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ECOPHYSIOLOGICAL RESPONSES OF SUBARCTIC SCOTS PINE TO ULTRAVIOLET (UV) RADIATION

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Abstract: The focus of our field studies in the subarctic of Finnish Lapland from 1997 onwards has been to investigate the effect of solar UV radiation on the ecophysiology of Scots pine. Our studies have indicated that solar UV-B_{BE} exclusion during 1997–2002 caused transient effects on the growth of both Scots pine seedlings and saplings, which may not be related to changes in Photosystem II efficiency, however. Studies of the phylloplane fungi of Scots pine needles showed that *Aureobasidium pullulans* (de Bary) Arnaud and *Cladosporium* sp. populations were found to decrease, and *Phoma* sp. to increase, with UV exposure, but there was no UV effect found for total populations. It was also shown that both UV-B radiation and increasing temperature enhance the nitrate reductase (NR) activity of Scots pine needles. On the other hand, our earlier studies have shown that the defence mechanisms (increase in the concentration of soluble phenolics, thickening of the epi- and hypodermal cell layers) of the Scots pine were functioning against ambient solar UV radiation. The daily UV dose rates during 1997–2002 were not very high and in our experiments, the exposure periods of three growing seasons were probably not long enough to cause greater effects that may be cumulative in nature and occur only after longer experimental periods.

Key words: Ultraviolet radiation, Scots pine, *Pinus sylvestris*, subarctic, ecophysiology, defence mechanisms, nitrate reductase (NR) activity, Photosystem II, phylloplane fungi

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INTRODUCTION

In the last 20 years, the largest stratospheric ozone depletion caused by anthropogenic chemicals has been measured over Antarctica but since the early 1990s, ozone depletion has also been observed over the Arctic. It has been predicted that subarctic ecosystems, which are adapted to low fluxes of UV-B, will be subjected to 14% increase in the annual UV dose in 2010–2020 relative to 1979–1992 conditions. The recovery of ozone levels back to the conditions in 1979–1992 depends strongly on the emissions of ozone depleting substances, e.g. CFCs (chlorofluorocarbons) and greenhouse gases (e.g. CO_2), and is not expected until 2040–2050 (Taalas *et al*. 2000). It is obvious that as long as anthropogenic ozone destroying reactions occur in the stratosphere, ozone depletion will continue and especially northern plant life will be confronted with increasing doses of ultraviolet-B radiation (UV-B 280–320 nm) (Weatherhead 1998; Björn 2002).

Many recent reviews on the response of terrestrial plants to UV-B radiation have been published (Laakso & Huttunen 1998; Searles *et al*. 2001; Björn 2002; Day & Neale 2002) some paying special attention to plant defence mechanisms against UV-B radiation (Jones & Hartley 1998; Bornman 1999; Cockell & Knowland 1999; Meijkamp *et al*. 1999; Jordan 2002). Long-term field studies in the subarctic of northern Sweden showed that enhanced UV-B can have both direct and indirect effects on heathland vegetation, ranging from reduced growth in dwarf shrubs to changes in reproductive output, insect herbivory and litter composition, all of which could have implications on the competitive balances between species within the ecosystem (Johanson *et al*. 1995; Gwynn-Jones *et al*. 1999; Phoenix *et al*. 2001; Björn 2002).

In the subarctic of Finnish Lapland, field studies investigating the plant response to UV radiation have basically involved either UV exclusion experiments, which manipulate the spectral balance of natural solar radiation (Turunen *et al*. 1999, 2002; Krywult *et al*. 2002), or UV enhancement experiments with spectral fluorescent lamps being able to predict future UV effects (Kinnunen *et al*. 2001; Laakso *et al*. 2001; Latola *et al*. 2001) (Fig. 1). To date, there is not enough information about the effects of long-term UV exposure on the ecophysiology of Scots pine in subarctic field conditions. The focus of our studies has been to investigate the effect of solar UV radiation on growth, biomass and the defence mechanisms of Scots pine seedlings and saplings.

Material and Methods

The UV experiments conducted in Finnish Lapland during 1997–2003 included both UV exclusion experiments and UV-B enhancement experiments with Scots pine (*Pinus sylvestris* L.) seedlings and saplings (Fig. 1). The UV exclusion experiment was based on different filters placed over plants. The following treatments were applied in our studies: (1) UV-B and UV-A exclusion (a clear acryl plate) and (2) UV-B exclusion (a clear polyester filter) as compared to (3) a control treatment with filter transmitting all UV radiation (a polyethene filter) and (4) ambient plants (without plastic filter). Spectral characteristics of the filters are illustrated in Fig. 2. All the experiments were arranged on a randomized block design with four treatments each replicated from five to ten times (Turunen *et al*. 1999, 2002; Turunen 2000; Krywult *et al*. 2002).

