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Stress-induced BVOC emissions from forests in Sweden

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Erica Jaakkola



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DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University, Sweden. To be publicly defended on Friday, the 8th of March 2024 at 09:30 am in Pangea auditorium, Geocentrum II, Sölvegatan 12, Lund.

Faculty opponent
Professor Mark J. Potosnak

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Abstract A changing climate is expected to lead to more extreme weather events, such as an increased frequency of droughts and forest fires. Changing forest conditions can offer benefits to species such as insects, including bark borers that thrive in warm conditions. Warmer temperatures also favor the acceleration of ozone (O ₃) production, which can cause stress on vegetation. Vegetation stress can have negative impacts on growth and can also result in increased tree mortality, negatively impacting global forests with deforestation, loss of biodiversity and associated ecosystem services. This thesis aimed to quantify the effect of forest stress from the European spruce bark beetle (<i>Ips typographus</i>), elevated O ₃ concentrations and forest fires by analyzing the biogenic volatile compound (BVOC) emissions from both healthy and stressed trees. The results of this thesis revealed that bark beetle infestations appear as a critical stressor, increasing the total BVOC emissions by 7 900%. Recovery after forest fires, on the other hand, indicated a 54% to 90% reduction in emission rates. Similarly, elevated O ₃ concentrations revealed an 80% reduction in BVOC emissions from mountain birch leaves. However, after exposure the emissions were instead boosted with 16% higher emissions compared to healthy leaves. In addition to the total emission rates, the importance of the individual compounds were highlighted in this thesis. Bark beetle infestations caused significant increases for all measured compounds, plus the addition of eucalyptol not seen from healthy bark. Even if there was a reduction in the total emission rates from the forest fire recovery and the O ₃ exposure, increases were seen for individual compounds. This can have substantial implications for atmospheric chemistry as certain compounds found to increase have a higher capacity for secondary organic aerosol (SOA) formation. Scaling up the impacts to cover all of Sweden, the study estimates a 2% increase in BVOC emissions when considering all stresses concurrently. This thesis provides an insight into how stress from drought, bark beetle and forest fire can have long-term impacts on BVOC emissions. The quantified emissions are an important contribution to our knowledge on vegetation response to stress. These results can be used as a basis for better prediction of future emission changes in atmospheric and ecosystem models. Additional applications of the thesis results can be to monitor forest status by using the quantified stress emissions as indicators of forest stress.		
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“Learning never exhausts the mind”
- Leonardo da Vinci

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Abstract

A changing climate is expected to lead to more extreme weather events, such as an increased frequency of droughts and forest fires. Changing forest conditions can offer benefits to species such as insects, including bark borers that thrive in warm conditions. Warmer temperatures also favor the acceleration of ozone (O₃) production, which can cause stress on vegetation. Vegetation stress can have negative impacts on growth and can also result in increased tree mortality, negatively impacting global forests with deforestation, loss of biodiversity and associated ecosystem services. This thesis aimed to quantify the effect of forest stress from the European spruce bark beetle (*Ips typographus*), elevated O₃ concentrations and forest fires by analyzing the biogenic volatile compound (BVOC) emissions from both healthy and stressed trees.

The results of this thesis revealed that bark beetle infestations appear as a critical stressor, increasing the total BVOC emissions by 7 900%. Recovery after forest fires, on the other hand, indicated a 54% to 90% reduction in emission rates. Similarly, elevated O₃ concentrations revealed an 80% reduction in BVOC emissions from mountain birch leaves. However, after exposure the emissions were instead boosted with 16% higher emissions compared to healthy leaves. In addition to the total emission rates, the importance of the individual compounds were highlighted in this thesis. Bark beetle infestations caused significant increases for all measured compounds, plus the addition of eucalyptol not seen from healthy bark. Even if there was a reduction in the total emission rates from the forest fire recovery and the O₃ exposure, increases were seen for individual compounds. This can have substantial implications for atmospheric chemistry as certain compounds found to increase have a higher capacity for secondary organic aerosol (SOA) formation. Scaling up the impacts to cover all of Sweden, the study estimates a 2% increase in BVOC emissions when considering all stresses concurrently.

This thesis provides an insight into how stress from drought, bark beetle and forest fire can have long-term impacts on BVOC emissions. The quantified emissions are an important contribution to our knowledge on vegetation response to stress. These results can be used as a basis for better prediction of future emission changes in atmospheric and ecosystem models. Additional applications of the thesis results can be to monitor forest status by using the quantified stress emissions as indicators of forest stress.

Populärvetenskaplig sammanfattning

Sveriges skogar påverkas av de hastiga globala klimatförändringarna. Inverkan av klimatförändringarna syns redan med både ökad frekvens och kraftigare extremväder som stormar, värmeböljor, torka och skyfall. Ett tydligt exempel är den extrema torka som drabbade hela landet år 2018. Till följd av torkan har det bland annat skett en explosionsartad ökning av antalet granbarkborrar som angriper och dödar granar i Sveriges skogar. Den värsta skogsbranden i svensk modern tid drabbade Mellansverige samma år och förhöjda halter av ozon uppmättes till följd av de förhöjda temperaturerna. Det står klart att klimatförändringarna påverkar oss på en märkbar nivå men utöver de direkta effekter som leder till att träd och skogar dör, är det inte riktigt lika tydligt hur skog och mark egentligen påverkas.

All vegetation interagerar med atmosfären där bland annat koldioxid är en vital del för att växter ska kunna leva och växa med hjälp av fotosyntes. Men utöver fotosyntesen har växter ytterligare interaktioner med atmosfären. Under fotosyntesprocessen tillverkas nämligen även andra ämnen som är användbara för växterna. Dessa ämnen är små kolväten som bland annat produceras för försvar mot till exempel insektsangrepp, men också mot förhöjda temperaturer eller mot oxidativ ozonstress som annars hade kunnat skada växters celler och vävnader. Kolvätena som släpps ut har en engelsk förkortning, BVOC, som kan översättas till biogena volatila organiska kolväten.

Syftet med denna avhandling var att analysera effekten av barkborreangrepp, oxidativ ozonstress samt återhämtning efter skogsbränder genom att mäta dessa BVOC utsläpp. Resultaten är tydliga från barkborrestudien, BVOC utsläppen från granbark ökade med 7 900 % vilket var den största uppmätta ökningen av alla studier. Skogsbränder och oxidativ ozonstress påverkade BVOC utsläppen i motsatt riktning, efter skogsbrand minskade utsläppen från skogsmark med upp till 90 % och under oxidativ ozonstress sågs en minskning med 80 %. En viktig upptäckt i denna avhandling var också att även om de totala utsläppen minskade, så uppmättes en ökning för vissa kolväten.

Denna upptäckt är av stor vikt eftersom BVOC utsläppen även påverkar en stor del av kemin i atmosfären. BVOC kan bland annat bilda sekundära organiska aerosoler, partiklar som påverkar atmosfären genom att bland annat direkt sprida och reflektera solstrålning. Aerosolerna bidrar även till att bilda moln. Det har gjorts upptäckter att vissa kolväten är bättre än andra på att bilda aerosoler, och det är även dessa kolväten som sågs öka vid stress, även om totalen minskar. Utöver dessa resultat bidrar denna avhandling också till en fördjupad förståelse av hur skog påverkas av stress förorsakad av klimatförändringar. Dessa resultat är även av stor vikt för att förbättra prognoser från modeller av atmosfärskemi och ekosystemmodeller.

List of Papers

- I. **Jaakkola, E.**, Gärtner, A., Jönsson, A. M., Ljung, K., Olsson, P. O. & Holst, T. (2023). Spruce bark beetles (*Ips typographus*) cause up to 700 times higher bark BVOC emission rates compared to healthy Norway spruce (*Picea abies*). *Biogeosciences*, 20, 803–826.
- II. **Jaakkola, E.**, Hellén, H., Olin, S., Pleijel, H., Tykkä, T., Holst, T. (2024). Ozone stress response of leaf BVOC emission and photosynthesis in mountain birch (*Betula pubescens* spp. *czerepanovii*) depends on leaf age. *Accepted for publication in Plant-Environment Interactions*
- III. **Jaakkola, E.**, Lindström, J., Kelly, J., Kljun, N., Holst, T. BVOC emissions from boreal forest floors during the first years after a wildfire: impacts of fire severity, stand age and management strategies. *Manuscript unpublished*
- IV. Holst, T., **Jaakkola, E.**, Biermann, T., Heliasz, M. & Holst, J. Variation of BVOC fluxes during three summer seasons at the Swedish Hyltemossa spruce forest site. *Manuscript unpublished*

Author contributions

- I. EJ conceived and designed the study with TH. EJ conducted the data collection and led the analysis with contributions from KL, AMJ, AG and POO. EJ wrote the paper with contributions from all co-authors.
- II. EJ conceived and designed the study with contributions from TH, HP and SO. EJ conducted the data collection. TT and HH performed the laboratory analysis and EJ led the data interpretation. EJ wrote the paper with contributions from all co-authors.
- III. TH conceived and designed the study with NK. TH conducted the data collection. EJ performed the data analysis. Data interpretation was done by EJ and JL with contributions from TH. JK contributed to data curation and visualization. EJ wrote the paper with contributions from all co-authors.
- IV. TH conceived and designed the study and conducted data collection. EJ and TH performed data analysis and data interpretation. EJ and TH wrote the paper with contributions from all co-authors.

Abbreviations

BVOC	Biogenic volatile organic compounds
SOA	Secondary organic aerosol
C	Carbon
H	Hydrogen
MEP	Methylerythriol phosphate
MVA	Mevalonate
DMADP	Dimethylallyl diphosphate
IDP	Isopentenyl diphosphate
LOX	Lipoxygenase
OH	Hydroxyl radical
O ₃	Ozone
NO _x	Nitrogen oxides
CH ₄	Methane
CCN	Cloud condensation nuclei
CDNC	Cloud droplet number concentration
SO ₂	Sulfur dioxide
ICOS	Integrated carbon observation system
ACTRIS	Aerosol, clouds and trace gases research infrastructure
ANS	Abisko scientific research station
GC	Gas chromatograph
MS	Mass spectrometry
EC	Eddy covariance
PTR-TOF	Proton transfer reaction – time of flight
ATD	Automated thermal desorption
ER	Emission rate
PAR	Photosynthetically active radiation
GPP	Gross primary production

HM	High-severity fire mature trees
HY	High-severity fire young trees
UM	Unburnt mature trees
MT	Monoterpene
SQT	Sesquiterpene
OXY	Oxygenated compounds
MBO	2-methyl-3-buten-1-ol
AMCH	4-acetyl-1-methylcyclohexene

Introduction

When spending time in a pine forest, it is inevitable to notice the fragrant, pine scent surrounding the air. The scent originates from the trees as they emit tiny gas-phase particles. During warm summer days, a blue colored haze can be noticed above the forest. It was only in the 1960s that the origin of this blue haze was given attention by Went, who was interested in why the blue colored haze occurred. Went (1960) formulated the hypothesis that the blue haze was in fact derived from these tiny terpene particles emitted by the forests. Despite the efforts to fill the knowledge gaps surrounding the phenomena since then, there is still a lot to learn.

The terpene particles emitted by forests are hydrocarbons, also named biogenic volatile organic compounds (BVOCs). BVOCs are chemical compounds emitted from above- and below-ground from different plant organs. The highest emissions of BVOCs originate from green leaves while the greatest variety come from flowers and fruits (Laothawornkitkul et al., 2009; Niinemets and Monson, 2013). The compounds are produced via photosynthesis and are suggested to have developed and changed throughout history with plant evolution and adaptation (Niinemets and Monson, 2013). These compounds are useful to the plants in signaling and as a defense from stress.

Extreme disruptions to environmental stability can lead to plant stress with severe impacts (Bussotti and Pollastrini, 2021), affecting BVOC emissions. Uncertainties remain about the extent and impact severity of different stresses. Most extreme stresses are expected to increase with climate change (Seneviratne et al., 2021). BVOC emissions are major contributors to the formation of secondary organic aerosols (SOAs) and reactions in atmospheric chemistry (Hallquist et al., 2009; Kulmala et al., 2003; Paasonen et al., 2013). Research on BVOC emissions is vital to understand how they impact the climate system, especially as climate change induced emission changes lead to difficulties in making future predictions with climate models (Grote et al., 2019).

Plant emission of BVOCs

There are many and diverse BVOCs — examples include terpenoids, alkanes, alkenes, alcohols, aldehydes, esters, ethers, and carboxylic acids (Maffei, 2010). The terpenoids share similarity in their structure with building blocks of one or more isoprene (C_5H_8) chains. The terpenoids from the monoterpene group typically consist of two chains (C_{10}) while the sesquiterpene group has three chains (C_{15}). Plants produce energy as primary metabolites via photosynthesis used mainly for growth. Some of the primary metabolites are utilized through secondary metabolism, with BVOCs produced through various synthesis pathways (Figure 1; Niinemets and Monson, 2013). The production pathway of the BVOCs is of particular interest because, depending on whether or not the plant is exposed to stress or other factors, different pathways may be elicited (Li et al., 2017; Loreto and Schnitzler, 2010). Knowing the originating pathways of BVOCs can then give a hint of the plant's status.

Isoprene and the main monoterpenes are produced from the same pathway, the methylerythriol phosphate (MEP) pathway (Li and Sharkey, 2013). This pathway can also produce some sesquiterpenes, but the majority of them are produced through the mevalonate (MVA) pathway (Loreto and Schnitzler, 2010). Common for these pathways is the production of similar substrates; dimethylallyl diphosphate (DMADP) and its isomer isopentenyl diphosphate (IDP) used as precursors for terpenoid production (Li and Sharkey, 2013). Other BVOCs are produced from other pathways, green leaf volatiles (C_6) are for example synthesized through the lipoxygenase (LOX) pathway (Loreto and Schnitzler, 2010), where linolenic acid is used as the substrate for production (Matsui and Engelberth, 2022). The LOX-pathway is activated upon plant damage (Matsui and Engelberth, 2022).

Emissions of BVOCs mostly occur continuously and are hence called *constitutive* emissions (Holopainen, 2011). But, when plants are exposed to stress, emissions can be *induced* and change in both compound composition and amount (Laothawornkitkul et al., 2009). The induction of certain compounds can provide insight into what pathways were activated and details of how the plant was affected.

By producing and emitting BVOCs, a plant can re-emit up to 10% of its fixed carbon (Niinemets and Monson, 2013). However, the benefits of emitting BVOCs outweighs the metabolic costs. One purpose of the constitutive BVOC emissions is to interact with the surrounding environment (Fineschi and Loreto, 2012). Plants interact with pollinators that have learned to recognize and distinguish certain plants by their BVOC composition. However, plants and insects have co-evolved and while the main use of plant BVOCs is to attract pollinators, herbivores have taken advantage of this by

learning how to tune in to the scent and use it to locate the plant (Brilli et al., 2009). Since the constitutive emissions are vital for plant reproduction, evolution did not favor the emissions to stop. Instead, plants evolved defense strategies with their BVOC emissions. Through direct defense, plants have learned to alter the BVOC composition upon herbivore attacks to act as a repellent (Fineschi and Loreto, 2012). They can also induce certain compounds that in high concentrations are toxic to some attacking insects (Krokene, 2015). The defense can also be indirect where they instead focus their resources on inducing emissions or changing the compound composition to attract the natural predators of the attacking herbivore (Fineschi and Loreto, 2012).

