



Photo. Aerial view of Adventdalen. Adventdalen is a glaciervalley, with the Adventriver ending in Isfjorden at the background of the photograph. UV lamp plots of Tromsø University and Vrije Universiteit Amsterdam are situated in the glaciervalley as well as at the slope of the glaciervalley at Isdammen (Photograph: J.Rozema).

Stratospheric ozone depletion: high arctic tundra plant growth on Svalbard is not affected by enhanced UV-B after 7 years of UV-B supplementation in the field

Jelte Rozema^{1,*}, Peter Boelen¹, Bjørn Solheim², Matthias Zielke², Alwin Buskens¹, Marieke Doorenbosch¹, Ruben Fijn¹, Jelger Herder¹, Terry Callaghan^{3,4}, Lars Olof Björn⁵, Dylan Gwynn Jones⁶, Rob Broekman¹, Peter Blokker¹ and Willem van de Poll⁷

¹Department of Systems Ecology, Institute of Ecological Science, Climate Center Vrije Universiteit, De Boelelaan 1087, 1081HV, Amsterdam, The Netherlands; ²Department of Biology, University of Tromsø, N-9037, Tromsø, Norway; ³Abisko Scientific Research Station, Royal Swedish Academy of Sciences, SE-981 07, Abisko, Sweden; ⁴Sheffield Centre for Arctic Ecology, University of Sheffield, X Taptonville Road, Sheffield, S10 5BR, UK; ⁵Department of Cell and Organism Biology, Lund University, Lund University, Box 117, SE-22362, Lund, Sweden; ⁶Institute of Biological Sciences, University of Wales, Aberystwyth; ⁷Department of Marine Biology, University of Groningen, Groningen, The Netherlands; *Author for correspondence (e-mail: jelte.rozema@ecology.falw.vu.nl)

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Abstract

The response of tundra plants to enhanced UV-B radiation simulating 15 and 30% ozone depletion was studied at two high arctic sites (Isdammen and Adventdalen, 78° N, Svalbard). The set-up of the UV-B supplementation systems is described, consisting of large and small UV lamp arrays, installed in 1996 and 2002. After 7 years of exposure to enhanced UV-B radiation, plant cover, density, morphological (leaf fresh and dry weight, leaf thickness, leaf area, reproductive and ecophysiological parameters leaf UV-B absorbance, leaf phenolic content, leaf water content) were not affected by enhanced UV-B radiation. DNA damage in the leaves was not increased with enhanced UV-B in *Salix polaris* and *Cassiope tetragona*. DNA damage in *Salix polaris* leaves was higher than in leaves of *C. tetragona*. The length of male gametophyte moss plants of *Polytrichum hyperboreum* was reduced with elevated UV-B as well as the number of *Pedicularis hirsuta* plants per plot, but the inflorescence length of *Bistorta vivipara* was not significantly affected. We discuss the possible causes of tolerance of tundra plants to UV-B (absence of response to enhanced UV-B) in terms of methodology (supplementation versus exclusion), ecophysiological adaptations to UV-B and the biogeographical history of polar plants

Introduction

While the depletion of stratospheric ozone as a consequence of the emission of CFC's has given rise to a reoccurring hole in the ozone layer over the Antarctic since 1974 (Molina and Rowland 1974; Farman et al. 1985), severe ozone depletion during the Arctic spring since the early 1990's has also been observed (McPeters et al. 1996; Newman et al. 1997; <http://www.esa.int>). While stratospheric ozone at the Antarctic spring is reduced from 300 to 100 Dobson Units, i.e. a 60–70% decrease and the ozone depleted area is very extensive, spring arctic ozone levels are rarely less than 150–200 Dobson Units and comprise a smaller depleted area (<http://www.esa.int/export/esaSA/SAHFROOSTCearth>). As a result of stratospheric ozone breakdown, increased solar UV-B reaches the earth (McKenzie et al. 2003; WMO 2003).