The UV-B enhancement experiments established on natural Scots pine forest and peatland sites in Sodankylä running from 2002 onwards are based on a modulated UV-B exposure system which maintains the UV-B exposure at a constant level of 46% increase corresponding to an ozone loss of about 20%. The UV-B facility at the forest site consists of 21 lamp arrays with a UV-B treatment, UV-A control and ambient control, providing altogether seven replicates of each treatment. The UV-B treatment is achieved by encasing the lamp tubes in a cellulose diacetate film that cuts off the radiation below 290 nm. Because the treatment results in an increase in UV-A, control with enhanced UV-A is included in the experiment. Lamps for this UV-A control are wrapped in a polyester film that excludes all UV-C and UV-B wavelengths. The ambient control treatment with equal shading, as beneath the UV arrays, is achieved with lamp frames.

These studies included measurements of the growth and biomass of Scots pine (Turunen 2000; Turunen *et al*. 2002) as well as chlorophyll fluorescence measurements for PSII (Photosystem II) efficiency (Turunen *et al*. 2002), UV-absorbing compounds particularly soluble phenolics (Turunen *et al*. 1999), light microscopical structure (e.g. epidermal and hypodermal thickness) (Turunen 2000), epiphytic microflora (King 2001) and the nitrogen metabolism (nitrate reductase activity) (Krywult *et al*. 2002) of Scots pine needles.

Results and Discussion

Our studies with the two separate three-year lasting UV exclusion experiments indicated that solar $UV\text{-}B_{BE}$ exclusion during 1997–2002 caused only transient effects on the growth of evergreen Scots pine at the subarctic. After the first year, the height increment of Scots pine saplings was significantly greater in saplings grown under

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Fig. 1. UV exclusion and UV-B enhancement experiments with Scots pine during 1997–2003 in Finnish Lapland. a – A UV exclusion experiment with Scots pine, White birch and Silver birch seedlings in Pallasjärvi (Phot. Jouni Puoskari), b – A UV exclusion experiment with Scots pine saplings with open-top field chambers in Sodankylä (Phot. Minna Turunen), c – a UV-B enhancement experiment with Scots pine seedlings in Sodankylä (Phot. Hanne Perälä), d – A UV-B enhancement experiment with adult Scots pine in Sammaltunturi (Phot. Minna Turunen).


a
b
c
d

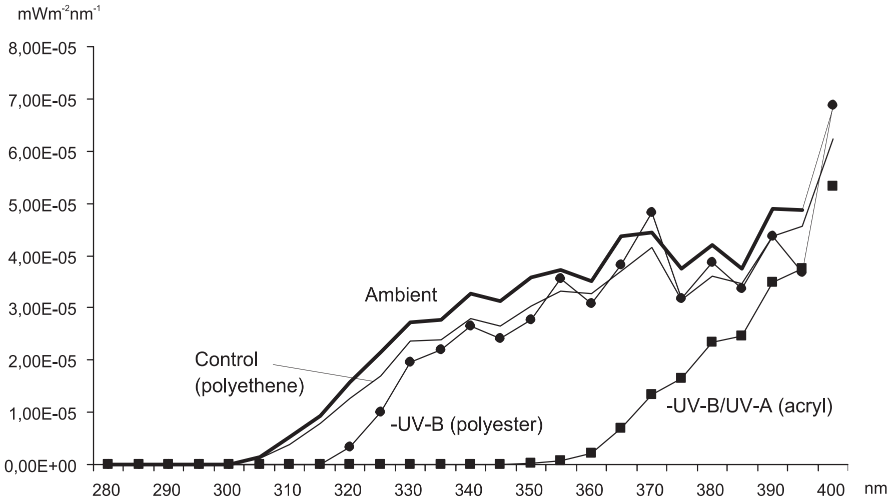

Fig. 2. The spectral characteristics of plastic filters used in the UV-exclusion experiment: ambient irradiance, control (transparent polyethene), UV-B exclusion (polyester), UV-B/UV-A exclusion (transparent acryl) (after Turunen *et al.* 1999, modified).

UV-B/UV-A exclusion when compared to controls (29%), but after the second and the third year, the effect was not statistically significant (Fig. 3). Similarly, UV-B/UV-A exclusion treatment accelerated the height increment (18–20%) of the Scots pine seedlings after the first year, and increased the dry weight of 1-yr-old needles (45–57%) after the second year but at the end of the experiment, no significant effects could be seen (Turunen *et al*. 2002).

