



Feeding of large pine weevil on Scots pine stem triggers localised bark and systemic shoot emission of volatile organic compounds

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ABSTRACT

Feeding by the large pine weevil (*Hylobius abietis* L.) causes severe damage to the bark of Scots pine (*Pinus sylvestris* L.) seedlings. We measured photosynthesis, the emission of volatile organic compounds from intact and weevil-damaged bark and systemic emissions from undamaged foliage. Feeding damage did not affect photosynthesis. Monoterpenes dominated the emissions from the feeding site, although some sesquiterpenes were also emitted. Weevil feeding increased bark emission of monoterpenes by nearly 4-fold and sesquiterpenes by 7-fold. The influence of weevil damage on systemic monoterpene emissions from shoots was more profound. Several compounds were substantially induced, including linalool, β -phellandrene, limonene and 1,8-cineole. Sesquiterpenes contributed only 1.2% of the total foliage emission, but comprised eight different compounds including (*E,E*)- α -farnesene, β -bourbonene and (*E*)- β -farnesene. The total emission of monoterpenes and sesquiterpenes from shoots was respectively 2.8-fold and 2.9-fold higher in the pine weevil damaged plants than the undamaged plants. As many of the induced compounds are highly reactive in the atmosphere and form organic aerosol particles, our results suggest that conifers damaged by insects could become a more important source of secondary organic aerosols than healthy trees.

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1. Introduction

Scots pine (*Pinus sylvestris*) is one of the most widely distributed conifers in the world with a geographical range from Scotland to the coastal area of eastern Siberia in Russia (Hämét-Ahti et al., 1992). It is a dominant tree species in European boreal conifer forests and has major economic importance in timber, pulp and paper industries. However, monocultured forest plantations of Scots pine have generated significant pest problems. Large pine weevil (*Hylobius abietis* L., Coleoptera: Curculionidae) adults emerge from conifer tree stumps and feed on the stem phloem and bark of young seedlings causing severe problems in cultivated areas (Örlander and Nilsson, 1999). Heavy infestations of this insect can result in the widespread loss of conifer seedlings for several years after plantation establishment in Europe (Danielsson et al., 2008; Dillon et al., 2008). Both large pine weevil sexes are attracted by volatile compounds, such as α -pinene and β -pinene emitted by fresh conifer stumps left during felling (Zagatti et al., 1997).

Conifer resistance to biotic damage is associated with constitutive and inducible defence compounds, i.e. a mixture of volatile monoterpenes (MTs), sesquiterpenes (SQTs) and non-volatile diter-

penes (resin acids) in the oleoresin (Trapp and Croteau, 2001), and with structural defences e.g., resin canals. Concentrations of MTs in current-year needle extracts of Scots pine seedlings are only 10–30% of those in current year stem bark extracts and (*E*)- β -caryophyllene was the only SQT detectable in extracted samples (Sallas et al., 2003). When plants are damaged by herbivores they emit volatile organic compounds (VOCs) (e.g., Arimura et al., 2004; Rasmann and Turlings, 2007). Oleoresin stored in the bark of conifer seedlings could be a significant source of VOCs (Ghirardo et al., 2010). Damage by bark phloem feeding insects causes massive resin flow that can passively release VOCs that may function as airborne signals within-plant. The defence compounds in conifers have been found to deter insect pests and fungal pathogens (Gershenson and Croteau, 1991) and act in direct and indirect ecological interactions (Mumm and Hilker, 2006; Gershenson, 2007). It has also been shown in conifers that volatiles are induced by herbivory and egg deposition in needles (Mumm and Hilker, 2006). These volatiles often function in the attraction of natural enemies of insect herbivores (Keeling and Bohlmann, 2006). Many of these volatiles are emitted by foliage but also from resin canals in stem (Sallas et al., 1999; Heijari et al., 2005) and roots (Janson, 1993), especially in monoterpene-storing conifers.

The induction of resistance in non-affected parts of a plant when a distant part of the same plant is challenged by a pathogen or herbivore is called induced systemic resistance (ISR) and it has

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been observed in conifers (Bonello et al., 2001, 2006). Previous research on systemically induced volatile organic compounds has revealed the involvement of three major signal-transduction pathways and their key intermediates; octadecanoid, shikimate and ethylene pathways producing: jasmonic acid (JA) salicylic acid (SA) and ethylene (ET), respectively. Evidence exists that SA, JA and ET are involved in localised and systemic induced defence responses in conifers (Fäldt et al., 2003; Heijari et al., 2005; Bonello et al., 2006; Zeneli et al., 2006). Local and systemically induced VOC emissions from needles of Scots pine have been found after egg deposition by pine sawfly (Hilker et al., 2002).

In this study we focus on emissions of volatile organic compounds (VOC) from Scots pine seedlings after stem bark wounding below the foliage by the large pine weevil, *H. abietis*. Our aim was to clarify the quality and quantity of both local emissions from the feeding site at the stem base and the systemic emission from intact shoots. Furthermore, this study will give insight as to how outbreaks of bark-feeding insects affect the quality and quantity of reactive carbon compounds emitted from conifers to the atmosphere and thus the possible consequences on atmosphere-biosphere interactions e.g., the formation of secondary organic aerosols from plant volatiles (e.g., Bonn and Moortgat, 2003; VanReken et al., 2006; Pinto et al., 2007; Boy et al., 2008; Spracklen et al., 2008; Hao et al., 2009; Jimenez et al., 2009; Virtanen et al., 2010).

