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Herbivore-induced BVOC emissions of Scots pine under warming, elevated ozone and increased nitrogen availability in an open-field exposure

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ABSTRACT

Climate change may promote the frequency of insect attacks such as outbreaks of the great web-spinning pine sawfly (*Acantholyda posticalis*) on Scots pine (*Pinus sylvestris* L.). We determined the emission rates of localized biogenic volatile organic compounds (BVOCs) from *A. posticalis*-fed branches, and systemic BVOCs from non-fed branches of Scots pine seedlings defoliated for two growing seasons by *A. posticalis* larvae. Seedlings were also exposed to warming, elevated ozone and higher nitrogen availability for three years in an open-field experiment. *A. posticalis* feeding increased localized emissions of total non-oxygenated monoterpenes 21-fold, total oxygenated monoterpenes 9.1-fold, total sesquiterpenes 11-fold and total green leaf volatiles 9.2-fold from insect-damaged shoots on the 7th day of feeding in June. Warming reduced the effects of herbivory on the emission rates of total non-oxygenated monoterpenes by 77%. However, the effect of herbivory on total sesquiterpene emissions was enhanced by 16-fold in combination with warming and elevated ozone. The localized emission rates of total BVOCs were linearly increased when feeding damage intensity by larvae exceeded 80%. After three weeks of continuous sawfly feeding, herbivory stress increased systemic emissions of total non-oxygenated monoterpenes 5.6-fold, total sesquiterpenes 5.6-fold and total green leaf volatiles 6.5-fold from the non-damaged branch of larvae-fed seedlings, and this effect on total non-oxygenated monoterpene emission was enhanced 8.6-fold with elevated ozone. Herbivory sporadically showed post-feeding effects still by the end of 12th week from the initiation of feeding, increasing total non-oxygenated monoterpene emissions 4.4-fold at elevated nitrogen level. Our results suggest that Scots pine, at least in seedling stage, will be a stronger source of BVOC emissions in future due to expected increase of sawfly outbreaks with climate warming and by increased herbivory interactions with abiotic climate change factors.

1. Introduction

Boreal forest zone of the northern hemisphere (taiga), the largest terrestrial biome of the Earth, covers about 33% of the world's total forest area (Taggart and Cross, 2009). This biome has suffered from the largest temperature increase (> 0.85 °C) over the period of 1880–2012 (Serreze et al., 2000; Folland et al., 2001; Stocker et al., 2013) and from increasing tropospheric ozone concentrations at a rate of 1–5 ppb per decade by the end of 20th century, with current ambient concentrations of 30–40 ppb (Wittig et al., 2007; Hartmann et al., 2013). However, there is a large yearly variation in ozone exposure throughout the European boreal forests (EMEP 2014, 2015, 2016). Scots pine (*Pinus sylvestris* L.) (Pinaceae) is a dominant conifer species of European boreal forests (FAO, 2010) and constitutes almost 50% of the total growing stock (2206 million m^3) in Finland (Peltola, 2009). Warming affects boreal forest ecosystems by increasing plant productivity and net N mineralization (Rustad et al., 2001; Allison and Treseder, 2008). Higher nitrogen availability caused by atmospheric deposition or fertilization usually enhances tree growth and carbon uptake in the northern forest ecosystems (Aber et al., 1989; Ollinger et al., 2002) that have been originally nitrogen limited. Tropospheric ozone, a phytotoxic gas is reported to reduce photosynthesis, growth and biomass production of boreal trees (Utriainen and Holopainen, 2001; Wittig et al., 2009; Ainsworth et al., 2012).

Climate warming increases insect populations and enhances both the intensity and frequency of their outbreaks (Williams and Liebhold, 1995; Bale et al., 2002). Warming induces northward and upward shift in the outbreak areas of forest defoliators due to better performance of boreal conifers at treeline (Wilmking et al., 2004; Soja et al., 2007). Insect species populations living in the high latitudes of boreal forest

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zone benefit from climate warming due to increase of their fecundity, generations per year, and by reduction of their mortality rate due to cold (Stange and Ayres, 2010). A 5 °C elevation in temperature increases the outbreak risk of sawfly (*Neodiprion sertifer*) in boreal pine forests by shortening the development period of insects' larvae by 37–41% (Kollberg et al., 2013).