Some plants emit BVOCs directly after they are produced, while some plants have the ability to store BVOCs in resin ducts or glands (Figure 1; Ghirardo et al., 2010). The BVOCs can then be emitted at a later stage when needed, for example when a plant is exposed to leaf wounding or herbivory (Brilli et al., 2011; Niinemets and Monson, 2013; Räisänen et al., 2009). As BVOCs are closely connected to plant metabolism, changes in temperature or light can have large impacts on the emissions (Rinne et al., 2002; Zeng et al., 2023). Generally, emissions increase with temperature and light until a certain threshold after which they either stabilize or decrease (Monson et al., 1992; Staudt et al., 2017). The light and temperature dependency also leads to distinct diurnal and seasonal patterns. BVOC emissions also change depending on the plant's development stage manifesting in varying ecosystem flux magnitudes throughout the growing season (Hellén et al., 2021; Holst et al., 2010; Song et al., 2023).

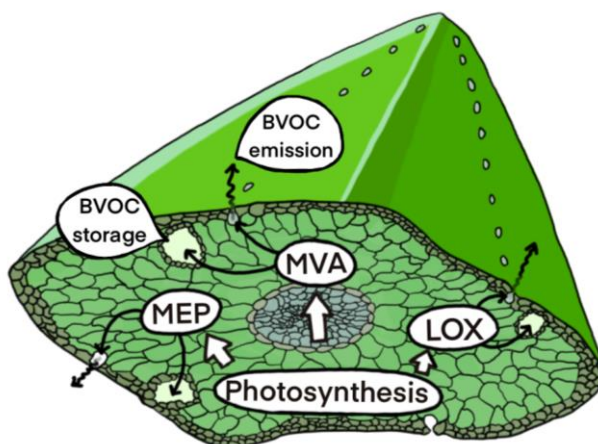


Figure 1. Simplified overview of BVOC emission and production pathways in a needle tip. BVOCs are produced through secondary metabolism from several pathways, for example the methylerythriol phosphate (MEP)-, mevalonate (MVA)- and lipoxygenase (LOX)-pathways. Upon production, BVOCs can be emitted directly through the stomata but also stored in the plant, for example in resin ducts of a needle.

BVOCs in the atmosphere

Global BVOCs emissions from plants are estimated to contribute around 400-800Tg of carbon to the atmosphere per year (Guenther et al., 1995; Maffei, 2010; Sindelarova et al., 2014). Once in the atmosphere BVOCs are highly reactive with atmospheric lifetimes of minutes to days (Acosta Navarro et al., 2014). They take part in several chemical chain reactions with large implications on the atmospheric conditions (Boy et al., 2022). Terpenoids are the most reactive group and are part of several gas-phase reactions, for example oxidative reactions with hydroxyl radicals (OH), ozone (O₃) and nitrogen oxides (NO_x; Laothawornkitkul et al., 2009; Monson and Baldocchi, 2014). The BVOC compounds and their oxidative products can also act as precursors to SOA or deposit onto surfaces (Goldstein and Galbally, 2007; Paasonen et al., 2013).

Depending on the atmospheric composition, BVOC-related reactions can have either positive (cooling) or negative (warming) effects on global warming (Figure 2). Tropospheric O₃ is a potent greenhouse gas and the net effect on global warming depends on the presence of NO_x in relation to BVOC. O₃ formation also depends on OH in the atmosphere that through oxidation increases O₃ precursors (Weber et al., 2022). However, BVOCs react with OH and decreases the atmospheric concentration. This indirectly causes a warming effect since the depletion of OH by BVOCs prevents their reaction with the greenhouse gas methane (CH₄) that instead gains a prolonged atmospheric lifetime (Peñuelas and Staudt, 2010; Scott et al., 2018).

BVOCs can also have a cooling effect through the formation or additional growth of SOA particles (Hallquist et al., 2009; Tunved et al., 2006). Increases of SOAs in the atmosphere have a cooling effect by scattering incoming solar radiation (Monson and Baldocchi, 2014; Paasonen et al., 2013). SOAs can also act as cloud condensation nuclei (CCN), which directly affects the energy budget of the Earth (Paasonen et al., 2013). The emitted BVOCs can lead to the activation and growth of the CCN, further affecting the energy budget by increasing the cloud droplet number concentration (CDNC) if the particles are large enough. High CDNC indicates more but smaller cloud droplets that further increase scattering and absorption of incoming solar radiation as well as increasing the albedo, consequently cooling the atmosphere (Monson and Baldocchi, 2014; Paasonen et al., 2013; Scott et al., 2018)

Additionally, BVOC depletion of OH also impacts the SOA particles. Reactions with OH and sulfur dioxide (SO₂) typically yield new aerosol particles but as OH is depleted, so is the formation of new aerosol particles. That leads to a reduction in CDNC, resulting in fewer and larger cloud droplets, reducing cloud albedo, and possibly creating a net warming (Weber et al., 2022).

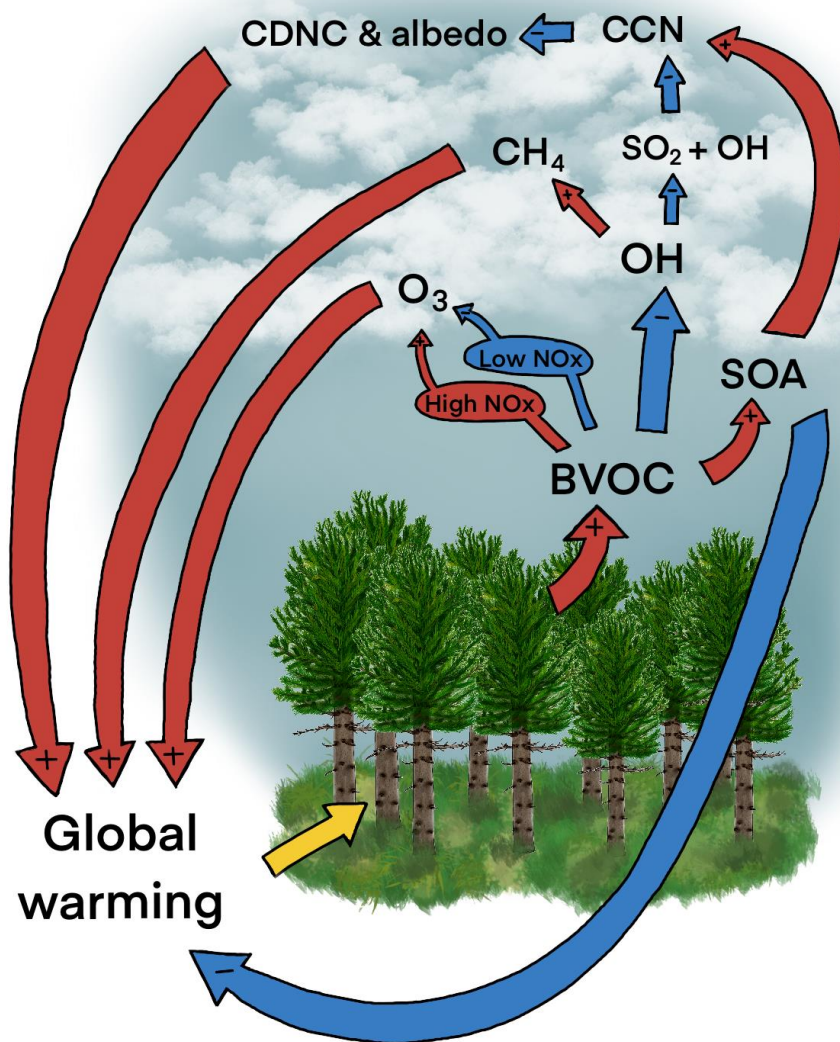


Figure 2. Conceptual illustration of BVOC reactions in the atmosphere in relation to global warming. Red arrows with a plus sign illustrate increase and blue arrows with a minus sign a decrease. Higher temperatures from global warming leads to increased BVOC emissions. Complex chemical reactions with BVOCs occur in the atmosphere. The concentration of nitrogen oxides (NO_x) determines if ozone (O₃) is produced or consumed where net production leads to increased warming. BVOCs also react with OH-radicals decreasing their concentration, resulting in prolonged lifetimes of CH₄ and increased warming. Depleted OH also leads to decreases in the secondary organic aerosol (SOA) formation capacity of sulfur dioxide (SO₂) resulting in decreased cloud formation capacity. BVOCs can be precursors of SOAs having a cooling effect through radiation scattering. SOAs also increases cloud condensation nuclei (CCN), however, a net decrease of SO₂ + OH can result in decreased CCN. This also decreases the cloud droplet number concentration (CDNC) and albedo, further increasing global warming. The figure is redrawn from Peñuelas and Staudt, (2010) and Weber et al. (2022).

Higher emission rates can further strengthen the feedback loops of some atmospheric reactions and processes. Model projections estimate increased BVOC emissions by 16% to 60% depending on global warming scenarios (Boy et al., 2022; Sporre et al., 2019). However, the projections carry large uncertainties as they are based on emission factors from empirical studies limited by the number of species and compounds (Guenther et al., 2012). Plant stress can lead to further variation in emission factors depending on the stress and the compound. This is not well represented in models such as the dynamic global vegetation model LPJ-GUESS (Schurgers et al., 2009), or the semi-mechanistic model MEGAN (Guenther et al., 2012), mainly because of the limited studies on the subject (Grote et al., 2019).

Plant stress

All plants experience different kinds of stress during their lifetime. Stress can be caused by biotic (such as herbivory or pathogens) or abiotic (such as temperature, drought and oxidative stress like O₃ exposure) agents. Stresses alone or in combination with others cause plants to alter their BVOC emissions. By inducing the emissions and altering the BVOC composition plants change their constitutive emission patterns as a protection. The majority of studies on plant stress find that the emission rates are usually induced compared to the constitutive emissions (Holopainen and Gershenson, 2010).

A combination of defense and interaction can be a useful tool for within- and between-plant signaling. A herbivore attacked plant induces its BVOC emissions or alters the compound composition. When these are emitted into the ambient air, other plant parts or other plants can respond by inducing their own defense BVOCs (Baldwin et al., 2006; Loreto and D'Auria, 2022). However, the induced BVOCs do not only lead to direct responses from neighboring plants, they can also have a priming effect. When plants sense the stress-signal, it can prime them to be prepared for a faster response later, when they might be attacked as well (Heil and Bueno, 2007; Ton et al., 2007). Another priming effect happens if a plant survives a period of stress. If the plant experiences stress again, it is better prepared and can have a faster response with induced BVOCs (Holopainen and Gershenson, 2010).

The effects of multiple stresses on plants have not been widely studied. It is common that plants in the field experience several stresses at once, for example higher temperatures in combination with increased herbivory (Holopainen and Gershenson, 2010). The combined effect can lead to different plant responses compared to when a single stress is experienced. A combination of biotic stress and abiotic stress resulted in additive stress response when herbivory was combined with temperature changes and

changes in O₃ (Gouinguéné and Turlings, 2002; Vuorinen et al., 2004), while it resulted in a decreased response when herbivory was combined with drought (Malone et al., 2023).

The majority of studies on plant BVOCs both healthy and stressed, alone and combined, have been tested in a laboratory setting (Bezerra et al., 2021; Faiola and Taipale, 2020; Huber and Bauerle, 2016; Schuman, 2023). The few studies conducted in the field often found contrasting outcomes compared to the similar experiments in a laboratory. This argues for the importance of measuring stress effects in the field; even if the plants are exposed to singular stresses, the natural habitat of the plants offer different conditions than what can be replicated in a laboratory. Some stresses can be hard to replicate in a laboratory and are best analyzed when they occur naturally, for example, insect infestations of the European spruce bark beetle (*Ips typographus*) or forest fires. Experimental stresses are equally as important to conduct in a laboratory as well as in the field, for example oxidative stress from O₃.

Stress on forests in Sweden

Forests comes to mind for many when Sweden is mentioned, as 69% of the total area is covered by forests (Roberge et al., 2023). Forests are important for the Swedish economy, evident by the large area (58% of total area) used as production forests (Roberge et al., 2023). This means that of all forests in Sweden, 84% are used for production. The majority of managed production forests in Sweden are planted with Scots pine (*Pinus sylvestris*) covering 40%, and the second most planted species is Norway spruce (*Picea abies*) covering 27%. Some forests not suitable for production, such as alpine forests with mainly mountain birch (*Betula pubescens* ssp. *czerepanovii*), cover up to 10% of the total land area of Sweden (Roberge et al., 2023).

Forests are important to Sweden and consequently lots of resources target the detection, mitigation and understanding of naturally occurring stresses, becoming more extreme due to climate change. Swedish forests suffered from a major drought in 2018 due to historically extreme temperatures and a large precipitation deficit (Lindroth et al., 2020; Wilcke et al., 2020). This led to further problems when the spruce bark beetle infestations exploded in the next years, killing about 1.1% of all spruces from 2018-2022 (Table 1; Roberge et al., 2023). The 2018 drought did not only cause bark beetles to thrive, it also resulted in the most severe wildfire season Sweden has experienced in modern history. From 1996 to 2018, 0.24% of the forest area in Sweden was burned, approximately 0.01% per year (Table 1; Högberg et al., 2021). In addition, another implication of the dry and warm year in 2018 was the unusually high levels of

near-surface O₃ (Karlsson et al., 2019). Alpine regions also experienced elevated O₃ during 2018 to 2022 in the Scandinavian mountains. Approximately 11 330 hours (around 472 days) were measured with concentrations higher than the recommended threshold of 40ppb (Table 1; SMHI, 2023; Directive 2008/50/EC).

Table 1. The size of forests in Sweden with reported damage from bark beetles, forest fires and elevated O₃. The damage is quantified as a sum between the years 2018 to 2022. Data on land cover and number of bark beetle killed trees were taken from the Swedish forest statistics (Roberge et al., 2023), the extent of forest fires was acquired from Högberg et al. (2021) and the hours of elevated O₃ concentrations were taken from the Swedish Meteorological and Hydrological Institute (SMHI, 2023).

Tree type	Land cover type	Land cover (1000 ha)	Stress type	Quantified effect from 2018-2022
Norway spruce	Production forest	5849	Insect attack from the European spruce bark beetle	1.1% of all trees killed
Scots pine	Production forest	8979	Forest fire	0.01% of forest burnt
Mountain birch	Alpine forest	2900	Elevated O ₃ concentrations above 40ppb	11 330 hours of exposure above threshold

The work in this thesis focuses on quantifying how constitutive emissions from trees change as a result of stress from spruce bark beetle, forest fires and elevated tropospheric O₃. These stressors in focus have the largest impacts on forests in Europe and are expected to increase with climate change (Cooper et al., 2014; Jönsson et al., 2012; Köster et al., 2021; Schelhaas et al., 2003), yet there still remains uncertainties about how they affect the common tree species in Sweden.