2. Materials and methods

2.1. Experimental plants and herbivores

Scots pine seedlings (2-years-old) were obtained from a commercial nursery (Taimityyllä Oy, Mäntyharju, Finland). Seedlings were individually planted in 7.5 l plastic pots in 2:1 (v/v) quartz sand (Ø 0.5–1.2 mm; SP Minerals Partek, Finland) and fertilized sphagnum peat (Kekkilä PP6, Finland). After planting, the seedlings were fertilized with a slow-release fertilizer (Taimiston kestolanos 9% nitrogen, 5% phosphorous, 5% potassium and 5% magnesium, 4% sulphur and micronutrients, Kemira Oyj, Finland), 4 g of which was added to the surface layer of the growth medium in each pot. The seedlings were grown outside with natural rainfall and supplementary watering as required.

Large pine weevils (*H. abietis* L., Coleoptera: Curculionidae) were collected from a saw dust storage heap of a sawmill (Iisveden Saha, Suonenjoki, Finland). Prior to experiments weevils were kept in an 8 °C controlled temperature room, they were stored in plastic containers filled with wood shavings and fed with small pine twigs.

2.2. Study site and design

The study site was the Kuopio campus research garden of the University of Eastern Finland (62°53'N, 27°37'E, and 80 m above sea level). The first experiment tested the effects of weevil feeding on systemic emissions from the shoots of Scots pine seedlings. Scots pine seedlings were grown on twelve separate wooden platforms. On six platforms, three Scots pine seedlings per platform were infested with large pine weevils (*H. abietis* L., Coleoptera: Curculionidae), while on the remaining six platforms the seedlings were non-infested controls. Seedlings to be infested were selected randomly and infested with two large pine weevil adults enclosed in mesh bags attached to basal stem bark of each seedling. Weevils were selected at random, irrespective of sex, based on earlier experiments where no differences were observed in their feeding activity (Heijari et al., 2005). Three days (72 h) after the initiation of feeding (June 4–7, 2007), the experimental insects were removed and volatile organic compounds (VOC) were collected from the whole foliage of 17 damaged and 16 non-damaged plants.

The second experiment tested the effects of weevil feeding on emissions from the site of damage. Five Scots pine seedlings were infested with weevils, as described above, and placed one per platform on five randomly separate platforms. A further five seedlings were selected as non-infested controls and placed on five different platforms. After 4 days (96 h) of feeding, seedlings were transported to the laboratory for collection of VOCs.

2.3. Photosynthesis measurements

Net photosynthesis (Pn) was measured from the top shoots of a subset of the sampled seedlings (8 damaged and 7 non-damaged seedlings). After measurements, the seedlings were harvested for determination of shoot dry weight (dried in an oven for 72 h at 60 °C) and needle area for use in Pn calculations. Pn measurements were conducted in direct sunlight, but with some of the light blocked with a light mesh fabric (Photosynthetically active radiation was on average \pm SD, $758 \pm 145 \mu\text{mol m}^{-2} \text{s}^{-1}$). Measurements were made between 10:00 AM and 3:00 PM with a CI-510 Ultra-light Portable Photosynthesis System (CID, Inc., Vancouver, WA, USA). The needle lengths of ten two-needle fascicles per annual shoot and the number of needles were measured. The total area (A_t) of needles was calculated using the model, $A_t = 4.2235 \times (\text{Mean needle length}) - 15.6835$ (Flower-Ellis and Olsson, 1993).

Pn: net photosynthesis rate ($\mu\text{mol/m}^2/\text{s}$) for the open system was calculated using the formula:

$$Pn = -W \times (C_o - C_i) = -2005.39 \times \frac{V \times P}{T_a \times A} \times (C_o - C_i)$$

where C_o (C_i) is the outlet (inlet) CO_2 concentration (ppm or $\mu\text{mol/mol}$), V is the volume flow rate (l/min), P is the atmospheric pressure (bar), T_a : air temperature (K), A : leaf area (cm^2), W : mass flow rate per leaf area ($\text{mol m}^{-2} \text{s}^{-1}$).

2.4. Collection of volatile organic compounds

We collected VOCs (mono-, sesquiterpenes and green leaf volatiles (GLV)) from the foliage of 16 non-damaged and 17 damaged Scots pine seedlings. The mesh bags on each tree were opened immediately before sampling and the feeding weevils were removed. Polyethylene terephthalate (PET) bags (size 45 cm \times 55 cm, LOOK, Terinex Ltd., Bedford, England) were heated at +120 °C for 1 h before collections to remove any contaminants from the bag, and subsequently cooled. The main shoot and side branches were enclosed inside the PET bag and fastened securely to the stem bark taking care not to damage any foliage. One of the two outermost bag corners was cut and an air inlet and data recording device were inserted and supported by a tripod. Clean charcoal-filtered and MnO_2 scrubbed air was pumped through Teflon tubing and into the bag at 600 ml min^{-1} to flush the system, and then reduced to 250 ml min^{-1} during collections. The remaining bag corner was cut and a stainless steel tube containing approximately 150 mg of Tenax TA-adsorbent (Supelco, mesh 60/80) was inserted and fastened into position. Air was pulled through the Tenax tube by battery-operated sampling pumps (Rietschle Thomas, Puchheim, Germany). The air flow through the Tenax tube was set to 200 ml min^{-1} with an M-5 bubble flowmeter (A.P. Buck, Orlando, FL, USA). The VOC collection system including pumps, air filters, Teflon tubing, data logging device and batteries was installed into a portable plastic toolbox. During the sampling period (30 min), the temperature, photosynthetically active radiation (PAR) and air humidity inside the plastic bags were monitored with a HOBO Micro Station Data Logger (MicroDAQ.com, Ltd., Contoocook, NH, USA).

To determine the impact of insect feeding on the emission of volatile organic compounds from stem bark we measured emis-

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