Environmental Pollution 157 (2009) 174–180

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Pine weevil feeding on Norway spruce bark has a stronger impact on needle VOC emissions than enhanced ultraviolet-B radiation

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Chronic exposure to enhanced UV-B radiation has little effect on volatile emissions of Norway spruce.

ARTICLE INFO

Article history:
Received 1 April 2008
Received in revised form 11 July 2008
Accepted 17 July 2008

Keywords:
Hylobius abietis
Picea abies
Terpenoids
Volatile organic compounds
Systemic responses

ABSTRACT

Plants can respond physiologically to damaging ultraviolet-B radiation by altering leaf chemistry, especially UV absorbing phenolic compounds. However, the effects on terpene emissions have received little attention. We conducted two field trials in plots with supplemented UV-B radiation and assessed the influence of feeding by pine weevils, *Hylobius abietis* L., on volatile emissions from 3-year old Norway spruce trees (*Picea abies* L. Karst.). We collected emissions from branch tips distal to the feeding weevils, and from whole branches including the damage sites. Weevil feeding clearly induced the emission of monoterpenes and sesquiterpenes, particularly linalool and (*E*)-β-farnesene, from branch tips, and the sums of monoterpenes and sesquiterpenes emitted by whole branches were substantially increased. We discovered little effect of UV-B radiation up to 30% above the ambient level on volatile emissions from branch tips distal to damage sites, but there was a possible effect on bark emissions from damage sites.
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1. Introduction

Anthropogenic release of halocarbons, e.g. chlorofluorocarbons, has resulted in a thinning of the stratospheric ozone layer facilitating the passage of increased levels of short wavelength (280–320 nm) ultraviolet-B (UV-B) radiation to the biosphere (Kerr, 1988, 1991; Madronich et al., 1995; McKenzie et al., 1999). Whilst rarely damaging in the field, UV-B radiation induces many morphological, physiological and biochemical changes in plants, including the elevation of phenolic compound concentrations in leaf tissue (e.g. Lavola, 1998; Rousseaux et al., 2004; Caputo et al., 2006). These changes influence interactions between plants and herbivores (Ballaré et al., 1996, 2001; Paul and Gwynn-Jones, 2003; Caputo et al., 2006).

In tobacco, solar UV-B radiation and simulated insect herbivory elicit overlapping responses both in terms of gene expression (Izaguirre et al., 2003) and accumulation of phenolic compounds (Caputo et al., 2006; Izaguirre et al., 2007). In particular, both stimuli elicit a down-regulation of genes encoding proteins of the photosynthetic apparatus, and up-regulation of genes that encode enzymes of the octadecanoid pathway, leading to the formation of jasmonic acid (JA) and other oxylipins (Izaguirre et al., 2003). Soybeans grown under ambient and attenuated UV radiation levels showed no differences in insect feeding induced volatile organic compound (VOC) emissions and there were no behavioural responses displayed by herbivore parasitoids, despite plants displaying morphological and physiological changes in response to UV radiation (Winter and Rostás, 2008).

To our knowledge the influence of above ambient UV-B radiation on volatile products of the octadecanoid signalling pathway and monoterpene and sesquiterpene emissions, all important indirect defence responses in plants (e.g. Holopainen, 2004; Dicke and Hilker, 2003), has not previously been addressed. However, Harley et al. (1996) observed that isoprene-emitting *Quercus gambelii* Nutt., grown in the field with supplementary UV-B simulating a 30% depletion of ozone, emitted isoprene in greater amounts than under ambient conditions. Furthermore, Tiiva et al. (2007) reported that supplementary UV-B radiation, simulating a 20% depletion of stratospheric ozone, increased isoprene emissions from a subarctic fen. Isoprene is thought to play a role in increasing the thermal tolerance of photosynthesis (Sharkey et al., 2001), or in protecting plants from oxidative damage (Loreto and Velikova, 2001).

For this study we selected Norway spruce (*Picea abies*), one of the most economically and ecologically important tree species in Finland, as a model on which to test the effects of above ambient UV-B radiation on insect-induced volatile emissions. As Norway spruce also grows in parts of southern Europe, including at high altitudes, we may expect a greater resistance to UV-B than in species restricted to Scandinavia. Indeed, current evidence suggests that conifers have a fairly high degree of tolerance to UV-B radiation (Day et al., 1992; Laakso and Huttunen, 1998; Turtola et al., 2006),

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0269-7491/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.envpol.2008.07.007

with thickness of epidermal tissue, and location, concentration and quality of UV absorbing compounds determining to what extent UV-B penetrates needles (Day et al., 1993). Young needles are more vulnerable to UV-B (DeLucia et al., 1992), which can damage the photosynthetic apparatus, and reduce photosynthetic capacity (Šprtová et al., 1999).