Spruce bark beetle infestations

The European spruce bark beetle targets the Norway spruce tree (*Picea abies*) for reproduction. They drill into the phloem of the spruce to create galleries to lay their eggs (Raffa, 1991). The bark beetles disrupts the vascular systems of the trees when they drill in the phloem, and if the attack is successful, larvae hatch and further disrupt the tree when they feed on the phloem. Eventually, the larvae pupate and evolve to new bark beetles and emerge from the tree through new holes to either swarm once more or hibernate until next spring. If the bark beetle infestation is extensive, and thus the disruption to the vascular system is large, the spruce can be killed (Raffa, 1991). However, spruce trees are not defenseless. By increasing resin flow in the trunk, bark

beetles can be submerged and drowned, or pushed out of the tree (Raffa, 1991). Resin also contains BVOCs, mainly monoterpenes that are toxic to bark beetles when the emissions are induced, and studies on conifers attacked by bark beetles have found evidence of increased monoterpene content at the attacked location (Amin et al., 2013; Eller et al., 2013; Ghimire et al., 2016). Comparisons of BVOC fluxes from healthy Norway spruce and infested Norway spruce have been done before (Ghimire et al., 2016), but the impact on emission rates over time and the emission changes from healthy trees that become infested still remains uncertain. Analysis of bark beetle infestation is of importance to increase the accuracy in model predictions of the stress BVOC emissions and impacts to SOA production, but is also of interest for the development of early detection methods and pest control (Moliterno et al., 2023; Stríbrská et al., 2023).

Elevated O₃

The majority of studies on the oxidative stress from O₃ on plants are either from potted seedlings usually conducted in a laboratory (Carriero et al., 2016; Hartikainen et al., 2012; Timkovsky et al., 2014) or from mature trees growing at experimental sites (Calfapietra et al., 2007). The outcome of elevated O₃ depends largely on the studied species and on the exposure concentration and duration. Potted saplings of birch exposed to low concentrations ranging from 40 to 100ppb over one to several weeks indicated increased emissions of monoterpenes compared to non-exposed birches (Carriero et al., 2016; Hartikainen et al., 2012). Birch saplings exposed to higher than 150ppb instead decreased their emission rates of monoterpenes (Timkovsky et al., 2014). Field measurements at leaf-scale from mature trees stressed by acute exposures of O₃ in the field are however scarce and are needed to realistically estimate the stress effects, as the differences in stress response between the laboratory and the field are large (Kigathi et al., 2009). Further research is also needed on the effect of the leaf age of plants and the potential recovery after oxidative O₃ stress to understand what damage different acute exposure concentrations have to the plant at different life stages. Expanding this knowledge will facilitate the development of more accurate models to estimate the stress induced by BVOC emissions (Grote et al., 2019).

Forest fires

Wildfires impact the forest floor by consuming vegetation and organic matter, leaving burnt charred surfaces (Bond-Lamberty et al., 2007). The intensity and severity of fires determine how much of the organic and mineral layers are affected. The main BVOC

compounds emitted from boreal forest floors are monoterpenes (Mäki et al., 2019a; Zhang-Turpeinen et al., 2021). After a low intensity fire, it can however take decades for the BVOC emissions to recover (Zhang-Turpeinen et al., 2021). It remains uncertain how the fire impacts the boreal forest floor during the first few years of recovery and how different fire severities affect emissions. The strategies after a fire vary and can potentially have large implications on BVOC emissions after a fire, as Swedish forests have many different owners and managers. Knowing how different management strategies impact BVOC emissions can help decide what is best suited for forest management. Having initially high emissions from salvage logging might impact nearby surviving forests as higher emissions can attract insects that can have further negative impacts on the already stressed forest (Kandasamy et al., 2023; Stríbrská et al., 2023).

Aims and objectives

Climate change has increased the frequency and intensity of naturally occurring stresses in Sweden, mainly from bark beetles, forest fires and O₃ exposure. The overall aim of this thesis was to study the impact of these stresses on vegetation. By quantifying the BVOC emissions from mature trees in the field, this thesis contributes to a deeper knowledge of the realistic emissions rates from forest ecosystems in Sweden. Conducting measurements over time further contributes to the knowledge of the natural variations of BVOCs. The thesis provides novel insights on trees' stress response in Swedish forests by quantifying the BVOC emissions from naturally occurring and experimentally applied stresses within realistic ranges. The main objectives of this PhD thesis were to:

- Analyze and quantify the BVOC emissions' change from un-stressed conditions to stressed conditions (Paper I-IV)
- Analyze how bark beetle infestations, forest fires and elevated O₃ affect BVOC emissions from forests over time (Paper I-III)
- Quantify emission patterns at ecosystem scale, the yearly variation and deviations of the emissions caused by changes in environmental factors (Paper IV)

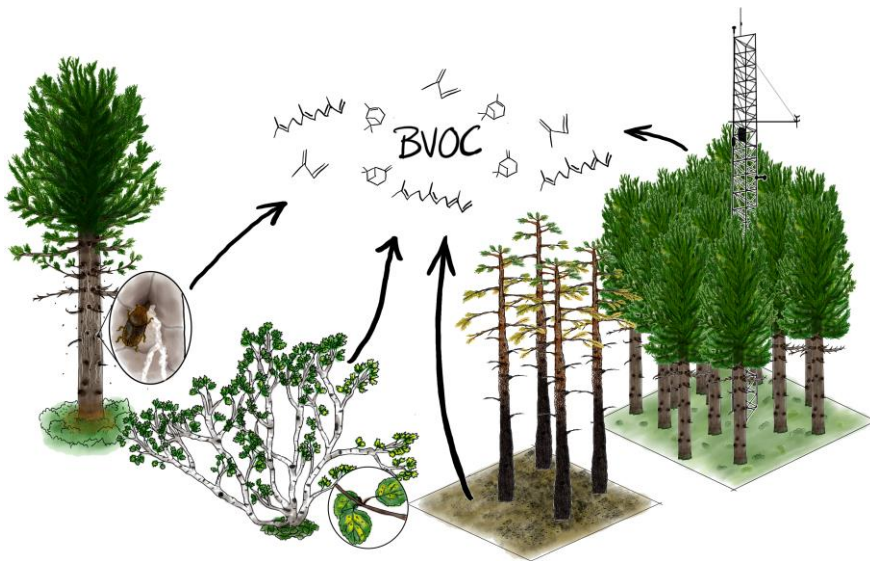


Figure 3. Schematic overview of the thesis aim to measure and analyze how different stresses affect BVOC emissions and ecosystem BVOC fluxes.

Material and Methods

Study sites

This PhD study focused on four forest areas in Sweden. Three of them are located in coniferous forests (Figure 4, Kårböle, Hyltemossa and Norunda), mainly consisting of the dominating tree types of Sweden, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The fourth site was located in a sub-Arctic mountain birch forest (*Betula pubescens* ssp. *czerepanovii*), dominating the alpine and mountain zones of Sweden (Figure 4, Abisko). The selected forests were either healthy upon measurements or had already been exposed to the stresses analyzed in the study.

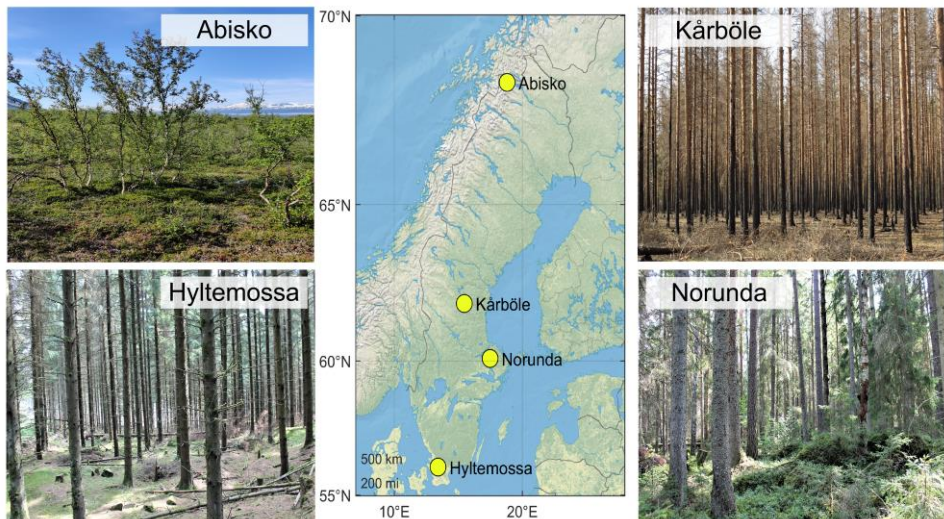


Figure 4. The study sites' location in Sweden and images of the main forest type (Photographs: Hyltemossa, Abisko and Norunda by author, Kårböle by Julia Kelly).

Hyltemossa and Norunda

BVOCs were measured from Norway spruce bark in managed forests in Hyltemossa and Norunda, research stations included in the Integrated Carbon Observation System (ICOS). Hyltemossa is in the nemoral zone in the south of Sweden (56°06'N, 13°25'E) and is dominated by Norway spruce (>97%) with an understory of mainly mosses. Norunda is closer to the boreal zone of Sweden (60°05'N, 17°29'E) and is a mixed forest of mainly Norway spruce (54%) and Scots pine (37%) with an understory of different shrubs. In 2019, the trees in Hyltemossa were around 40 years old and on average 19 m tall, while the trees in Norunda had a mixed age of around 60-80 years and up to 110 years old, with an average height of around 25 m.

Being part of the ICOS network, these sites are long-term research stations making them ideal for measuring the BVOC emissions from Norway spruce. Previous studies had measured BVOC emissions from the trees at these sites, providing background information on the constitutive emissions (van Meeningen et al., 2017b; Wang et al., 2017). In addition, the Hyltemossa site provided the perfect opportunity to lure bark beetles to a couple of isolated spruces, enabling the measurements of BVOCs from the healthy spruces and allowing an examination of how the emissions evolved as the spruces were infested. In 2019, there had already been ongoing infestations in Norunda, presenting the opportunity to gather additional measurements from infested trees.

The site in Hyltemossa is also a part of the Aerosol, Clouds and Trace Gases Research Infrastructure (ACTRIS) network, making the addition of BVOC flux measurements to the already existing eddy covariance tower ideal. From this flux tower, BVOC measurements over a healthy Norway spruce stand were collected between 2019 to 2021 providing long-term above-canopy BVOC flux observations.

Abisko

The Mountain birch trees in the Swedish sub-Arctic were considered an optimal candidate for the experiments of exposure to elevated O₃. This is an area that does not experience as high O₃ concentrations compared to other areas in northern Europe (Klingberg et al., 2019), but the Arctic air quality is expected to degrade with future increased Arctic shipping (Gong et al., 2018). Measuring the impacts of increased O₃ concentrations on birch trees in this area can thus yield key insights into how future BVOC emissions might change as O₃ increases. Leaf measurements of photosynthesis and BVOCs were taken from Mountain birch trees in a forest located in the nature reserve at the Abisko Scientific Research Station (ANS) in the Swedish sub-Arctic

(68°20'N 19°02'E). The area is dominated by Mountain birch growing on heathlands and meadows with patches of wetlands. The trees included in the study were all without visual stress before starting the experiments of exposing their leaves to O₃.

Kårböle

Forest floor BVOC measurements were taken in a forest area located close to Ljusdal in central Sweden (61°56'N, 15°28'E). The area is dominated by Scots pine with an understory of lichens and shrubs. In 2018, wildfires were raging in the forest, causing damage of different severities; low severity fires with mainly ground fires leaving surviving trees and high severity fires causing all trees to die. Six different sites in the forest area were used in the study. One was a control site with unburnt trees and the other five were all affected by wildfires at different severities, stand ages and post-fire forest management. This site created an ideal opportunity to study how these different factors impacted BVOC emissions as they were all located within 3 km of each other, making accessibility easier and comparisons available. Measurements were taken up to four years after the fire with the intention to compare how BVOC emission recovery differed. Differences in recovery were derived from differences in stress impacts, with slower recovery implying higher levels of stress.

Measurement techniques

There are several ways to measure gas fluxes such as BVOCs, either at ecosystem level or at smaller scale from chamber enclosures. The majority of the measurements in this PhD study (Paper I-III) were done with different chamber enclosures, all using a dynamic chamber technique. The dynamic chamber technique is a flow-through system where incoming air is often ambient air filtered from contaminants and the outgoing air is enriched with the emitted compounds. An advantage of this method is that it enables environmental variables to be kept constant and close to ambient conditions (Ortega and Helmig, 2008). Measurements of gas concentrations can then be taken from the inlet and outlet of the chamber and used to calculate the emission rates. When the incoming air is filtered from volatiles, measurements of the emitted volatiles in the enclosure are simplified and with available control of environmental conditions, several experimental studies can be made with this method. After the samples have been collected from the chambers, they can be analyzed in a laboratory to identify and quantify the chemical compounds using a gas chromatograph mass spectrometry system (GC-MS).

The measurements in Paper IV were done at a larger scale by measuring the BVOC fluxes above canopy continuously from a flux tower. In this way large-scale and long-term variations in BVOC fluxes could be accounted for.

Chamber enclosures

Three different chamber enclosures were used in this PhD project, each specifically intended for measurements from bark, forest floor and leaves (Figure 5). Both the bark and the forest floor chambers were connected to a custom built pump box to make it a dynamic system. Using the dynamic technique was desirable to achieve stable conditions similar to the ambient environment to measure the constitutive and potentially stress-induced emissions with little influence from artificial changes in environmental factors. The leaf chamber was a part of an already-built pump system used for photosynthesis measurements (LI-6400XT, LICOR, Lincoln, NE, USA). The chamber head outlet was adapted to split the air stream to enable BVOC sampling while simultaneously measuring photosynthesis. Detailed descriptions of the chambers and measurement setup can be found in their respective papers (bark chamber, Paper I; forest floor chamber, Paper III; and leaf chamber, Paper II).

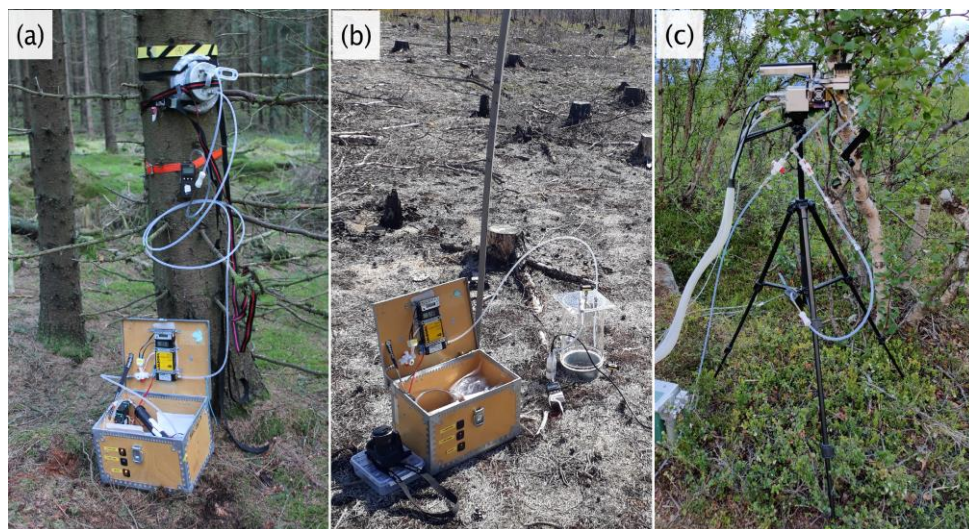


Figure 5. The chamber enclosures used in the study, (a) bark chamber, (b) forest floor chamber and (c) leaf chamber.