In the present research project effects of enhanced UV-B radiation on plant species of a high arctic tundra ecosystem, Adventdalen (78°15' N, 16°30' E) on Svalbard are being studied. A UV-supplementation field experiment was started in 1996 on Svalbard (Björn 2002). The UV lamp supplementation experiment includes a long-term (7 years) and a short term (2 years) field experiment simulating 15 and 30% ozone depletion. A similar UV-B supplementation field experiment is running at the Antarctic Island of Signy (Boelen et al. 2005, this volume). The tundra ecosystems studied on Svalbard, form part of the arctic area with severe ozone depletion during springtime (Newman et al. 1997; <http://www.esa.int>). The UV-B lamp experiments on Svalbard are unique because they cover a longterm (7 years) assessment of effects of enhanced UV-B on tundra plants. The majority of the tundra plants is long-lived and some species (e.g. *Cassiope tetragona*, *Dryas octopetala*) have evergreen leaves and shoots, i.e. perennial aerial parts photosynthesizing more than one summer season and receiving high UV-B radiation for several years. Alternatively the deciduous polar willow is shedding its leaves at the end of the polar summer.

UV-B effects on cyanobacterial nitrogen fixation are discussed by Solheim et al. (2002); Bjerke et al. (2003); Solheim et al. (2006, this volume); (Zielke et al. 2003; Zielke 2004). In addition the study of effects of enhanced UV-B on the arctic tundra is

relevant because the tundra plant species encounter severe climatic stress and may therefore be vulnerable to enhanced UV-B. Furthermore, cold and frost may exacerbate temperature dependent DNA damage caused by UV-B by preventing repair (Li et al. 2002).

It is therefore hypothesized that plant species of the high arctic tundra will be vulnerable to enhanced UV-B. We expect DNA damage to increase with enhanced UV-B with reduced growth and plant biomass as a result. In particular gametophyte moss plant length growth of *Polytrichum hyperboreum* and inflorescence length growth of *Bistorta vivipara* may be reduced. Changes of morphological and ecophysiological parameters may reflect adaptations to UV-B to prevent UV-B damage.

The purpose of the present paper is to describe and analyse effects of enhanced UV-B radiation on tundra species cover, plant density, morphological, ecophysiological and reproductive parameters.

Material and methods

Site descriptions

The field work was done in the summer period (June–September) of 1999, 2000, 2002 and 2003.

The Adventdalen site represents a flat valley floor on glaciofluvial and fluvial deposits with *Salix polaris* and the mosses *Polytrichum hyperboreum* and *Sanionia uncinata* as the dominant tundra plant species (Table 1). *P. hyperboreum* is frequently sporulating (see Figures 1 and 2), while *S. uncinata* bears no spore capsules. The Adventdalen site is ca 5 m above stream level surface and about 200 m away from the stream bed of the river in the center of Adventdalen. The site can be characterized as a moist open tundra vegetation on glaciofluvial and fluvial deposits, mainly sandur (Kristiansen and Sollid 1987). The Isdammen site is near the Isdammen water reservoir of Longyearbyen on a mountain slope, circa 30 m above sea level on marine deposits (Kristiansen and Sollid 1987). The Isdammen site is drier than the Adventdalen site, and the soil has a higher organic matter content.

Vegetation cover of the tundra plant species in the large UV plots irradiated from 1996–2002 was assessed (Tables 2, 3). The tundra plants, e.g. *Salix*

Table 1. List of tundra plant species present at the Isdammen and Adventdalen site.