VOC emissions are substantially modified quantitatively and qualitatively by insect feeding, which can be mimicked using defence elicitors, for example methyl jasmonate (MeJA). Application of MeJA to Norway spruce saplings increases emissions of sesquiterpenes by over 30-fold and monoterpenes by approximately 2-fold with greater than 100-fold increases in linalool (Martin et al., 2003). The number of traumatic resin ducts and the concentration of terpenes in stem tissue of conifers are also increased after MeJA application, leading to a reduction in bark beetle (*Ips typographus* L.) colonisation (Erbilgin et al., 2006) and decreased bark area removed by the large pine weevil (*Hylobius abietis* L.) (Heijari et al., 2005). Feeding by white pine weevils on bark induces VOC emissions in Sitka spruce (*Picea sitchensis* (Bong.) Carr), with a similar profile to that of methyl jasmonate-induced plants (Miller et al., 2005). However, jasmonic acid and wounding pre-treatments of Norway spruce did not significantly affect the feeding activity, oviposition or adult emergence of the white pine weevil (*Pissodes strobi* Peck) (Nicole et al., 2006). Conifer bark defence against bark beetles has been thoroughly reviewed by Franceschi et al. (2005).

We hypothesised that long-term exposure to enhanced UV-B radiation would affect the VOC emissions from Norway spruce and in particular monoterpene and sesquiterpene emissions synthesised de novo following herbivore damage. We conducted two field trials in an ultraviolet exposure facility to test this hypothesis. We used weevils (*H. abietis* L., Coleoptera: Curculionidae) which feed on tree bark and can reach outbreak levels on Scots pine and Norway spruce seedlings in Finland to exert biotic stresses, and used an air entrainment system to collect VOCs. We evaluated the effects of weevil feeding and UV-B radiation on localised and systemic induction of VOCs by collecting emissions from whole branches and the tip of the branch located distal to the damage site.

2. Materials and methods

2.1. Trees and insects

Norway spruce (*P. abies* (L.) Karst.) seedlings originating from a registered seed orchard (seed stock 113: Kangasniemi, Finland, 61° 54′ N, 26° 40′ E, 100 m a.s.l) were grown for 3 years at a forest nursery (METLA Suonenjoen tutkimustaimitarha, Suonenjoki, Finland). Seedlings were re-potted in 5 L black polyethylene pots containing a 1:1 mixture of M-6 Sphagnum peat and quartz sand (grain size 0.5–1.2 mm, Maxit Oy, Helsinki, Finland) on May 18, 2004 and transferred to wooden platforms at the Ruohoniemi experimental field site of the University of Kuopio Research Garden (Turtola et al., 2006). During May, plants were watered and nutritionally supplemented twice per week with 0.1% Superex 5 fertilizer (Kekkilä Oyj, Tuusula, Finland). During the summer months (June–August) plants were watered twice per week and nutritionally supplemented once per week. In 2006, when the feeding experiments were conducted, the fertilizer concentration was increased to 0.2%.

In 2007 further measurements were taken from three year old saplings, grown at ambient UV-B, of the same origin as the previous experimental trees. Saplings were planted in 5 L polyethylene pots and grown in the University of Kuopio Research Garden.

Pine weevils *H. abietis* L. were collected from spruce and pine logs at a sawmill area in Suonenjoki (Iisveden Metsä Oy). Adult weevils were stored at 8 °C in plastic containers and provided with cut pine branches as a food source. Weevils were starved for 24 h prior to the start of experiments to encourage feeding.