Continuous large-scale measurements

Ecosystem scale BVOC fluxes can be measured using the eddy covariance (EC) method. The EC method calculates the turbulent fluxes by co-variance of high frequency wind data and the fluctuations of the BVOC concentrations measured from the same sample volume (Burba, 2013). The measurements are done at high frequency (10 to 20Hz) to include all relevant eddies. To quantify the BVOCs at trace level, the eddy-covariance method can be coupled with a proton transfer reaction – time of flight – mass spectrometry system (PTR-TOF-MS). Using the PTR-TOF-MS, a wide range of BVOCs can be measured simultaneously at high time resolution at 10Hz (Graus et al., 2010). This measures the continuous BVOC concentrations in real time. This is an advantage compared to the chamber enclosure techniques where BVOC concentrations are measured in the field and later analyzed in the laboratory. The disadvantage is that the PTR-TOF-MS cannot distinguish between the different compounds of the same mass, as the chamber measurement analyzed using GC-MS in the laboratory can. The two systems are however a great complement to each other where GC-MS can be used to correctly identify the detected compounds and PTR-TOF-MS for rapid quantification (Majchrzak et al., 2018).

BVOC sampling

The off-line BVOC sampling from the chamber enclosures were done using adsorbent tubes which were later analyzed in the laboratory while BVOC fluxes were continuously measured from the flux tower using PTR-TOF-MS.

Adsorbent tubes

The majority of the PhD project was based on collecting BVOCs with the off-line sampling method. The BVOCs were collected from the chambers using stainless steel cartridges (Markes International Limited, Llantrisant, UK) packed with two adsorbents, Tenax TA (a porous organic polymer) and Carbograph 1TD (graphitized carbon black). BVOCs were captured in the tubes by extracting air from the chambers using pocket pumps (Pocket Pump, SKC Ltd., Dorset, UK). Depending on each study application, the sample time and air flow through the pump varied but to avoid the tubes becoming saturated, approximately 5-6 liters were always sampled. When the samples had been taken, they were stored in a refrigerator and later analyzed in the laboratory. Specific details on the sampling method are found in each paper.

Laboratory analysis

The collected adsorbent tubes were analyzed in three laboratories following similar procedures. The sample cartridges were analyzed using a two stage automated thermal desorption (ATD) coupled with a GC-MS from different factories and with specified settings depending on the sub-study. Using the ATD-GC-MS system enables the identification and quantification of the sampled BVOCs at high sensitivity, even for compounds with similar mass. The separation of compounds with similar mass was vital to the thesis' aims to analyze the stress effect on BVOCs as stress can be seen as shifts in compounds while the total emissions remains the same (Holopainen and Gershenson, 2010).

The ATD-GC-MS method was similar for all samples. A first stage desorption was carried out where the cartridges were heated to high temperatures to release the captured BVOCs onto a cold trap. A second desorption was done by flash heating the cold trap, re-releasing the BVOCs at higher concentration and improved sensibility before the volatiles are led to the GC-MS column. The GC ovens were heated to release the volatiles to the MS to identify the compounds depending on their retention time and mass spectra. Standard compounds with known concentrations were prepared and analyzed in a similar procedure as the samples to confirm and quantify the compounds. Detailed descriptions of the laboratory analysis settings can be found in the respective papers.

Emission calculations

When the BVOC concentrations per sample had been acquired in the laboratory, they were calculated as emission rates (ER) following Ortega and Helmig (2008; Eq 1):

$$ER = \frac{(C_{out} - C_{in})Q}{A} \quad (\text{Eq. 1})$$

Where C_{out} and C_{in} ($\mu\text{g L}^{-1}$) are the outlet and inlet BVOC concentrations, Q is the flow rate (L min^{-1}). Depending on the chamber application, A represents the measurement area (m^2) or the dry weight (g) resulting in the units of the ER being either $\mu\text{g m}^{-2} \text{h}^{-1}$ or $\mu\text{g g}_{\text{dw}}^{-1} \text{h}^{-1}$. The bark and forest floor emission rates were based on the measurement area obtained from the chamber bases while the leaf emission rates were based on the dry weight which were acquired by harvesting and drying the leaves.

The emission rates from the chamber measurements of the bark beetle and forest fire campaigns were normalized by temperature and photosynthetically active radiation using standard values of 30°C and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ following Guenther et al. (1993).

This was done to improve comparability of the results within the study but also with other studies. More details about the standardization and emission rate calculations are found in the respective papers.

PTR-TOF-MS

The PTR-TOF-MS coupled with the EC flux system in Hyltemossa was used to sample high frequency data on selected BVOCs. The high frequency wind fluctuations were measured using a sonic anemometer at 27m on the tower. The air was sampled continuously from the tower through a thermally insulated intake to the PTR-TOF-MS with the sample frequency of 10Hz. The PTR-TOF-MS data was processed using the PTRwid-software (Holzinger, 2015). The high frequency BVOC data was then aligned with the sonic anemometer output at the same temporal resolution and using EddyPro to calculate the fluxes. Only data passing the criteria for well mixed conditions (friction velocity greater than 0.3m s^{-1} ; Lindroth et al., 2020) was used. Further details can be found in Paper IV.

Temperature sensitivity calculations

In addition to the analyzed BVOC emissions in Paper I and Paper IV, calculations on the temperature sensitivity were done using a Q_{10} relationship (Lloyd and Taylor, 1994). The calculations were done following Seco et al. (2020) where the resulting Q_{10} coefficient represents the increase in emission rate for every 10°C temperature increase. Calculating the Q_{10} coefficient for the yearly continuous BVOC measurements in Hyltemossa (Paper IV) or between healthy and infested spruce bark (Paper I) can reveal differences in the Q_{10} coefficient that indicate increased temperature sensitivity. The analysis of temperature sensitivity adds insights to the overall thesis aims by seeing how stress impacts BVOC emissions compared to un-stressed conditions. Details on the calculations can be found in Paper I.

Field campaigns

The overarching aim of the PhD thesis was to analyze how stress affects plants' BVOC emissions. To do this, several field campaigns were done throughout the years of 2019-2022 focusing on different stress factors on different plant parts and plant material. An overview of the campaigns, dates, plant material, stress and in which paper the results are presented is found in Table 2.

Table 2. The dates of field campaigns performed during the thesis work, their location, plant material, exposed, measured stress factor and in which paper the results are presented.

Year and date of campaigns	Location	Plant material	Stress factor	Paper
Year 2019: 4-6 May, 4-6 and 13 June, 2-4 July, 30-1 July/August, 26-27 August	Hyltemossa & Norunda	Norway spruce bark	Insect infestation of the European spruce bark beetle	I
Year 2020: 28-4 June/July 28-3 July/August	Abisko	Mountain birch leaves	Oxidative stress from ozone	II
Year 2019: 19-20 July Year 2020: 1-3 August Year 2021: 3-6 August Year 2022: 30-31 July 2-4 August	Kårböle	Scots pine dominated forest floor	Post wildfire	III
June-August 2019-2021	Hyltemossa	Norway spruce forest	Long term ecosystem monitoring (no intentional stress)	IV

Insect infestation of the European spruce bark beetle

One of the main stresses to forests in Sweden between 2018 and 2022 were infestations of the spruce bark beetle, killing 1.1% of all Norway spruces (Table 1). To study the effect of this substantial stress, healthy and infested Norway spruce bark BVOC emissions were measured. By studying the stress from insect infestation of European spruce bark beetles we aimed to evaluate the changes in BVOC emission rate and composition from healthy to infested Norway spruce bark. The emission and compound composition were also measured over time to see how the ongoing infestation influenced tree defense over time (Figure 6). The main hypothesis was that the BVOC emissions would be higher from infested bark compared to healthy bark, and infested tree emissions would decline over time. The severity of the infestation was monitored by recording the amount of holes drilled and relating it to the emission rate profiles. Field work was carried out during the summer of 2019 with six campaigns measuring both healthy and infested Norway spruce trees. Five of the campaigns were done in Hyltemossa with continuous measurements on the same spruces over the season, where two were infested by spruce bark beetles by the third campaign. One additional campaign was carried out in Norunda on already infested spruce trees. This allowed for measurements of the healthy-to-infested process as well as the emission rate profiles of already infested trees. Detailed descriptions of the experimental setup can be found in Paper I.

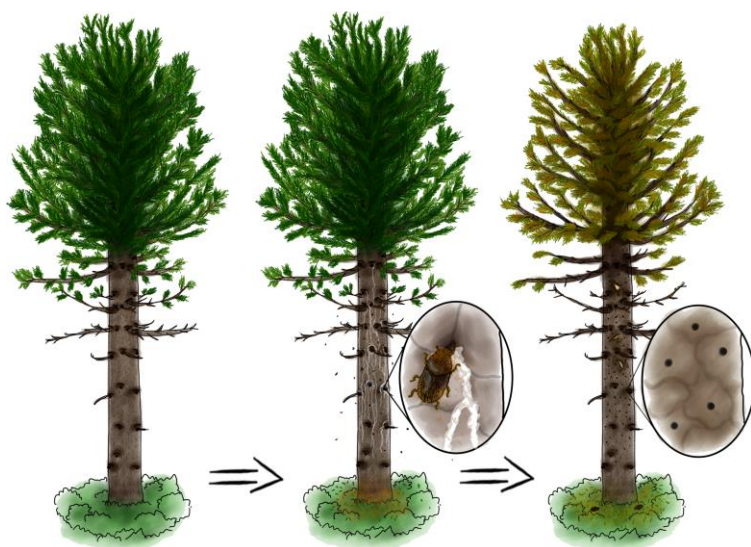


Figure 6. A conceptual overview of Paper I's aim. BVOC measurements were taken from spruce trees that were unaffected by bark beetles and later from spruce trees with ongoing infestations of bark beetles and in the end from trees dying of successful infestation.

Oxidative stress from O₃

We measured the oxidative stress on mountain birch leaves to analyze differences in un-stressed to stressed conditions and evaluate stress over time. The main objective with studying acute elevated O₃ concentrations was to investigate how this impact the photosynthetic rate and BVOC emissions from leaves of mature Mountain birch trees in the field (Figure 7). We aimed to study the effects of leaf age on BVOC emissions and photosynthetic rate and to see if increased O₃ concentrations had different impacts depending on the age. We studied the effects of different O₃ concentrations to identify thresholds in plant defense for carbon assimilation and BVOC emission and to analyze the recovery of birch leaves after exposure to elevated O₃. To capture the differences in leaf morphology and season, BVOCs were collected at two field campaigns from young and mature leaves respectively. The above- described pump box and leaf chamber were connected to an O₃ monitor and an O₃ generator with further details described in Paper II. The experimental setup was designed to expose leaves initially to 0ppb O₃, then increase the concentration to 40ppb, 80ppb and eventually 120ppb with periods of no exposure in between to simulate recovery phases. All leaves were sampled at all O₃ concentration and recovery steps, following the previously described adsorbent tube sampling method with details found in Paper II.

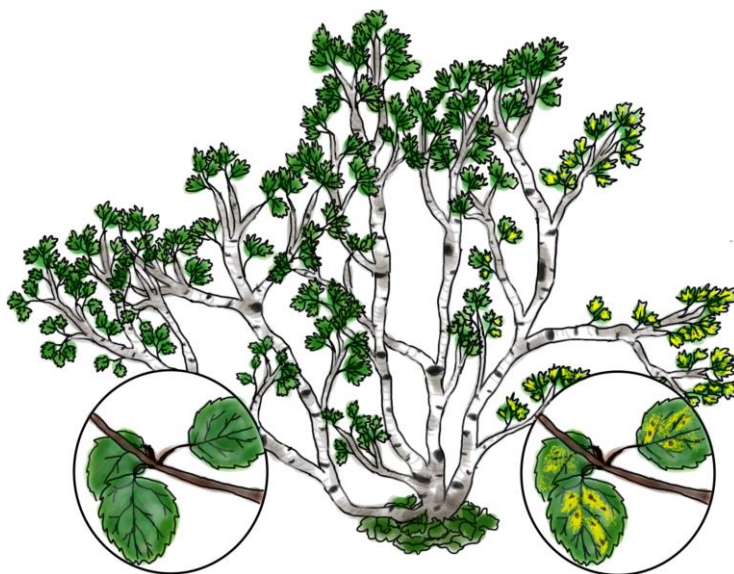


Figure 7. A conceptual overview of the aim of Paper II. BVOC measurements were taken from healthy mountain birch leaves that were sequentially exposed to elevated O₃ with new measurements taken at several steps. The experiment was done on young leaves in the early summer and mature leaves later in summer.

Recovery after forest fire

The severe 2018 drought in Sweden led to widespread wildfires providing a unique opportunity to study the impact on BVOC emissions during the first years of forest recovery (Figure 8). The area of Kårböle comprised of sites with different fire severity and post-fire management strategy. Thus we could evaluate how these factors affected BVOC emission recovery after the fire. We hypothesized that emissions would be low from the burnt forest floor compared to the unburnt forest floor, but as the forest floor started to recover after the fire, emissions would start to increase. The emission rate recovery was also expected to vary between sites, in for example the post-fire management strategy with salvage logging, which would initially have high emission rates that would decrease rapidly due to the emissions of litter and tree debris. BVOC measurements were taken using a forest floor chamber system to study the fire impact on the recovering forest floor. Four plots were measured at each site: two plots where the soil organic layer and litter were removed and two without any manipulation. Measurements were taken every year between 2019 to 2022 to see the impact and recovery after fire. To facilitate the comparisons of emissions, measurements of soil moisture, incoming PAR, chamber temperature and soil temperature were also taken during the BVOC sampling and used to normalize the emissions. Detailed descriptions of the sites and measurements are found in Paper III.