Plant species	Isdammen	Adventdalen
<i>Salix polaris</i>	x	x
<i>Cassiope tetragona</i>	x	–
<i>Dryas octopetala</i>	x	–
<i>Oxyria digina</i>	x	–
<i>Bistorta vivipara</i> (= <i>Polygonum viviparum</i>)	x	x
<i>Pedicularis hirsuta</i>	x	x
<i>Saxifraga hirculus</i>	x	–
<i>Luzula confusa</i>	–	x
<i>Festuca rubra</i>	–	x
<i>Polytrichum hyperboreum</i>	x	x
<i>Equisetum arvense</i>	–	x
<i>Peltigera aphota</i>	–	x
<i>Sanionia uncinata</i>	x	x
<i>Stellaria crassipes</i>	x	–
<i>Carex misandra</i>	x	x
<i>Saxifraga oppositifolia</i>	x	–
<i>Saxifraga hieracifolia</i>	x	–
<i>Alopecurus borealis</i>	x	–

Nomenclature after Rønning (1996) and Elvebakk (1994).

polaris and *Cassiope tetragona* are small and have only rarely shoots longer than 10–15 cm (Johnstone and Henry 1997, see Figures 1 and 2), and considering the total number of tundra plant species at Isdammen and Adventdalen (about 15–20) (Table 1), the relief (flat valley floor Adventdalen site) and homogeneity of the tundra soil, as well as the obvious visual homogeneity of the tundra vegetation (Figure 1) at Adventdalen and Isdammen, it is reasonable to assume that the 135×270 cm² of the large UV plots cover representative parts of the tundra vegetation.

The spatial distribution of the small UV lamp plots was chosen randomly, but in more detail such that *Salix* and *Cassiope* (Isdammen) or *Salix* and *Polytrichum* (Adventdalen) were well represented. The total cover of the tundra vegetation was about 80% (Isdammen) and 65–70% (Adventdalen) in the 7 year irradiated plots. Total vegetation cover of the small UV lamp plots at Isdammen and Adventdalen was 80% and 65–85% respectively (Table 2).

Experimental design, UV supplementation systems at Isdammen and Adventdalen

Both at Isdammen and Adventdalen eight sets of metal frames holding UV-B fluorescent tubes were

installed over the tundra vegetation since 1996 (Björn 2002).

There are four control sets (ambient UV-B) and four sets simulating 15% ozone depletion (enhanced UV-B) as described by Johanson et al. (1995a, b) and Solheim et al. (2002).

In June 2002, 16 additional mini-UV lamp sets were installed over the tundra vegetation both at Isdammen and Adventdalen adjacent to the existing sets already installed in 1996 (Figure 1). At each site 4 of these mini UV lamp sets are controls (C) with wooden bars replacing the fluorescent UV-B tubes, 4 sets represent UV-A treatments, where Mylar foil blocked UV-B and UV-C, but transmitted UV-A radiation emitted by the lamps, and two sets of 4 lamps with cellulose acetate foil blocking UV-C radiation, transmitting UV-B (and UV-A) simulating 15 and 30% ozone depletion (referred to as UV-B1 and UV-B2), with a longer lamp burning period in the latter case. Radiation spectra of the four treatments applied and details of the UV-B dosimetry and electronics of the lamp switch control system are given by Boelen et al. 2005 (this volume). The sites for the small UV lamps were chosen in such a way that *Salix polaris* and *Polytrichum hyperboreum* were dominantly present (Adventdalen site) or *Salix polaris* and *Cassiope tetragona* (Isdammen site). Treatment and control plots were randomised.

In 2002 and 2003 both the large and small UV supplementation systems operated from mid June until late August-beginning of September. Then the large UV fluorescent lamps were removed, while frames with lamp-holders remained at the tundra. The small lamp systems were removed completely and stored during winter time.