The great web-spinning pine sawfly *Acantholyda posticalis* (Matsumura) is a widespread, insect species causing damage on the pine forests of the central and eastern Europe and is expected to become a serious pest in northern and western Europe with the current warming (Voolma et al., 2016). *A. posticalis* has recently caused mass outbreaks in Scots pine forests in Siberia, Estonia (Voolma et al., 2009) and South-Western Finland (Vapaavuori et al., 2010). *A. posticalis* overwinters in two larval stages – eonymphs (diapause in soil) and pronymphs (pupate and develop into adults) – only few centimetres below the soil. The overwintering larvae in the soil are protected by an insulating shield of needle litter and snow, thus ensuring for better survival during long winter in the northern Europe (Voolma et al., 2016). Larvae of sawfly feed on pine needles from June to early July. The larvae first cut fresh pine needles of new and older generations and feed on them later inside their webs close to the branch bark.

Boreal conifer forests are major sources of biogenic volatile organic compound (BVOC) emissions, which mainly comprise of isoprene, monoterpenes (MTs) and sesquiterpenes (SQTs). BVOCs from boreal forests contribute 30–35% to the annual global BVOCs emitted from world's total vegetation (Kesselmeier and Staudt, 1999; Taggart and Cross, 2009). BVOCs function in oxidative-and thermo-protection of plants and in signalling with other plants and organisms (Peñuelas and Llusià, 2003; Heil and Karban, 2010; Loreto and Schnitzler, 2010). BVOCs promote plant growth, reproduction and defence against herbivores, pathogens and abiotic stresses (Peñuelas and Llusia 2003; Dicke and Baldwin, 2010; Holopainen and Gershenzon, 2010; Loreto and Schnitzler, 2010; Possell and Loreto 2013). BVOCs yield tropospheric ozone by catalysing a photochemical reaction with nitrogen oxides (NO_x) (Matyssek and Sandermann, 2003; Pinto et al., 2010). On the other hand, in reactions with ozone and hydroxyl (OH) and nitrate (NO_3) radicals (Atkinson and Arey 2003) BVOCs participate in the formation of secondary organic aerosols (SOA) in the lower atmosphere (Virtanen et al., 2010; Hao et al., 2011; Ehn et al., 2014; Joutsensaari et al., 2015). SOA further develop into cloud condensation nuclei (Ehn et al., 2014), the atmospheric concentrations of which are estimated to double in the regional scale due to BVOC emissions from boreal conifer forests (Spracklen et al., 2008).

Both elevated ozone concentrations and higher temperatures have been found to increase the emissions of BVOCs from conifers. Ozone concentration of 50 ppb nearly doubled emissions of dominant MTs from Scots pine in two-year-lasting open top chamber exposure (Heiden et al., 1999), and also slightly elevated ozone (1.4 × ambient concentration) exposure increased emissions of several BVOCs from Norway spruce in an open-field experiment (Kivimäenpää et al., 2013). Warming of 1 °C + ambient and elevated ozone 1.5 × ambient concentrations, increased the emission rates of several BVOCs from Scots pine and the effect was enhanced by elevated soil N availability (Kivimäenpää et al., 2016).