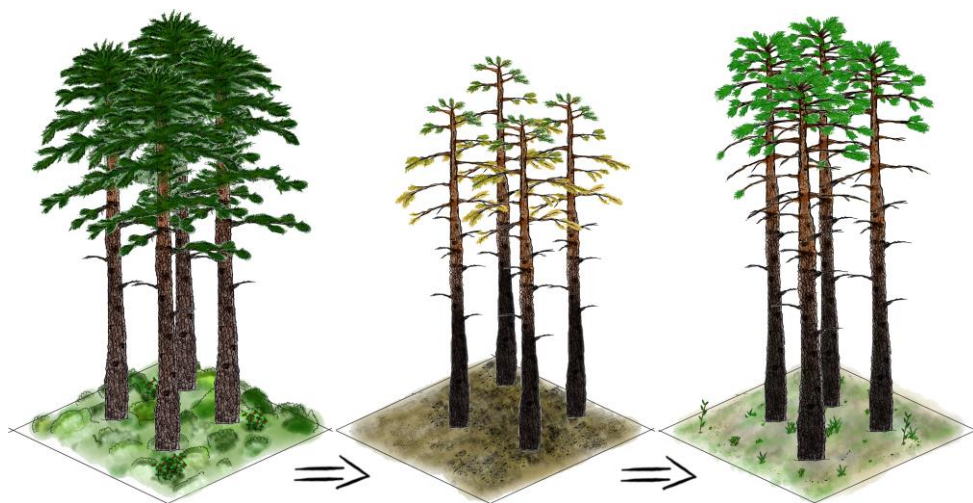


Figure 8. A conceptual overview of the aim of Paper III. The effect of forest fires on BVOC emissions were analyzed by measuring the emissions of healthy forest floor, burnt forest floor one year post fire and the recovering forest floor up to four years post fire.

Long-term BVOC flux measurements

This project aimed to quantify the BVOC emission patterns from a managed Norway spruce production forest in Hyltemossa located in southern Sweden (Figure 9). The long-term and continuous BVOC emissions contributed to the final aim of the thesis of analyzing yearly variations in BVOC emissions. The aim was also to measure the constitutive emissions on ecosystem level to use as background emission for what a healthy spruce forest emitted. By conducting long-term continuous measurement, the BVOC fluxes could also be compared with environmental factors to analyze if any potential deviations in emissions could be a result from different environmental conditions and potentially stress. To achieve this, flux measurements were sampled from an eddy covariance tower located at the ICOS research station in Hyltemossa with a PTR-TOF-MS. Measurements were ongoing during June to August from 2019 to 2021 to capture summer trends and yearly variations. The managed Norway spruce forest in Hyltemossa was around 40 years old during the sampling period. Since the sampling site also was an ICOS station, several measurements of atmospheric variables were taken at the same time as the BVOC fluxes. This allowed for correlations with measurements of example net ecosystem exchange, air temperature and humidity, incoming solar radiation and sensible and latent heat fluxes. This made Hyltemossa the optimal location to also find correlations between the BVOC fluxes and atmospheric measurements from ICOS.

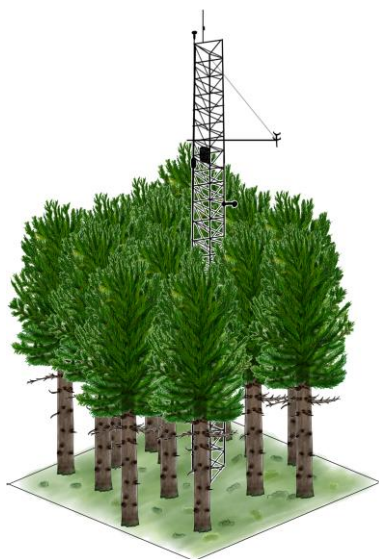


Figure 9. A conceptual overview of Paper IV's aim. Long-term ecosystem monitoring of BVOC fluxes in a managed spruce forest. Measurements were sampled from 2019 to 2021 allowing for the capture of summer trends as well as annual variations.

Results and Discussion

BVOC emission variability

To fully understand how BVOC emissions from plants are affected by stress, it is essential to first make sense of what the constitutive emissions from un-stressed vegetation look like and how they vary over time. Since BVOCs are a result of secondary metabolism affected by several environmental factors, they have a natural pattern to vary diurnally, seasonally and yearly. To capture this variability, the sub-projects of the PhD took place at different times and over several years, adding further evidence and knowledge around the natural variations of the constitutive emissions and the influence on stress emissions.

Ecosystem BVOC flux measurements

The study in the Norway spruce production forest in Hyltemossa, Skåne, brings evidence of the yearly variations in BVOC fluxes. Fluxes were measured in the summers of 2019-2021 where the summer (June to August) average fluxes of monoterpenes were highest in 2019 ($0.75 \pm 1.1 \text{ nmol m}^{-2} \text{ s}^{-1}$ mean \pm standard deviation) compared to 2020 and 2021 with similar summer averages ($0.61\text{-}0.63 \pm 0.4 \text{ nmol m}^{-2} \text{ s}^{-1}$). The full summer daily maximum monoterpene flux was also highest in 2019 ($26 \text{ nmol m}^{-2} \text{ s}^{-1}$) compared to 2020 and 2021 (5.1 and $3.4 \text{ nmol m}^{-2} \text{ s}^{-1}$, respectively). To date, few studies of ecosystem BVOC fluxes in Norway spruce forests have been carried out, with many instead focusing on chamber measurements of the needles or other parts of the tree (Jaakkola et al., 2023; van Meeningen et al., 2017a). There are also few studies of flux measurements in the nemoral vegetation zone to which Skåne belongs (Hagen et al., 2013). One study in Denmark in 1997 found daily monoterpene fluxes of $0.78 \text{ nmol m}^{-2} \text{ h}^{-1}$ (Christensen et al., 2000). Further studies on ecosystem BVOC fluxes in Norway spruce forests were carried out in the temperate zone in Germany in 2001-2002 (Graus et al., 2006) and the Czech Republic in 2014 (Juráň et al., 2017). The monoterpene daytime average has only been reported from the Czech Republic at $1.29 \text{ nmol m}^{-2} \text{ h}^{-1}$, which is higher than both the full summer daytime averages from the PhD study in Hyltemossa and the study in Denmark. Comparing Hyltemossa to

Denmark, the average full summer monoterpene fluxes in 2019 align. Even if the fluxes from 2020-2021 are around $0.16 \text{ nmol m}^{-2} \text{ h}^{-1}$ lower than the ones in Denmark, the Danish fluxes fall within the range of one standard deviation. Several factors could explain the higher daytime average fluxes from the Czech Republic, such as differences in the leaf area index, biomass and forest density. Another explanation could be the different vegetation zones; spruce has occurred naturally over time in the Czech republic, whereas Norway spruce was planted in Denmark and Skåne (Tollefsrud et al., 2008). It is also the case that variations may not only be due to environmental factors, but different genotypes of trees have been found to emit different BVOCs (Bäck et al., 2012), which may be the case with these spruce forests.

When comparing the average daytime fluxes, it is clear that the monoterpene fluxes in 2019 were not always similar to other years. In June 2019, the highest hourly average monoterpene flux was $3.3 \text{ nmol m}^{-2} \text{ h}^{-1}$, but with a high standard deviation ($5 \text{ nmol m}^{-2} \text{ h}^{-1}$; Figure 10). In June 2020 and 2021 the highest hourly average fluxes were $0.9\text{-}1 \text{ nmol m}^{-2} \text{ h}^{-1}$ for both years, making the June fluxes in 2019 stand out with three times higher emission rates than 2020 and 2021. However, in both July and August the highest hourly average flux ranged between 0.4 to $1.27 \text{ nmol m}^{-2} \text{ h}^{-1}$ for all years (Figure 10). As the highest hourly average fluxes in 2020 and 2021 and July and August in 2019 are in line with the $2 \text{ nmol m}^{-2} \text{ h}^{-1}$ found previously it might indicate that the observed high fluxes in Hyltemossa are single events and do not represent the constitutive ecosystem flux. Instead, this might indicate that some stress factor was affecting the emission rates at those times.

When looking at the average diel cycles of air temperature and gross primary production (GPP) of the forest, there are no large deviations in June that could explain the high monoterpene fluxes in 2019 (Figure 10). However, the daily measurements in June revealed high temperatures early in the month with diurnal temperatures ranging from 10°C to 26°C . These early season high temperatures could be one influencing factor that boosted the BVOC emissions in 2019, showing higher diel averages. Fluxes of isoprene were also measured during the years, indicating a similar pattern with unusually high fluxes in June 2019 (data not shown). Measurements were also taken of net ecosystem exchange, incoming solar radiation, soil water content and O_3 concentrations (data not shown, details in Paper IV). However, none of these parameters could contribute with any clarification. Other than the high early June temperatures, there must be an additional explanation to the exceptionally high fluxes in 2019.

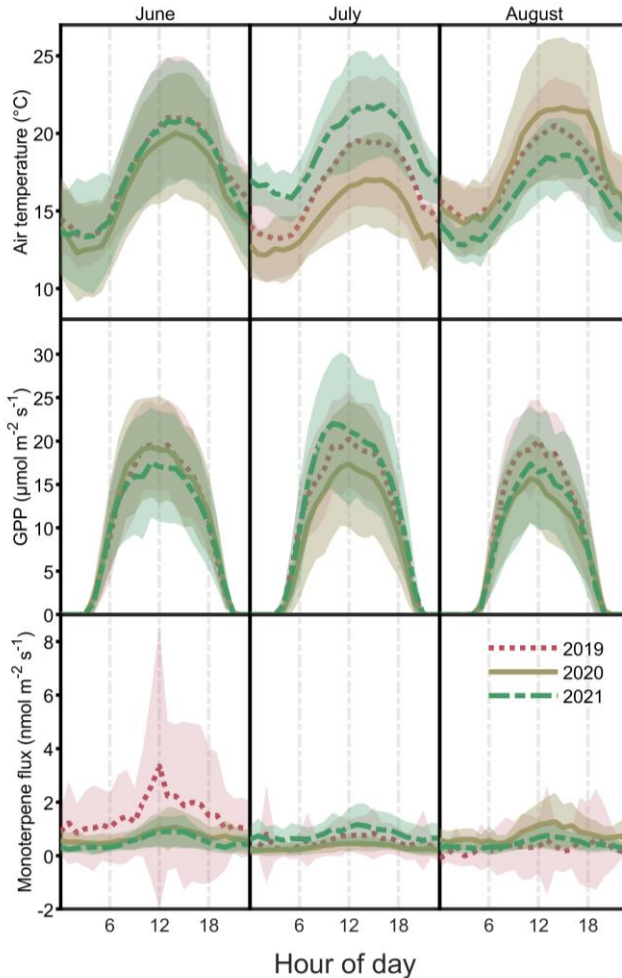


Figure 10. Diel cycles of hourly averages of air temperature, gross primary production (GPP) and monoterpene fluxes for the summer months June, July and August for the years 2019, 2020 and 2021. The lines represent the hourly average where the shaded areas represent ± 1 standard deviation where colors represent the years (red = 2019, yellow = 2020, green = 2021). The vertical axes for each variable share the same scale indicated by the left axis. Air temperature and GPP were acquired from the ICOS research station in Hyltemossa (Heliasz et al., 2023a).

The additional explanation, mentioned in the introduction to this thesis, might be the severe drought in Sweden in 2018 that resulted in stress on the forests, both from secondary effects such as the bark beetle infestations, but also from the drought itself (Lindroth et al., 2020). Drought stress can lead to defoliation and the mortality of Norway spruces as well as root mortality (Solberg, 2004). The summer of 2018 also

had higher temperatures than usual that can increase needle fall the same and following year (Kouki and Hokkanen, 1992). This could have happened in Hyltemossa in 2018 and could be revealed through exceptionally high monoterpene emissions from the dropped needle and roots as storage emissions the year after. However, what is not explained by the heat- and drought-induced storage emissions is the increased emissions of isoprene at the same time as the monoterpene emissions. Isoprene is not stored in the needles, but the temperature dependency can possibly explain the high emissions as they could be linked to the early June high temperatures measured in 2019 (Laothawornkitkul et al., 2009; Zeng et al., 2023).

The increase in emissions due to high temperatures can potentially be an additional indirect effect of the drought in 2018, leading to increased temperature sensitivity. BVOCs from many plants, monoterpenes in particular, are emitted exponentially with temperature and generally follow a predictable pattern (Guenther et al., 1993). When calculating the temperature sensitivity of the monoterpene fluxes using a Q_{10} relationship (more details in Paper I and Seco et al. (2020)), it is clear that 2020 and 2021 follow a similar trend that might then be the predictable pattern in Hyltemossa (Figure 11). However, the relation looks different for the fluxes in 2019. The Q_{10} value in 2019 is about 20% higher than in 2021, indicating that the temperature sensitivity is higher in 2019. The spread of the flux data is also greater in 2019, making it uncertain if any increase in flux is a result of an increase in temperature. This supports the hypothesis that the high monoterpene fluxes could be storage emissions resulting from the heat and drought the previous year. The addition of litter on soil has also been shown to increase the Q_{10} value and thus the temperature sensitivity of soil respiration (Zhuang et al., 2023). Thus, the higher Q_{10} can also be a result of the increased litter on the forest floor in 2019.

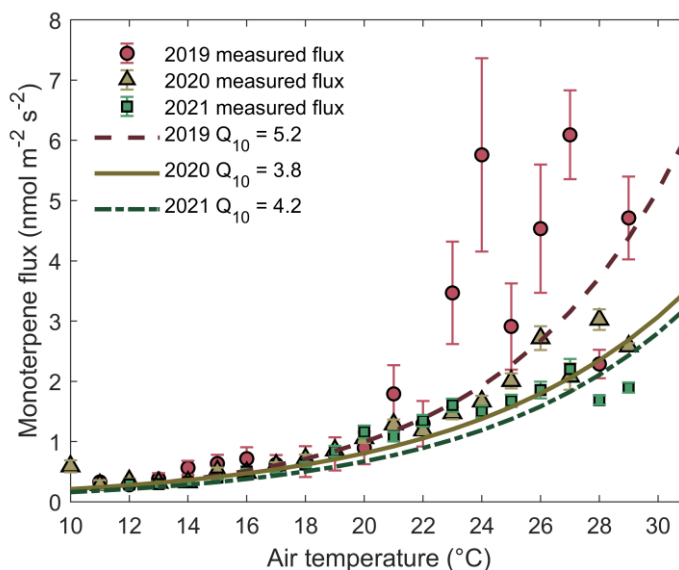


Figure 11. Relationship of the monoterpene fluxes above the forest in Hyltemossa with the air temperature measured at 50m from the nearby flux mast at the ICOS research station in Hyltemossa (Heliasz et al., 2023a). The plotted data points are the average of the observed fluxes binned into 1 °C bins. All fluxes pass the criteria for well mixed conditions (friction velocity greater than 0.3 m s^{-1} ; Lindroth et al., 2020), and are not limited by light (PPFD greater than $1000\ \mu\text{mol m}^{-2}\text{ s}^{-1}$). The standard errors are represented by the error bars. The years are plotted in different colors (red = 2019, yellow = 2020, green = 2021). The plotted lines show the exponential Q_{10} relationship for the monoterpene fluxes for each year (equation 5 in Paper I, with T_0 set to 0 °C).