Field sampling and measurements

Vegetation cover

Vegetation cover was assessed in the subplots of the large UV plots (47.5×57.5 cm², Adventdalen; 47.5×76.7 cm², Isdammen) at August 14, 2002 and August 13 in 2003 (Isdammen), July 27, 2002, and August 13, 2003 (Adventdalen) as well as in the small UV plots at August 14, 2002 and July 31, 2003 (Isdammen), July 27 in 2002 and at July 31 in 2003 (Adventdalen) by visual estimation. 1% vegetation cover relates to 5×5 cm² or 5×6 cm² in

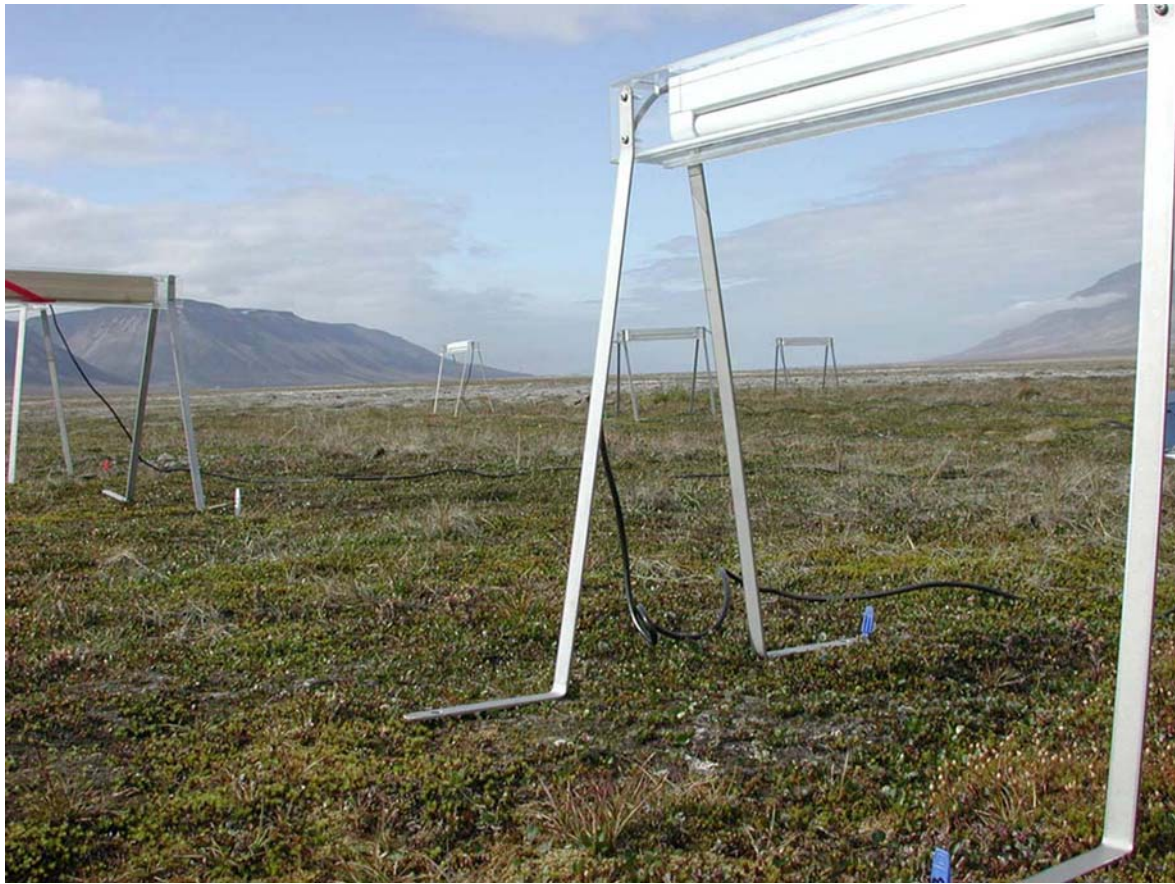


Figure 1. Small UV lamp at the Adventdalen site, with *Salix polaris* and sporulating *Polytrichum hyperboreum* (right foreground). Height of the lamps is 50 cm, the area below the lamps homogeneously UV-B irradiated is $50 \times 60 \text{ cm}^2$. The stainless steel frame was fixed to the tundra soil with tent-pegs. Photograph J. Rozema.

the Adventdalen and Isdammen plots respectively. In addition, digital photographs of all plots have been taken with a NIKON coolpix 990, 995 (3.2 MP) and a 5700 digital camera. The percentage cover estimates have been checked with the digital photographs of the (sub) plots.