Herbivory by bark-feeding *Hylobius abietis* is known to increase both localized emissions of BVOCs (Heijari et al., 2011) from herbivore-attacked part and systemic BVOC emissions (Heijari et al., 2011; Kovalchuk et al., 2015) from the non-damaged part of herbivore-attacked Scots pine. Needle feeding by sawflies *Diprion pini* and *Neodiprion sertifer* increased the localized emissions of total MTs and total BVOCs from Scots pine shoots, and *N. sertifer* feeding increased the systemic total MT emissions from pine shoots (Ghimire et al., 2013). A ten percent defoliation by *A. posticalis* nearly doubled the emissions of oxygenated monoterpenes (MT-ox) and tripled that of total SQTs (Kivimäenpää et al., 2016), and this mild herbivory enhanced the effects of warming and repressed the effects of ozone on BVOC emissions in the following spring (Kivimäenpää et al., 2016). A weak positive correlation was found between 3-carene emissions and herbivore damage intensity in Scots pine in a previous study (Kivimäenpää et al., 2016). A positive correlation between VOC emissions and the extent of damage by herbivores/pathogens on deciduous tree species has been found (Copolovici et al., 2011, 2014).

This study is aimed to fill a gap in our knowledge – how a prolonged foliar herbivory affects BVOC emissions of conifers under multiple, abiotic climate change factors. This issue is yet unaddressed, despite the growing threat of sawfly outbreaks in the pine forests of northern Europe with the current and predicted climate warming (Niemelä et al., 2001). The current field study is based on the same multi-factorial (elevated ozone, elevated temperature, two nitrogen levels and herbivory) experimental design in open-field as our earlier paper by Kivimäenpää et al. (2016). The previous work quantified only localized BVOC emissions of Scots pine under milder herbivory damage of one growing season (Kivimäenpää et al., 2016), this study has focused on both the localized and systemic shoot BVOC emissions of Scots pine seedlings in response to herbivory damage of two summers (2012–2013) with an intensive damage in the later year. Furthermore, we addressed the interactions between severe herbivory and abiotic factors (warming, elevated ozone and higher nitrogen availability) that affected the experimental seedlings over three years in this study.

Our specific objectives were: (1) to determine how the localized BVOC emission rates from Scots pine foliage were affected by *A. posticalis* feeding both alone or in combination with warming, elevated ozone and increased soil nitrogen availability; (2) to find out the relationship between localized BVOC emission rates and the proportion of needles consumed by *A. posticalis* larvae; and (3) to assess how *A. posticalis* feeding alone, and in interaction with the included climate change factors, affect the emission rates of systemic BVOCs from Scots pine shoots along the growing season.

2. Materials and methods

2.1. Experimental design

Scots pine (*Pinus sylvestris* L.) (Pinaceae) seedlings were exposed to elevated ozone, warming, two levels of nitrogen availability and herbivory in a three-year multi-factorial experiment, started in summer 2011 and ended in autumn 2013, run in an open-field exposure site of Kuopio campus (62°53′42″N, 27°37′30″E, 80 m above sea level) of the University of Eastern Finland. This study is based on the same experimental design that was used by Kivimäenpää et al. (2016) but it focusses on the BVOC emission data of summer and autumn 2013 in response to herbivory feeding during two growing seasons (2012 and 2013). Results of BVOC emissions and some needle structural and physiological responses of Scots pine shoots in response to moderate herbivory damage, elevated ozone, warming and soil nitrogen availability during summer 2012 and spring 2013, with a detailed experimental setup, have been reported by Kivimäenpää et al. (2016).

Three-year-old potted seedlings of Scots pine were used for the experiment conducted in 2013. The seedlings were randomly distributed to eight circular exposure plots (diameter 10 m), four of which were ambient ozone plots and the other four elevated ozone plots. Each plot comprised two rectangular subplots (190 × 140 cm), one of which was for ambient temperature and another for elevated temperature treatment. Each subplot had 18 experimental seedlings, but also included other 12 seedlings along the lengths of the subplot to provide them a similar shading and microclimatic conditions. Half of the seedlings of each subplot received a target dose of 120 kg N ha^{-1} y^{-1} in the beginning of growing seasons in 2011 and 2013, referred to as elevated nitrogen treatment (N+). The other half of the seedlings, lacking additional fertilization, is denoted as lower nitrogen treatment (N-). Thus, including herbivory, the experimental design comprised four replicates (n = 4) in each treatment combination. Water content of