Boreal forest floor BVOC emissions

To measure boreal forest floor recovery after a wildfire we conducted both unburnt (control) and burnt forest floor measurements. In addition to the recovery from stress, yearly variations from a healthy boreal forest floor were measured. Measurements were taken at the same time once a year so no seasonal variation could be examined. The variations in BVOC emission rates between the years from the healthy boreal forest floor are large: the total emission rates range from 14 to $91\ \mu\text{g m}^{-2}\text{ h}^{-1}$ with an increasing pattern each measurement year (2020 to 2022; Figure 12). The main emitted compounds were 3-carene and α -pinene for all years (Figure 12). The yearly variations in BVOC emission rates from the healthy boreal forest floor could be explained by changing environmental factors. July and August 2020 were unusually cold compared to the 20-year average air temperature in the area (1 °C colder; data not shown, details in Paper III). This might explain the low emission rates from the healthy forest floor that year (Figure 12).

To compare the emissions from the healthy boreal forest floor with other studies, the average monoterpene emission rates from 2020 to 2022 were calculated, resulting in emissions of $41 \pm 29 \mu\text{g m}^{-2} \text{h}^{-1}$. This is comparable with other studies on forest floor emissions from similar Scots pine-dominated forests that found monoterpene emissions ranging from 4 to $40 \mu\text{g m}^{-2} \text{h}^{-1}$ (Aaltonen et al., 2011; Mäki et al., 2019b), with exceptionally high monoterpene emissions measured in spring at around $300 \mu\text{g m}^{-2} \text{h}^{-1}$ (Hellén et al., 2006). All three mentioned studies were measured in the same boreal forest in Hyytiälä, Finland, in different years, offering further evidence of the yearly variations from these ecosystems. The unburnt areas compared in the study were all from the same age, a stand of mature Scots pine. If the areas were at different ages, that could explain the variations as BVOC emissions have been found to change with vegetation age (Zhang-Turpeinen et al., 2021).

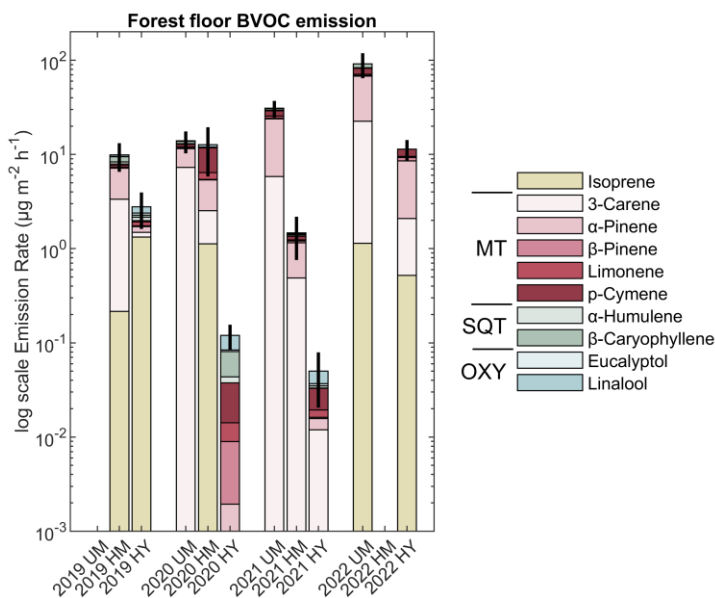


Figure 12. BVOC emission rates ($\mu\text{g m}^{-2} \text{h}^{-1}$) from boreal forest floor measured at unburnt areas with mature trees (UM), high-severity fire with mature trees (HM) and high-severity fire with young trees (HY). Yearly measurements were taken in July/August between 2019-2022. The emission rates are presented in log scale to facilitate the comparison between sites and years with high variation. The emitted compounds are presented in different color schemes where monoterpenes (MT) are red, sesquiterpenes (SQT) green and oxygenated compounds (OXY) blue. Isoprene is separated on its own and colored yellow. The black lines represent the standard deviation of the total emission rates.

For the burnt areas, measurements were taken from high-severity fire sites from both mature (HM) and young (HY) pines. This adds an additional layer that can influence the emissions as BVOCs are found to change with vegetation development (Bracho-

Nunez et al., 2011). The fire severity was similar at both sites. But, the young trees were completely burnt and killed by the fire while the mature trees were killed by the fire but had remaining canopy needles. In 2019, the emission rates from the burnt mature tree forest floor contained more monoterpenes compared to the burnt young tree forest floor (Figure 12). This difference could be explained by the litter that was combusted when the HY trees were killed by the fires, rather than age. The mature trees had shed almost all needles the year after the fire, contributing to higher monoterpene emissions in 2019. To see the impacts of the fire further in the soil, the top organic layer was removed, resulting in no litter interference. This revealed that there were still similar differences in the emission rate profiles (details in Paper III).

The BVOC emissions from HM and HY were different as they recovered from the fire. The emission rates two years after the fire (2020) were 100 times higher from HM compared to HY and the emission rates from HM were also similar to the unburnt site that year ($13 \mu\text{g m}^{-2} \text{h}^{-1}$; Figure 12). The emission rates also remained higher for HM compared to HY the third year, although not as much (30 times higher). There is a data gap for HM four years after the fire, but HY indicated increasing emission rates. This may be explained by the increased vegetation cover in 2022 compared to 2020 (Paper III). Even if the healthy soil emission rates varied widely, so did the emission rates from the burnt soil, and more so when comparing the young and mature trees.

BVOC emissions from birch leaves

The influence of age on BVOC emission rates was also apparent in the study of mountain birch leaves (Paper II). The results revealed that young leaves had a more various composition of BVOCs with higher contributions of oxygenated compounds (OXY) compared to the mature leaves that mainly emitted monoterpenes, specifically the compound α -pinene (Figure 13). This is in line with similar studies on birch species, reporting that the trees mainly emit monoterpenes, OXY and sesquiterpenes with a shift in emission profile as the leaves age, from a majority of sesquiterpene and OXY emissions to monoterpenes (Haapanala et al., 2009; Hakola et al., 2001; Hellén et al., 2021). The emission rates varied between the leaves of both ages, with an average total emission rate from the young leaves of $189 \pm 189 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$ (mean \pm standard deviation) and the mature leaves and average total emission rate being more than double ($456 \pm 876 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$). The observed increase in emission rate from young to mature leaves was however not significant ($P = 0.57$). The high variability evident by the high standard deviation can explain the non-significant result.

In addition to the different emission patterns found from un-stressed young and mature leaves, the stress response to O₃ exposure was also different. Lower emission rates from young leaves (a decrease of 80%) was observed upon exposure to 80ppb O₃, but the BVOC composition remained similar. When mature leaves were exposed to 80ppb, the emission rates were almost 100% lower, and unlike the young leaves, the emission composition changed to mainly contain sesquiterpenes and OXY, dominated by β-farnesene and 2-methyl-3-butene-2-ol (MBO; Figure 13). The difference in stress response between the young and mature leaves was even more profound at exposure to 120ppb. The young leaves were found to react in the opposite way when exposed to 120ppb compared to 80ppb and had increased emission rates of 24% compared to healthy emissions, while the mature leaves still had lower emission rates than the healthy leaves, similar to the exposure at 80ppb (Figure 13). The young leaves also altered the emission composition to contain more sesquiterpenes compared to the healthy leaves, while the mature leaves also altered the composition to increase emissions of monoterpenes compared to the exposure of 80ppb (Figure 13).

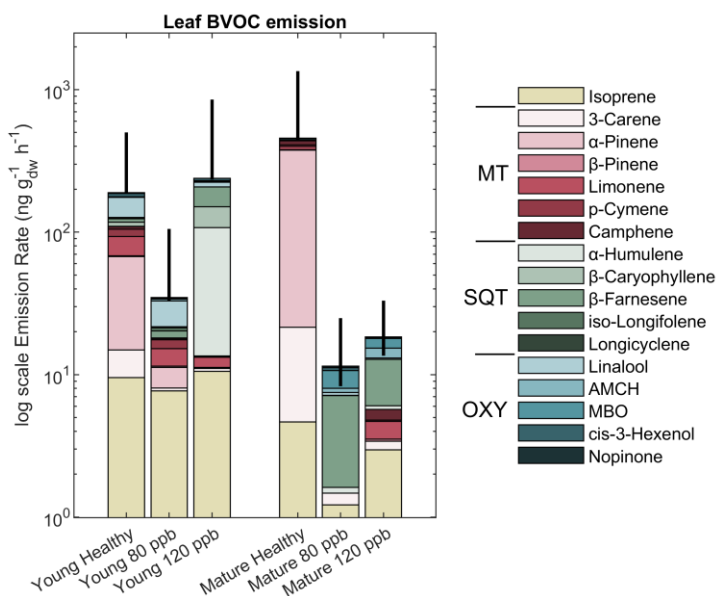


Figure 13. BVOC emission rates ($\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$) from mountain birch leaves at different ages (young and mature) and different exposures of O₃ (80 and 120ppb) measured twice in the summer of 2020. The emission rates are presented in log scale to facilitate the comparison between the different ages. The emitted compounds are presented in different color schemes where monoterpenes (MT) are red, sesquiterpenes (SQT) green and oxygenated compounds (OXY) blue, where MBO is abbreviated from 2-methyl-3-buten-1-ol and AMCH from 4-acetyl-1-methylcyclohexene. Isoprene is separated on its own and colored yellow. The black lines represent the standard deviation of the total emission rates.

Increased sesquiterpene emissions when plants are exposed to O₃ have previously been reported (Bourtsoukidis et al., 2012) and can be an indication that the plant is experiencing stress and is responding with increased defenses in the form of induced sesquiterpenes. The sesquiterpene group is one of the most reactive BVOC groups and has been found to have very fast reactions with O₃, explaining why a sesquiterpene induction was observed (Frazier et al., 2022). Young leaves induced their sesquiterpenes later (120ppb) than the mature trees that already induced sesquiterpene emissions at 40ppb (Paper II). An explanation to this difference could be that the mature leaves have been primed by low-concentration O₃ in the ambient air (Li et al., 2017) compared to the young leaves and therefore have boosted defenses with faster response times.

Norway spruce bark BVOC emissions

Other than whole ecosystem fluxes, forest floor and leaf emissions, emissions from bark of Norway spruce trees were also measured. Un-stressed emission variations from bark were also observed. Non-infested Norway spruce bark had total emission rates ranging from 4 to 38 $\mu\text{g m}^{-2} \text{h}^{-1}$ where the lowest emissions were measured in July and the highest in August (Figure 14). The main emissions were from the monoterpenes α -pinene and 3-carene with little contributions of other compound groups. However, in May, emissions of the sesquiterpene α -humulene were observed at 5 $\mu\text{g m}^{-2} \text{h}^{-1}$, which was the highest emission of sesquiterpenes from non-infested bark this season (Figure 14). Terpenoids are transported and stored in the xylem sap of Norway spruce contributing to the bark emissions (Duan et al., 2020) and the temperature dependency of monoterpenes can explain the emission variations – it was colder during the measurements in May and July compared to other times (Paper I). As the temperatures in May were low, this cannot explain the high contributions of sesquiterpenes at that time. One potential explanation could be that spring had just started with maximum temperatures of 22°C in the preceding weeks. The sesquiterpene emissions in May could then indicate the start of the growing season at an earlier development stage for the spruces. Due to these uncertainties, more studies are needed to draw robust conclusions.

Compared to the non-infested bark, the seasonal emissions from infested bark had higher variability, but this has a natural explanation as being caused by the infestation itself. At the beginning of the infestation in 2019 (June), the emissions were highest and can be explained by the active spruce defense. The defense continues either until the spruce fends off all beetles and the attack subsides, or the infestation is successful and the spruce is killed. A successful attack is seen in August where the bark beetles had taken over the trees infested in Hyltemossa, indicative of the lower emission rates in

August compared to June and July/August (Figure 14). To prevent further spread of the infestations, the infested trees in Hyltemossa were taken down before the new generations of bark beetles could emerge, therefore ending the data collection. It would be desirable to have continuous measurements after the tree is killed to track the emission changes over time. Measurements in May of trees infested the previous year do however indicate that emissions continue at higher rates than the healthy bark even the next summer (Figure 14). There could be implications relating to the spruces killed by the bark beetle even the following year.

Low emission rates in July are apparent deviations in the seasonal emission pattern for both infested and non-infested bark. This can be explained by the weather; as previously discussed, it was cold when the measurements were made, but the weather was also poor with heavy rain showers and wind gusts that can influence the emission rates from the tree, as well as the ability to capture the BVOCs with the measurement technique.

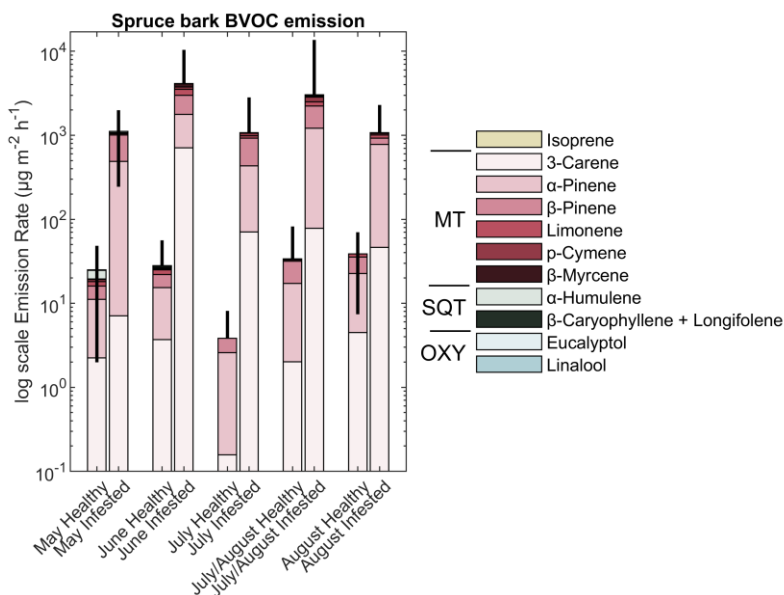


Figure 14. BVOC emission rates ($\mu\text{g m}^{-2} \text{h}^{-1}$) from both healthy and infested Norway spruce bark measured throughout the summer in 2019. The emission rates are presented in log scale to facilitate the comparison between sites and months with high variation. The emitted compounds are presented in different color schemes where monoterpenes (MT) are red, sesquiterpenes (SQT) green and oxygenated compounds (OXY) blue. Isoprene is separated on its own and colored yellow. The black lines represent the standard deviation of the total emission rates.

The average BVOC emission stress response

The sub-studies in the PhD project revealed the natural variability of the BVOC emissions, regardless of if stress is present or not. What is also apparent is that even if the emission rates have variations, there are visible effects beyond these variations that result from the stress factors studied throughout the PhD project. The average stress effect for bark beetle infestations, forest fires and O₃ exposure was found to have implications of varying degrees. The biggest stress response on the total BVOC emission rates came from bark beetle infestations, which resulted in increased emission rates of 7 900% (Figure 15a), from 26 to 2 090 $\mu\text{g m}^{-2} \text{h}^{-1}$. Comparing needle emissions from Norway spruce using the highest calculated Norway spruce monoterpene needle emission in 2019 (170 $\mu\text{g m}^{-2} \text{h}^{-1}$, see Paper I), the average healthy bark emissions contribute to around 15% of the tree emissions (27 $\mu\text{g m}^{-2} \text{h}^{-1}$). However, when the bark is infested, the emissions are 1 200% higher than the needle emissions, substantially increasing the emissions from the whole tree. Further comparison of the above canopy summer monoterpene flux average between 2019-2022 (417 $\mu\text{g m}^{-2} \text{h}^{-1}$, derived from Paper IV) reveals that needles contribute to 40% of the monoterpene emissions while healthy bark contributes to 6%. The measured monoterpene emissions from infested bark are five times higher than the measured above canopy flux, increasing the emissions by 400% at m^2 level, not taking into account potential within canopy consumption.