The growth and biomass changes due to UV exclusion observed here may not be related to changes in PSII (Photosystem II) efficiencies since there were no significant differences in the chlorophyll fluorescence (F_v/F_m) of either Scots pine seedlings or saplings in the UV exclusion treatments (Turunen *et al*. 2002). Earlier studies report either a decrease or no effect in the photosynthesis (or PSII) of forest tree seedlings due to ambient solar radiation or enhanced UV-B exposure (e.g. Naidu *et al*. 1993; Sullivan & Teramura 1994; Baker *et al*. 1997; Drilias *et al*. 1997; Schumaker *et al*. 1997). It could be speculated that the subtle growth reductions caused by UV radiation here might have occurred indirectly through a shift in carbon allocation into UV-absorbing compounds (Turunen *et al*. 1999) at the expense of the photosynthetic area rather than directly through a reduced photosynthetic rate per unit area (Sullivan *et al*. 1996; Allen *et al*. 1998; Laakso *et al*. 2000).

Phylloplane fungi are exposed to solar irradiance for long periods, and may therefore be

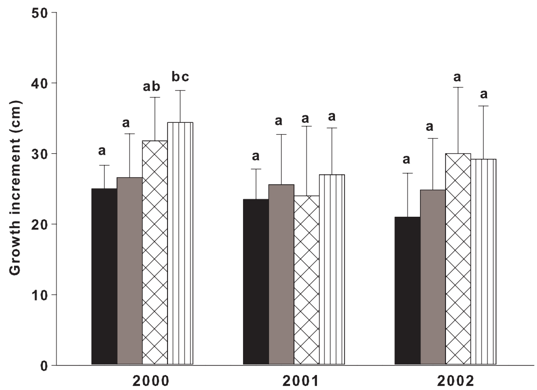

Fig. 3. Growth increment (cm) of Scots pine saplings in a UV exclusion experiment during 2000–2002 in Sodankylä, Finland. See Figs 1b and 2 for the experiment. The treatments are marked as follows: ambient (black), control (grey), UV-B exclusion (cross-hatching), UV-B/UV-A exclusion (vertical stripes). The values are expressed as means with the standard deviations for ten treatment replicates in each column. The different letters (a, b, c) above the columns indicate the statistical significances between treatments at the $p < 0.05$ level within each year and each growing season in Tukey's HSD test.

affected by direct effects of UV-B or indirectly through changes to their host, e.g. due to increased concentration of soluble phenolics (Ayres *et al*. 1996; Newsham *et al*. 1997). For fungi it is easier to adapt to the UV-B exposure than higher plants, as they can reproduce rapidly to evolve to tolerate the higher UV-B environment. This may however lead to different fungal populations being present in higher UV-B environment. For example *Aureobasidium pullulans* (de Bary) Arnaud is able to produce clumps of dark, thick-walled chlamydospores that enable them to survive UV exposure and desiccation. This is particularly important when living on plants such as the Scots pine that increase water retention in response to UV-B (Ingold & Hudson 1993).

In this study, the phylloplane populations of fungi of the needles of Scots pine saplings in the UV exclusion experiment were tested by direct plating and serial dilution and inoculated onto malt extract agar. It was found that *Aureobasidium pullulans* (de Bary) Arnaud and *Phoma* sp. were the dominant types of phylloplane fungi in early summer and autumn, and *Cladosporium* sp. in the mid-summer. The *Aureobasidium pullulans* (de Bary) Arnaud and *Cladosporium* sp. populations were found to decrease, and *Phoma* sp. to increase with UV exposure, but there was no UV effect found for total populations (King 2001) (Fig. 4).

Little is known about the effects of UV radiation on the nitrogen economy of forest trees, particularly on the nitrate reductase (NR) activity in subarctic ecosystems where nitrogen is a growth-limiting factor. Nitrate reductase has a key role in nitrogen fixation and assimilation in most terrestrial plants as it is the enzyme responsible for the reduction of nitrate (NO_3^-) to nitrite (NO_2^-). This step includes the entire metabolic pathway leading to incorporate inorganic forms of nitrogen (nitrate) into amino acids. Although the availability of nitrate from soil is believed to be the most important factor controlling NR activity, the age of the plant tissue, its water status, intensity of light, temperature, the time of the day (due to diurnal changes of enzyme activity), the presence of other active chemical compounds (e.g. oxidants) as well