Morphological parameters

Leaf thickness measurements Salix polaris

Leaf thickness measurements of *Salix polaris* and collection of leaves in the field were done August 8–August 14, 2002. The thickness of 20 randomly selected leaves, was measured twice with a regular analogue thickness meter, with a resolution between 0.01 and 0.005 mm, and the average value was taken.

Water content, fresh and dry weight of leaves Salix polaris

At least 20 leaves were randomly collected from each plot, stored in plastic bags, and fresh weight was measured in the lab within less than an hour after sampling. The leaves were air dried for 7 days and overnight in a stove (80 °C) and weighed again.

Length growth male gametophyte Polytrichum hyperboreum

Length of male gametophyte moss plants of *Polytrichum hyperboreum* was measured from the last developed antheridium to the top of the longest leaf of 25 randomly chosen moss plants in the large UV lamp plots of Adventdalen, August 11, 2003, (Figure 2). It is assumed that new growth of the male moss plants out of the antheridium tissue started at the same time. Length of other moss

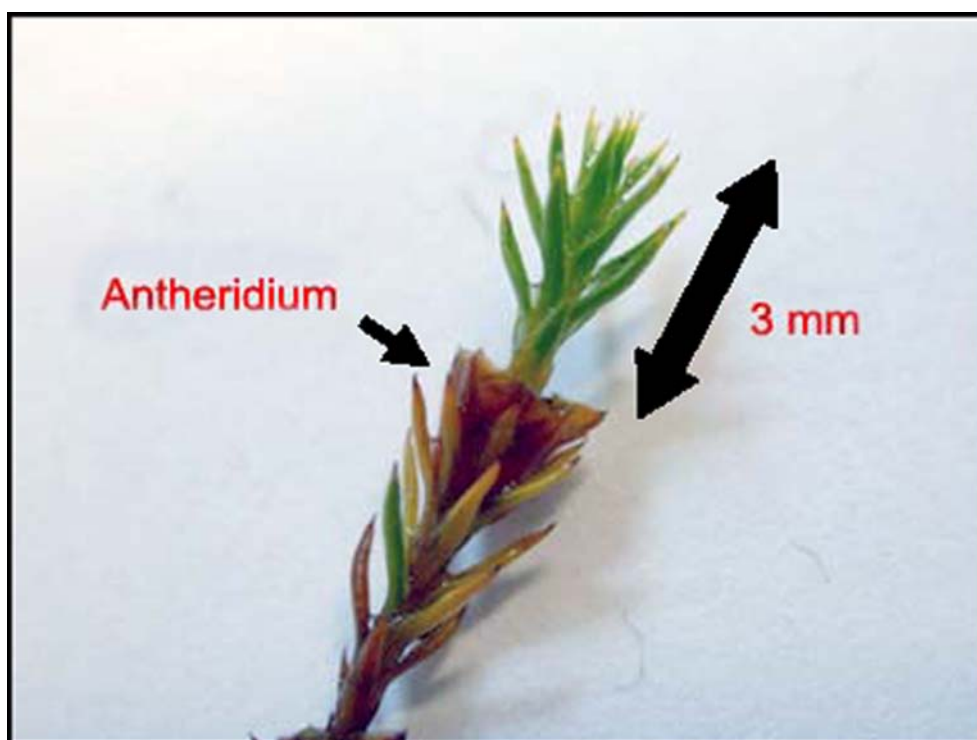


Figure 2. Length growth of male gametophyte moss plant of *Polytrichum hyperboreum* after the last developed antheridium. Photograph Jelger Herder.

Table 2. Vegetation cover of tundra plant species exposed to enhanced UV-B for 6 (2002) and 7 years (2003) (large UV lamp plots), expressed as percentage ground cover, or number of plants per plot (*Oxyria digyna*, *Bistorta vivipara*, *Stellaria crassipes*, *Saxifraga hirculus*).