Bark beetle infestations severely affect the trees, something that is visible from the extreme increase in their BVOC emission rates. Since the increase in emission rates is so high, it not only affects the trees' ability for carbon assimilation, but the high monoterpene emission rates can also have severe impacts on the atmospheric chemistry, especially if large areas are affected. The largest increases were from p-cymene, β -myrcene and limonene (39 000%, 36 000% and 10 000% increase), but all compounds observed from healthy spruce bark increased. Additionally, emissions of eucalyptol were found from infested bark but not from healthy bark (Table 3). The high increases in emission rates for the mentioned compounds can have large implications, especially for limonene that has been found to have high impacts on O₃ and OH reactivity even when the increases are minor (Mcglynn et al., 2023). Other compounds, for example the monoterpene α -pinene, have been found to have high SOA yield and even more so the sesquiterpene β -caryophyllene (Faiola et al., 2018; Lee et al., 2006).

There is no question that from the studied stress factors, bark beetle infestations caused the highest stress response from the trees. However, vegetation stress is not only seen from extreme emission increases, it is also indicated by a decrease in emission rates or a change in the emitted compounds. Total emission decreases were seen after a forest fire

event in 2018 where the emissions decreased by 54% one year after the fire and continued to further decrease. After four years the emission rates had decreased by 90% compared to the healthy average total emission rates between 2020-2022 ($45 \mu\text{g m}^{-2} \text{h}^{-1}$; Figure 15b). The average emission rates from the burnt areas include areas with young and mature trees, high and low severity fires and different management strategies with natural succession or salvage logging and re-planting creating a realistic average of how recovery after a fire looks in Sweden (Paper III). It was expected that the total emission rates would decrease, as much of the biomass and vegetation is combusted by the fire. It is worth highlighting, however, that even if the total emission rates decreased one year after the fire compared to the healthy forest floor, certain compounds actually increased. Isoprene, eucalyptol and linalool all had increased emissions one year after fire (Table 3). The average healthy emissions of eucalyptol and linalool were only small contributions to begin with ($0.1 \mu\text{g m}^{-2} \text{h}^{-1}$), with slightly higher emission rates of isoprene ($0.4 \mu\text{g m}^{-2} \text{h}^{-1}$). Linalool and eucalyptol have previously deviated from the general diurnal emission patterns of other monoterpenes emitted from boreal forests, indicating that they can come from different sources (Hellén et al., 2018). This can potentially explain why they had increased average emissions one year after the fire, as the other sources of emissions from the understory vegetation are combusted. All three compounds are also emitted based on light availability compared to the majority of monoterpenes that are temperature dependent (Bouvier-Brown et al., 2009; Hakola et al., 2006, 2012), offering a further explanation for the emission increases as the forest floor has more light after a fire.

It is also worth noting the differences in emissions increasing for the individual sites depending on tree age and management strategy, where the mature trees survived at higher rates but dropped a lot of needles contributing to higher monoterpene emissions compared to the young trees that were combusted (Paper III). The same was seen for the salvage-logged site, where the monoterpene emissions one year after fire were the highest of all sites, explained by the litter and tree debris left behind after the logging (Paper III).

Two years after the fire, linalool was the only compound with higher emission rates compared to the healthy average. Additional explanations to the linalool emissions could be the stress that the forest floor was subjected to. Linalool emissions from pine branches increased when pines were infested by weevils, potentially caused by the exposed resin from the wounds (Blande et al., 2009). Increased tree debris of bark pieces were seen in the plots at that time, potentially resulting in similar resin storage emissions. This is also supported by the fact that no compounds from the burn sites average had higher emissions than the healthy average the third year after the fire, potentially from lack of storage emissions (Table 3). The total emission rates were on

average 90% less in the fourth year after the fire compared to the healthy forest floor with no individual monoterpene, sesquiterpene or OXY increases. There were, however, increases of isoprene in the fourth year that could be a result of the natural succession with fast growing pioneer species that are high isoprene emitters (Artaxo et al., 2022; Hanson et al., 1999; Holopainen, 2013).

It can take decades for burnt forests to recover from fire and regain the BVOC emissions (Zhang-Turpeinen et al., 2020). Following the recovery process in the first few years gave several insights into what the main sources of emissions might be. Continuing measurements could give more insights into how the recovery might differ depending on tree age, fire severity and management strategy, and help identify the turning point for the emission rate decrease.

Table 3. The emissions from unstressed Norway spruce bark ($\mu\text{g m}^{-2} \text{h}^{-1}$), Mountain birch leaf ($\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$) and boreal forest floor ($\mu\text{g m}^{-2} \text{h}^{-1}$) and the change (%) after stress. Some compounds were not measured all year which is indicated by n.d. (no data). NaN values indicate that there is no possibility of calculating the % since there is no emission. Inf indicates that there was no emission before the stress meaning that the increase not quantifiable. MBO is abbreviated from 2-methyl-3-buten-1-ol and AMCH from 4-acetyl-1-methylcyclohexene.

Compound	Bark beetle		Ozone			Forest fire				
	Control ($\mu\text{g m}^{-2} \text{h}^{-1}$)	Infested (%)	Control ($\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$)	O ₃ (%)	Recovery (%)	Control ($\mu\text{g m}^{-2} \text{h}^{-1}$)	Year 1 (%)	Year 2 (%)	Year 3 (%)	Year 4 (%)
Isoprene	0	NaN	7.0	-28	35	0.4	37	-41	-65	22
Monoterpene										
3-Carene	2.5	7134	11.4	-97	-53	11.5	-56	-31	-59	-94
α -Pinene	11.3	6582	211.1	-100	39	22.5	-46	-81	-75	-89
β -Pinene	8.0	8328	2.1	-96	15	0.5	-48	-58	-60	-50
Limonene	1.9	10739	21.5	-93	-48	1.4	-34	-49	-89	-93
p-Cymene	0.4	39366	11.6	-95	-46	5.2	-85	-69	-95	-86
Camphene	n.d.	n.d.	16.9	-98	-10	n.d.	n.d.	n.d.	n.d.	n.d.
β -Myrcene	0.3	36559	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Sesquiterpenes										
α -Humulene	1.1	782	0.5	3591	32	0.6	-57	-74	-86	-99
β -Caryophyllene	n.d.	n.d.	4.6	100	-86	3.4	-83	-89	-92	-100
β -Farnesene	n.d.	n.d.	3.8	321	56	n.d.	n.d.	n.d.	n.d.	n.d.
iso-Longifolene	n.d.	n.d.	0.4	-32	58	n.d.	n.d.	n.d.	n.d.	n.d.
Longicyclene	n.d.	n.d.	0.8	-87	-83	n.d.	n.d.	n.d.	n.d.	n.d.
β -Caryophyllene + Longifolene	0.5	4583	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Oxygenated compounds										
Eucalyptol	0	Inf	n.d.	n.d.	n.d.	0.1	21	-29	-87	-71
Linalool	0	NaN	24.9	-75	-23	0.1	288	147	-72	-86
AMCH	n.d.	n.d.	0.3	532	127	n.d.	n.d.	n.d.	n.d.	n.d.
MBO	n.d.	n.d.	5.3	-59	2	n.d.	n.d.	n.d.	n.d.	n.d.
cis-3-Hexenol	n.d.	n.d.	5.9	-64	-19	n.d.	n.d.	n.d.	n.d.	n.d.
Nopinone	n.d.	n.d.	1.3	-80	-74	n.d.	n.d.	n.d.	n.d.	n.d.
Total emission rates										
Total	25.9	7960	329.3	-80	16	45.5	-54	-66	-75	-90

BVOC emission decrease from stress was also witnessed when mountain birch leaves were exposed to acute increased O₃ concentrations. The average total emission rate of mountain birch leaves exposed to O₃ concentrations of 80 and 120ppb decreased by 80% compared to the healthy leaf emissions (Figure 15c). However, similarly to the forest fire recovery, that was not the case for all individual compounds. When the leaves were exposed to O₃, all compound emission rates decreased, except some of the sesquiterpenes (α -humulene, β -caryophyllene, β -farnesene) and an OXY (4-acetyl-1-methylcyclohexene (AMCH)). As mentioned previously, this can be explained by the sesquiterpenes high reactions with O₃. They are part of the plant defense against oxidative stress and are induced instead of monoterpenes (Frazier et al., 2022; Marchica et al., 2021). AMCH is an oxidation product from limonene, and the measured high increase of AMCH (500%) during O₃ exposure further reveals active defense against oxidative stress (Fick et al., 2001; Hakola et al., 1994). When the O₃ exposure ended, the first 30 minutes of recovery revealed a 16% increase in emission rates compared to the healthy leaves (Figure 15c). During the 30-minute recovery time, the leaves did not return to the same emission patterns as before the O₃ exposure. Instead, induced emissions of isoprene, monoterpenes (α -pinene and β -pinene), sesquiterpenes (α -humulene, β -farnesene and iso-longifolene) and OXY (AMCH and 2-methyl-3-buten-1-ol (MBO)) were seen. This reveals that in the immediate time after acute O₃ exposure, even with no O₃ present, the leaves are still affected by the stress. The increase of isoprene and the monoterpenes with reported oxidative protection capacities (Fick et al., 2001; Hakola et al., 1994) along with the increased OXY emissions might indicate prolonged effects from the exposure, or altered patterns due to the priming effect of the high concentrations. Similarly the increase of some sesquiterpenes provide oxidative defense against O₃, where high external doses of β -farnesene protect leaves against O₃ damage (Palmer-Young et al., 2015).

The high-induced sesquiterpene emissions both during O₃ exposure (up to 3 500%) and after (30% to 60%) reveal that the leaves induced their stress defense during the events. It can be said with certainty that the leaves' response to the acute O₃ exposure resulted in lasting effects up to 30 minutes after the O₃ exposure stopped. However, it remains uncertain how long the induced emission effect lasts or if the plants would have primed defense for longer periods. Primed defenses have been seen from tobacco plants, *Nicotiana tabacum*, up to 48 hours after exposure to O₃ compared to no exposure (Kanagendran et al., 2018). Similar primed defenses were seen from sage plants (*Salvia officinalis*), but after continuous O₃ exposure at 120ppb for 5 hours per day they stopped emitting the induced sesquiterpene compounds, potentially due to lost ability or interest in investment (Marchica et al., 2021). However, the recovery after acute exposure might reveal different long-term patterns.

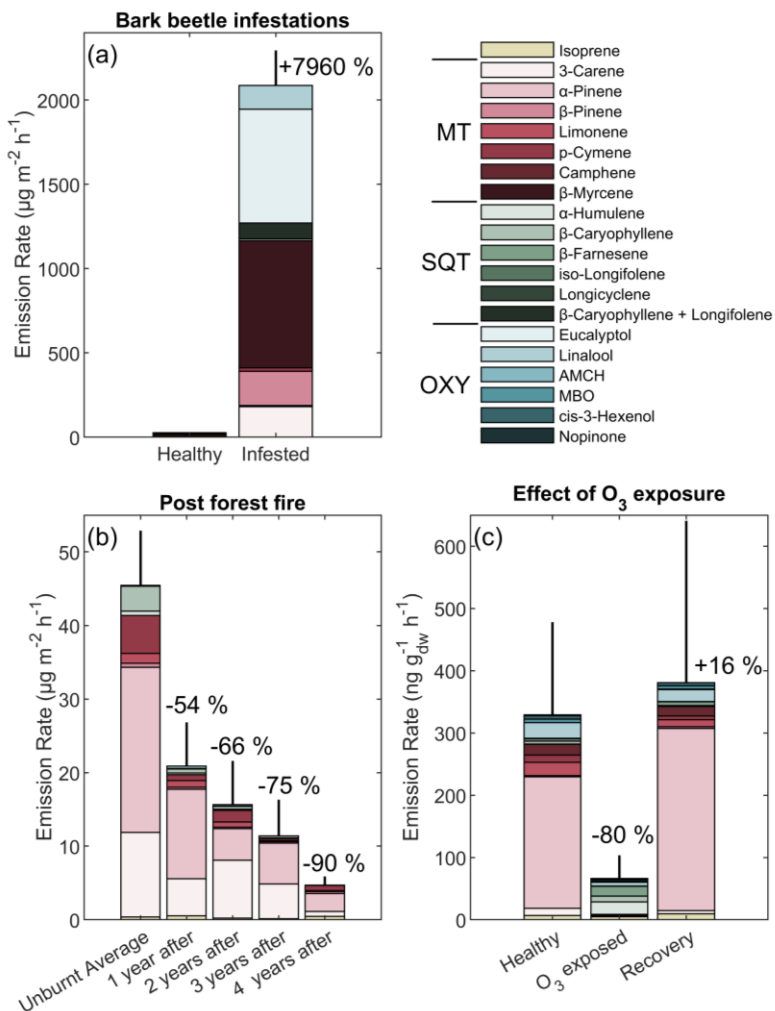


Figure 15. The stress effect on BVOC emission rates from (a) bark beetle infestations comparing healthy and infested Norway spruce bark, (b) forest fire comparing unburnt and burnt forest floor and the recovery until four years post fire and (c) O₃ exposure comparing healthy and O₃ exposed at 80 and 120ppb mountain birch leaves and the recovery after exposure. The numbers in the figures indicate the percentage increase or decrease in emission rates compared to the healthy state. The emitted compounds are presented in different color schemes where monoterpenes (MT) are red, sesquiterpenes (SQT) green and oxygenated compounds (OXY) blue, where MBO is abbreviated from 2-methyl-3-buten-1-ol and AMCH from 4-acetyl-1-methylcyclohexene. Isoprene is separated on its own and colored yell. The black lines represent the standard deviation of the total emission rates.

Large-scale implications from stressed vegetation

The stress on trees and vegetation is increasing with climate change. In Sweden between 2018-2022, 1.1% of all Norway spruces in production forests were killed by spruce bark beetles, 0.01% of all forests were burned and the alpine forests in the Scandinavian mountains were exposed to O₃ concentrations above 40ppb, the recommended threshold for O₃ concentrations (Directive 2008/50/EC), during approximately 11 330 hours (Table 1). The alpine O₃ concentrations are thus above the recommended threshold about 25% of the time. The small-scale effects of the stresses studied in this thesis indicate that bark beetle infestations are the main contributor to induced total emissions, followed by recovering mountain birch leaves and finally the forest floor recovering from forest fire. To place the results in a broader context, the stress-induced or reduced BVOC emissions can be applied to the whole of Sweden based on the land cover area and estimated stress extent summarized in the introduction (Table 1).