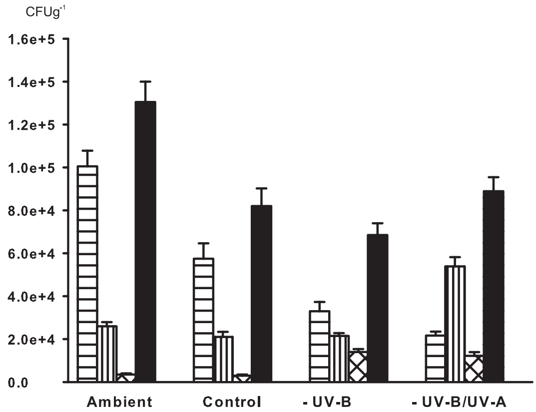

Fig. 4. Dominating fungal populations ($CFUg^{-1}$, colony forming units per gram of needle fresh weight) of 10^{-3} dilution plates on needle surfaces of Scots pine saplings in a UV exclusion experiment in October 2001 in Sodankylä, Finland. Columns are as follows *Phoma* sp. (horizontal stripes) *Aureobasidium pullulans* (vertical stripes), W. yeast (cross-hatching), total populations (black). See Fig. 1b and 2 for the experiment. Modified figure from King (2001).

as UV radiation may influence enzyme activity. Measuring NR activity gives important information about the intensity of nitrate assimilation and when combined with other parameters, it provides a view on the general physiological status of the plants being investigated (Norby 1989; Norby *et al*. 1989; Krywult *et al*. 1996; Krywult & Bytnerowicz 1997).

The response of the Scots pine nitrogen metabolism to UV radiation was studied using both UV exclusion and UV-B enhancement experiments during 2000–2003 in Sodankylä, Finland. The results from both experiments indicate that UV-B radiation is enhancing the nitrate reductase (NR) activity. In the UV exclusion experiment, needles of Scots pine saplings grown under UV-B/UV-A exclusion had the lowest NR activity, UV-B exclusion intermediate and the control the highest. It was also found that during cold days, there was no difference in NR activity between control and ambient but during warm days, Scots pine saplings grown under the control filter had significantly higher NR activity than the ambient plants. This result indicates that the 'greenhouse effect' caused by control filters enhances NR ac-

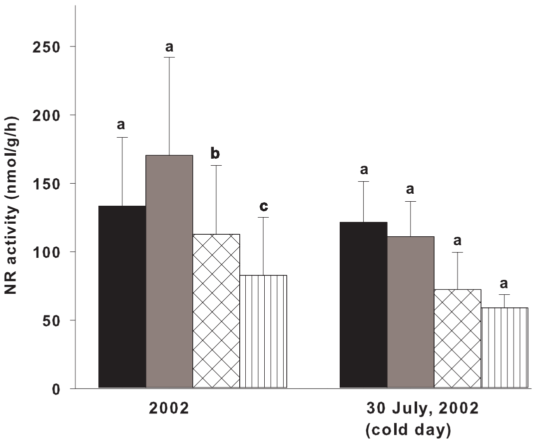

Fig. 5. NRA (nitrate reductase activity) in Scots pine needles during the growing season in 2002 and separately during a cold day on 30 July 2002. See Figs 1b and 2 for the experiment. The treatments are marked as follows: ambient (black), control (grey), UV-B exclusion (cross-hatching) UV-B/UV-A exclusion (vertical stripes). The different letters (a, b, c) above the columns indicate the statistical significances between the treatments at the $p < 0.05$ level in Tukey's HSD test (Krywult *et al*., unpubl. data).

tivity. In the UV-B enhancement experiments with Scots pine seedlings, enhanced UV-B increased NR activity, but there was no difference between the control and UV-A control (Krywult *et al*., unpubl. data) (Fig. 5).

The daily UV dose rates during 1997–2003 were not very high**,** and the exposure periods of three growing seasons in our experiments were probably not long enough to cause greater effects that may be cumulative in nature and occur only after longer experimental periods. It was also shown that the defence mechanisms of the Scots pine saplings and seedlings were functioning against solar UV radiation. The latter is clearly supported by our measurements from the same plants and earlier studies by others which indicated that the epidermal tissue of the foliage of the *Pinus* species contains high quantities of wall-bound and soluble UV absorbing compounds (Schnitzler *et al*. 1996; Turunen *et al*. 1999; Turunen 2000). Longer-term field studies with a large number of treatment replicates (10–20) are needed however in order to detect the cumulative characteristics of the UV responses.

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