sites (Loreto et al. 2014), and thus, changes of precipitation may predict distribution of isoprene and MT emitters. High isoprene emitters such as *Quercus* spp. capable of quenching atmospheric $O_3$ could replace low or non-isoprene emitters such as *Acer* sp. (Lerdau 2007). Moreover, warming and improved growth may offset inhibitory effects of elevated $CO_2$ on isoprene emitters and increase total forest isoprene emissions (Sharkey and Monson 2017). Continuous monitoring of BVOCs has been suggested to be used as one of the potential monitoring methods of ecosystem level effects of climate change and adaptation capacity of forest vegetation community composition (Vautz et al. 2018).

Forests form large ecosystems, biomes, where the composition of tree species is mainly defined by precipitation and temperature and the species are optimally adapted to these conditions. Boreal and temperate deciduous forests may transition to shrubland or grassland if precipitation will become low (Smith and Smith 2015) and warming promotes this process (Bergengren et al. 2001). At the forest ecosystem scale, the vegetation response to climate change, such as more frequent drought, can be rapid. The change in the tree species composition from mesic deciduous trees to more drought-tolerant species in the temperate forest zone has taken place in two decades (Zhang et al. 2018b). In the boreal zone, the increase in temperature by 4 °C and precipitation increase of 10% in a century will substantially increase the proportion of deciduous *Betula* species and

change the proportions of *P. sylvestris* and *P. abies* leading e.g. to an over 400% increase in isoprene emission in most northern forests if *P. abies* becomes more common (Kellomäki et al. 2001). An increasing proportion of isoprene in forest BVOC emissions may reduce MT-based BVOC nucleation and CCN formation (Kiendler-Scharr et al. 2009).

Trees connect air and soil gas and water exchange, and in this way, they have a certain capacity to localise the climate (Alkama and Cescatti 2016). Forests are important in attracting rain at longer distances from the sea by evaporating moisture to the air and supporting cloud formation and rain intensity (Sheil and Murdiyarso 2009; Sheil 2018). The rains in more distant continental areas are "recycled" water based on evapotranspiration of the coastal forests, and the CCNs formed from reactive BVOCs of forest trees have important roles in this water recycling process (Sheil 2018). Anthropogenic land-use change from forests to agricultural land drives the global decreasing trend for isoprene and MT emissions (Hantson et al. 2017). Massive deforestations (Bala et al. 2007; Nakamura et al. 2017) may break the water recycling gradient from coastal areas to inner continental areas leading to extended desertification (Sheil and Murdiyarso 2009). This means that the evapotranspiration and BVOCs emitted by one forest stand might not improve the climatic conditions of only the emitter stand, but the most important beneficiary could be a forest stand located hundreds of kilometres downwind from the BVOC emission site (Joutsensaari et al. 2015).

BVOCs in the atmosphere are biological (stress vs. non-stress) indicators (Vautz et al. 2018) that produce valuable information of tree condition and can be used to improve forest management. As climate is changing, BVOC emissions will change and eventually will help plants to adapt to new conditions. Remote sensing with satellites that estimate $CO_2$ uptake by vegetation with a photosynthetic reflectance index (PRI) (Reuter et al. 2017) can be used for monitoring of atmospheric formaldehyde (HCHO), a major atmospheric breakdown product of isoprene, as a proxy for BVOCs (Foster et al. 2014; Kefauver et al. 2014). Combined with PRI data (Kefauver et al. 2013), BVOC monitoring with satellites can be used for online monitoring of large areas of forest to indicate early warning signs for climate change effects, such as tropospheric $O_3$ injuries (Kefauver et al. 2013). Aircrafts can be used e.g. for intensive online sampling and analysis of atmospheric BVOCs (Hu et al. 2015), but close-to-canopy remote sensing of forest BVOC emissions with drones will be possible with advanced sensor techniques (Chang et al. 2016). The ICOS measurement tower network in Europe allows simultaneous and continuous monitoring of BVOCs from soil surface, canopy layer and the atmosphere above the forest stand (Lappalainen et al. 2009; Kulmala et al. 2013). The data of monitoring stations can be combined with the data of satellite measurements and used for modelling of forest responses to climatic changes and the strength of the feedback loops of forests to BVOC, aerosols and clouds (Kulmala et al. 2013).

## Concluding remarks

BVOCs in forests have a multitude of functions at various scales, and it is obvious that due to the enormous diversity of primary BVOCs and their atmospheric reaction products, we only understand a minor part of their role in forest ecosystem function. Plants face a diverse range of metabolic and physiological challenges, which can build up when the climate is changing rapidly. With rapid development of the field of chemical ecology, terpenoid secondary compounds have been shown to play major defensive roles in the survival of trees and in various ecosystem interactions including large-scale ecosystem and biosphere–atmosphere feedbacks such as the roles of BVOCs in control of precipitation. For better understanding of the role of BVOCs in forest ecosystems, it is essential that the basic processes related to BVOC biosynthesis, transportation and emissions are better known. We know how e.g. herbivorous insects and their natural enemies perceive molecular BVOC signals, but we still do not fully know how other plants are sensing the "cry for help" signals released by attacked plants. When the molecular basis of plant-to-plant signalling is unravelled, it will open possibilities to reduce and control the stress of growing forest trees caused by e.g. extreme weather conditions related to changing climate, herbivore and pathogen attack and forest management activities.

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