Hyltemossa is a Norway spruce production forest with approximately 597 spruce trees per hectare (Heliasz et al., 2023b). Using this estimate to cover the whole of Sweden, approximately 3.5 billion mature spruce trees grow in production forests in Sweden, from which 38 million trees were killed by spruce bark beetle between 2018-2022. From the average monoterpene flux measured in Hyltemossa those years (417 µg m⁻² h⁻¹), around 211Gg monoterpenes were emitted per year from healthy Norway spruce production forests in Sweden (Table 4). Using the emission rates measured from infested Norway spruce bark, around 0.7Gg monoterpenes per year was emitted from the bark beetle killed trees in Sweden the same years. The bark beetle infestations in Sweden between 2018 and 2022 would then result in 0.3% increased monoterpene emissions per year (Table 4). Even if bark is a small part of the total ecosystem fluxes (6%) and if only 1.1% of trees were infested and killed, it would still result in an estimated 0.3% increase in monoterpene emissions in all of Sweden.

Using similar calculations, estimations were done on the large-scale impacts of boreal forest fires. About 0.01% of the forests in Sweden are expected to burn every year and, as the measured forest fire area is dominated by Scots pine plantation forests, the land cover area of Scots pine was used for this estimate (Table 1). This resulted in around 900 hectares burnt every year in Sweden. Since the effects were measured one to four years after the fires with different emission results, this was included in the calculations to have both the recovery after fire each passing year as well as the new fires each year. The total emission rates from boreal forest floor in unburnt Scots pine plantations across all of Sweden would result in emissions of 36Gg BVOCs per year, which would on average only be 0.001Gg BVOC per year from the burnt forest floor. However, the average is based on the emissions in the first year of around 0.002Gg to the fourth year

of 0.0005Gg, resulting in the average emissions decreasing by 20% (to 29Gg per year) when taking forest fires from Scots pine forest floors into account. This estimate only includes the average number of fires per year in Sweden, and with climate change, more extremes could occur. This happened in 2018 when 25,000 hectares of Swedish forest were burnt, equal to around 27 years of average fires. The direct emissions of BVOCs from the fires themselves have not been measured or accounted for in the estimate. BVOCs are directly affected by the combustion of storage cells and through fire generated heatwaves (Ciccioli et al., 2014). It is a complex situation when BVOCs are emitted by fires as there are additional reactions that occur within the fire plumes before the compounds reach the atmosphere outside of the fire areas (Ciccioli et al., 2014).

Looking at the forest statistics in Sweden, there is no actual inventory of mountain birch forests (Roberge et al., 2023). However, it has been stated that 2 900 hectares are alpine forests, which are mainly dominated by mountain birch (Pividori et al., 2016). Using an interactive interpolated map from SMHI (SMHI, 2023) showing the hours of measured O₃ concentrations higher than 40ppb, measurements from 10 points along the Scandinavian mountains were used to calculate the yearly average hours above 40ppb for 2018-2022. The total hours between 2018-2022 above 40ppb was 11 330, which is around 25% of the total time period. This is however a rough estimate and local variations occur. From the measurements on healthy mountain birch leaves in Abisko and using the estimated land cover of mountain birch, around 37Gg of BVOCs are emitted per year in Sweden. The contribution of BVOCs from mountain birch to the yearly emissions from Sweden is almost the same as the healthy Scots pine forest floor (Table 4), indicating that they do not have substantial contributions considering that the main BVOC emissions are from the tree canopy (Laothawornkitkul et al., 2009; Niinemets and Monson, 2013). When quantifying the stress effect from the hours above 40ppb, the recovery phase was included in the calculations – but as only 30 minutes of recovery were measured, half of the total exposure hours were used for the recovery emission rates. This resulted in emissions from the O₃ stressed mountain birches of 13Gg per year and in adding the hours without O₃ stress, the yearly emissions increased by 33% to 49Gg per year. On a large scale, this increase was the largest compared to the other two stresses, but it also comes with the biggest uncertainties in regards to the stress extent estimations. Even with the uncertainties, the recovery period was only measured and calculated for 30 minutes and still contributes to the large increase, suggesting that the increase is potentially underestimated.

Based on these estimations, if all of the studied stresses occurred at the same time in one year, it would lead to an increase in BVOC emission rates of 2% from these ecosystem types from all of Sweden (Table 4).

Table 4. The yearly BVOC emissions (Gg year⁻¹) from healthy and stressed forests in Sweden. The calculated emission rates are based on the results presented in the thesis and the estimation of forest land cover and stress in Sweden quantified as a sum between the years 2018 to 2022. Data on land cover and number of bark beetle killed trees were taken from the Swedish forest statistics (Roberge et al., 2023), the extent of forest fires were acquired from Högberg et al. (2021) and the hours of elevated O₃ concentrations were taken from the Swedish Meteorological and Hydrological Institute (SMHI, 2023). The emission change (%) is calculated from the yearly average estimated healthy state emission and the combined emission rates from stressed and healthy trees.

Tree type	Stress	Healthy state emission rate (Gg year ⁻¹)	Stress emission rate (Gg year ⁻¹)	Combined emission rate (Gg year ⁻¹)	Emission change (%)
Norway spruce	Insect attack from the European spruce bark beetle	211	0.7	212	0.3
Scots pine	Forest fire	36	0.001	29	-20
Mountain birch	Elevated O ₃ concentration above 40ppb	37	12	49	33
All tree types		284	13	290	2

As previously discussed, induced BVOC emissions from stress can have large-scale implications not only to the trees, but also on the local or regional climate as the BVOCs take part in atmospheric chemical reactions. When modelling the impact of doubled BVOC emissions as a result of increased biomass, studies have found that there are increases in O₃ and CH₄ concentrations as well as enhanced SOA production (Cao et al., 2022; Weber et al., 2022). Cao et al. (2022) estimated increases of 16% in ambient O₃ and 73% in SOAs due to increased BVOC emissions from increased biomass in 2018 compared to 1981. Because of climate change, biomass in boreal forests is estimated to increase by around 95% by 2100 (Mekonnen and Riley, 2023). If the BVOC emissions in Sweden increase because of increased biomass, it adds even more implications to the regional climate. The resulting combined stress emission change from the studies in this thesis resulted in a 2% increase from the vegetation in Sweden, solely due to stress. This does not only add to the increased emission rates enhancing O₃, CH₄ or SOAs, but also to the complexity of the atmospheric chemistry as this thesis also showed that the emission profile changes to more reactive compounds. It is thus not only important to model and consider the emission increases, but also to take into account the emission profile change.

Suggestions for future research

Plant emissions of BVOCs are affected by several intricate interactions with factors controlling the emissions, like temperature, light, water availability and wind (Peñuelas and Llusà, 2001). In addition, the emissions are further affected by stress, such as the studied stresses in this thesis. Measuring BVOC emissions is of strong relevance to understand plant physiology, plant ecology and interactions with atmospheric chemistry.

The results in this thesis add to the understanding on constitutive emissions and their changes with the natural variations in growing seasons and between years. In addition, this thesis investigated the impact of stress from bark beetle infestations, oxidative O₃ stress and recovery after forest fires. This revealed differences in the stress response, both between stresses but also within the stress where the total emissions revealed different patterns compared to the individual compounds. It is important to continue the analysis of stress-related BVOC emissions to fully understand the complex interactions, but also to look into the emitted compounds. Moreover, future research needs to add more long-term measurements to cover the variability of the BVOCs emitted constitutively, but also to analyze the long-term stress effects (Faiola and Taipale, 2020). Taking the exposure time into account is crucial for the comparison of stress responses with other studies, as pointed out in this thesis where bark beetle emissions were found to be extremely high at the start of an infestation but decrease over time. Similarly, the measured stress response of O₃ was different depending on the leaf age and the recovery after forest fire indicated decreased total emission rates over the years. The O₃ exposure also led to increased emissions after the stress subsided, but this was only measured for 30 minutes after the stress. A longer measurement series would give further indications as to how elevated acute O₃ concentrations affect leaves in the long term. More data is needed with regards to the time in relation to the stresses and over longer time series to facilitate the comparison as well as a deeper understanding.

As empirical studies of BVOC emissions can provide the foundation for predictions and modeling future climates, the results from this thesis can be directly incorporated in future modeling studies. Current models have several restrictions, some due to the limitations in empirical studies, as the majority are conducted in a laboratory and up-scaled from those results (Kigathi et al., 2009; Schuman, 2023). Another limitation is from the processes incorporated in models. The majority of models use constant emission factors throughout the growing seasons to simulate the BVOC emissions (Berg et al., 2013; Bergström et al., 2014), when they in fact vary both in un-stressed and stressed conditions, as proven by this thesis. Furthermore, the model of aerosol dynamics and gas phase (ADCHEM, Roldin et al., 2011) takes into account BVOCs

as SOA precursors, however, only defined by direct emissions and emissions from storage where monoterpenes are considered to mainly be storage emitted. Therefore, future research should focus further on improving BVOC emission-related processes in models. One approach incorporated processes to predict the future emissions from plant stress by connecting the stress emissions to the active biosynthetic pathways (Grote et al., 2019). As seen by this thesis, that approach requires further research at compound level in order to find out what pathways are activated by which stress. Moreover, this can be different for different plants, motivating the need for further research of the same stress but from several plants or ecosystems.

The results in this thesis highlight the importance of looking at the compound level when studying the effects of stress. Another future direction is to look at the chirality of compounds, not covered in this thesis. Current research has given little attention to the enantiomers of the emitted compounds, but the different forms have been proven to have different diel cycles in the presence of drought (Byron et al., 2022). The different enantiomers were also suggested to be emitted differently, either directly upon production or from storage pools (Byron et al., 2022). Studies including the enantiomers will provide further ways to understand the processes behind the stress response. Analysis of the chirality of emitted compounds can also further help improve the output from the mentioned models as the emitted enantiomers also offer hints to the emission origin.

Currently, the majority of all BVOC studies are conducted in a laboratory. A potential reason as to why most studies on BVOC emissions are conducted in the laboratory is the possibility of controlling the environmental settings (Schuman, 2023). This makes it easier to draw conclusions about any potential stress impact without interference from other factors. However, this is rarely the case in the field where plants are often exposed to concurrent stresses. For example, insect herbivory often occurs with drought or heat stress and several more combinations are common (Faiola and Taipale, 2020). More studies on trees in their natural environment are needed.

Not only is there a need for more stress-related research in the future, more resources are needed to investigate how the stress responses differ within plants. One part of the plant might react to a stress differently than other parts, for example in regards to the bark beetle infestations. The effect of the infestation on needle emissions that might also be impacted has not been investigated in this thesis. The question remains whether the stress would increase or decrease the emissions from the needles. Studies also suggest that neighboring plants not subjected to the stress can adjust their emissions in response to the stress emissions from other plants (Schuman, 2023). Future research could not only focus on the direct impact of the stressed plant, but also on the indirect effect the plant emissions have on other plants.

Conclusion

Trees and vegetation are affected by various stresses in different ways. This is apparent from the results of this thesis where the largest impacts in emission rates were from the bark beetle-infested Norway spruce trees, with almost 8 000% increased bark emission rates, highly indicative of the stress and defense of the spruces. The results also showed that other kinds of stresses have different responses. Both stress from the recovery years following a forest fire in a boreal forest and O₃ exposure on mountain birch leaves revealed different responses. Contrary to the bark beetle infestations, both O₃ exposure and forest fire recovery measurements revealed that the total emission rates decreased. These results can be intuitive, as in the case of a forest fire where vegetation, the main BVOC emitter, is combusted or when O₃ is present in the air and emitted compounds are oxidized. However, from these stresses it was apparent that even if the overall pattern was a decrease, there were still some compounds that had increased emission rates. A key outcome from the thesis is the need to study impacts on compound level and not only the total emissions. Some increasing compounds have been found to be the most atmospherically reactive and also have the highest SOA yield, giving them potential to have substantial influence after emission, even when overall emissions decreases.

This thesis provides initial results and input to how stresses from drought, bark beetle and forest fire can have long-term impacts. BVOC emissions are naturally affected by environmental factors, causing variation in emissions. This was seen especially from the Hyltemossa above canopy flux measurements, where temperature was a driving factor in the emissions and similar temperatures in 2020 and 2021 resulted in similar daily monoterpene emission patterns and Q₁₀ values. However, large deviations were seen for the monoterpene emissions in 2019, despite not deviating much in air temperature and GPP compared to the other years. This is believed to be because of the drought in 2018 causing prolonged effects due to the potential increase in needle litter and fine root mortality. Prolonged effects were also seen from the bark beetle infestations where a tree infested in 2018 autumn still had induced emissions in 2019 spring compared to healthy trees. This is something important to consider in predictions of climate change impacts on vegetation as stress events can have long term impacts and additional studies are needed to understand more about how long the effects lasts and to examine potential changes to the emission profiles.

Through this thesis, the understanding of how plants react to stress has progressed, but more importantly the thesis also highlights the need for additional measurements and experiments. It still remains uncertain how, for example, Norway spruce needles are affected by bark beetle infestations, or if the remaining needles of a surviving burnt Scots pine have increased or decreased emissions. Studying the effects of different plant parts other than the ones directly affected by stress could further understanding of the connections within plants. The combination of stresses is also important. As the thesis work was all done in situ, the trees were already growing in their natural habitat and were subjected to ambient conditions. This indicates that the stress effects measured might have already been in motion due to changed ambient conditions that could be perceived as stressful to the plant, making the results of this thesis even more realistic than if it was performed experimentally in a laboratory.

Based on this thesis, stress-induced BVOC emissions from forests in Sweden increased the monoterpene emission rates by 2% from all production forests of Norway spruce and Scots pine and the alpine regions with Mountain birch trees. This rough estimate of 2% is calculated from the small-scale measurements conducted on Norway spruce bark, Scots pine forest floor and Mountain birch leaves. The regional increase could be much larger, as seen from the bark beetle infestations substantially increasing the emissions, but also from the variations in emission rates from forest fires due to management, severity and age. Mountain birch leaves were responding differently to O₃ exposure depending on their leaf age, and there is a potential for larger implications in atmospheric chemistry when young trees are exposed compared to old trees as they increased their sesquiterpene and OXY emissions earlier and at higher rates. The 2% estimate was also only based on three different stresses; in reality, there are several more stresses present not covered by this thesis, both different kinds of stresses but also stresses in combination. This can potentially affect the BVOC emission rates even more.

The results from this thesis provide knowledge of the constitutive emissions from Norway spruce canopy fluxes and Norway spruce bark, mostly considered of little importance but observed to have contributions of up to 15% of the Norway spruce BVOC emissions with needles and bark combined. The constitutive emissions from boreal Scots pine forest floor were also measured with large yearly variations, highlighting the importance of repeated measurements. Constitutive emissions from mountain birch leaves provide further details as to how they change with age, where the emission profiles differed the most. All of these constitutive emissions provide vital information that can be used as inputs in models for predicting future emissions. More importantly, the main results on how the emission changed in the presence of stress provide even further knowledge for making more accurate predictions.

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