2.2. UV-B enhancement plots

The UV-irradiation facility is described in detail by Turtola et al. (2006). It consisted of 12 plots, each including a rectangular wooden platform (3.0 × 1.2 m) 2.5 m above which an aluminium frame of the same dimensions was supported by metal poles. Each frame held six equally spaced fluorescent tubes (Philips TL40/12, Philips Lighting BV, Eindhoven, The Netherlands). The plots were arranged in a randomised block design with four replicates of three treatments: ambient control, enhanced UV-A control and enhanced UV-B. The ambient control UV-B levels were achieved by naturally occurring solar radiation, lamps were not functional. The enhanced UV-B treatment was obtained by covering the lamps with cellulose diacetate filters (100 μm; Expopak Oy, Jäminkipohja, Finland), which eliminate UV-C radiation with a wavelength below 290 nm. UV-B and a small amount of UV-A pass through the filter, and consequently a UV-A control was required. The UV-A control was achieved by covering lamps with a polyester film (125 μm; Mylar D, Trafomo AB, Sweden), which eliminates both UV-B and UV-C radiations. The ambient UV-B levels were measured from the centre of the first ambient control plot by a weatherproof erythema detector (type PMA 1102 Analog, Solar Light Co., Glenside, PA, USA). Each enhanced UV-B plot was irradiated relative to this control value, with enhanced UV-B levels measured centrally in each plot (see Table 1 for irradiance levels). The lamp intensity of each plot was adjusted once per minute to maintain the supplementary UV radiation at 30% above the ambient level. When solar irradiation fell below 10 mW m^{-2} the lamps were automatically switched off, and were removed during the winter period. On each platform there were 10 saplings arranged in two parallel lines of 5, the pots within each line were spaced 50 cm apart and the two lines were spaced 70 cm apart.

2.3. Branch tip emission experiment

Nine plots were selected, three for each treatment. Within each plot two trees were selected from one end of the platform to be infested with three weevils and two control trees were selected from the opposite end of the platform (1.5 m from the infested trees) to avoid any priming effect of the infested trees on control trees. One infested tree and one control tree were established per plot on each of two consecutive days at the end of June 2006. Both infested and control trees had a fabric mesh sleeve fastened over the inner half of one branch. In addition, infested trees had three weevils added to the sleeve. Volatiles were collected from the branch tips distal to the sleeves five days (120 h) after the establishment of treatment on the first batch of trees. Rain imposed a delay of one day on the second set of collections, thus these trees had been infested for 6 days. Collections were made from control and infested trees on each platform concurrently. Branch tips were enclosed in pre-cleaned (oven baking: 120 °C, 1 h) multi-purpose cooking bags (polyethylene terephthalate (PET), vol. 3 L, Look, Terinex Ltd., UK) (Stewart-Jones and Poppy, 2006). The bags were fastened around the branch enclosing all the needle growth on the outermost half of the branch (Fig. 1a). Although the bags were 3 L in capacity, this was reduced to approximately 2 L after fastening to trees. One bottom corner of the bag was cut and an air inlet tube was inserted. Air was pumped through a filter and an MnO_4 scrubber to remove ozone and into the bags at a rate of 205 mL min^{-1}. When the bags had expanded and the air had circulated the other bag corner was cut and a stainless steel tube (ATD sample tubes, Perkin Elmer Corp, Norwalk, CT, USA) filled with Tenax TA adsorbent mesh 60/80 (Supelco Inc., Bellefonte, PA, USA) was inserted. Air was pulled through the tube by a vacuum pump (Model (N022AN.18)

Table 1
The monthly means of biologically effective UV-B radiation (kJ m^{-2} d^{-1}) during the two growing seasons

	2005						2006					
	Ambient[a]			UV-B[b]			Ambient[a]			UV-B[b]		
	Mean ± SD	H	L	Mean ± SD	H	L	Mean ± SD	H	L	Mean ± SD	H	L
June	1.954 ± 0.610	3.132	0.673	2.614 ± 1.075	3.932	0.872	3.491 ± 2.232	7.766	0.431	3.988 ± 2.043	9.059	0.533
July	2.524 ± 0.814	3.512	0.553	3.000 ± 1.019	4.321	0.553	2.247 ± 0.790	3.546	0.615	2.857 ± 0.929	4.566	0.866
August	1.788 ± 1.415	5.940	0.134	1.788 ± 1.398	5.940	0.134	1.523 ± 0.542	2.638	0.503	1.883 ± 0.641	3.300	0.580
September	0.490 ± 0.349	1.378	0.037	0.490 ± 0.344	1.378	0.037	0.320 ± 0.243	0.828	0.037	0.413 ± 0.312	1.085	0.044

SD indicates the standard deviation of each monthly mean. H indicates the monthly high and L the monthly low.
[a] Ambient values represent the reference to which the enhanced values were set.
[b] UV-B values are an average of the four enhanced ozone plots.

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