Site	Isdammen		Adventdalen		
	Control	UV-B	Control	UV-B	
<i>Salix polaris</i>	2002	22.5(2.1)	17.3(1.3) $p=0.386$ n.s.	42.8(2.1)	30.4(3.4) $p=0.125$ n.s.
	2003	31.3(3.1)	26.3(2.4) $p=0.253$ n.s.	42.5(2.5)	42.5(2.5) $p=1.000$ n.s.
<i>Cassiope tetragona</i>	2002	42.4(2.4)	53.5(2.9) $p=0.134$ n.s.	–	–
	2003	48.8(4.3)	45.0(7.9) $p=0.563$ n.s.	–	–
<i>Sanionia uncinata</i>	2002	17.5(1.3)	14.1(1.1) $p=0.275$ n.s.	17.1(2.1)	30.2(4.3) $p=0.282$ n.s.
	2003	11.3(1.3)	6.3(1.3) $p=0.057$ n.s.	15.0(2.0)	18.8(1.3) $p=0.200$ n.s.
<i>Polytr. hyperboreum</i>	2002	–	–	4.9(0.6)	9.1(1.6) $p=0.198$ n.s.
	2003	–	–	16.3(2.4)	13.8(3.1) $p=0.834$ n.s.
<i>Dryas octopetala</i>	2002	5.0(0.9)	5.0(1.3) $p=0.449$ n.s.	–	–
	2003	10.0(3.5)	7.5(1.4) $p=0.704$ n.s.	–	–
<i>Festuca rubra</i>	2002	6.1(6.1)	10.9(10.5) $p=0.961$ n.s.	13.4(4.5)	9.8(1.8) $p=0.490$ n.s.
	2003	–	–	21.3(3.1)	22.5(4.8) $p=0.834$ n.s.
<i>Stellaria crassipes</i>	2002	3.3(1.4)	3.8(2.5) $p=0.978$ n.s.	–	–
<i>Oxyria digyna</i>	2002	2.0(0.5)	3.8(0.4) $p=0.035$ n.s.	–	–
<i>Peltigera aptosa</i>	2002	8.9(4.9)	4.3(4.1) $p=0.497$ n.s.	3.4(1.7)	4.6(0.14) $p=0.145$ n.s.
<i>Bistorta vivipara</i>	2002	2.8(0.8)	2.2(0.3) $p=0.548$ n.s.	12.9(6.8)	21.2(6.9) $p=0.431$ n.s.
<i>Saxifraga hirculus</i>	2002	5.8(3.6)	5.9(2.9) $p=0.865$ n.s.	–	–
<i>Crustose lichen</i>	2002	6.5(1.7)	4.6(1.4) $p=0.481$ n.s.	18.8(2.9)	15.9(5.4) $p=0.656$ n.s.

Average values and standard error of the mean (based on all subsamples). The anova's were carried out with the average values of the four lamp units per treatment.

Table 3. Vegetation cover of tundra plant species *S. polaris*, *P. hyperboreum*, *S. uncinata* and *Cassiope tetragona* exposed to enhanced UV-B for 1 (2002) and 2 (2003) years (small UV lamp plots), for the other species cover estimates of 2002, expressed as percentage ground cover, or number of plants per plot (*Oxyria digyna*, *Bistorta vivipara*).

Treatment		Control	UVA	UVB1	UVB2	<i>p</i> value
Adventdalen						
<i>Salix polaris</i>	2002	38.0(4.2)	42.5(4.8)	41.3(3.1)	55.0(20.4)	0.125
	2003	28.8(11.3)	43.6(6.3)	32.5(3.2)	37.5(6.0)	0.518
<i>Polytrichum hyperboreum</i>	2002	19.0(1.3)	32.5(6.6)	26.3(2.3)	18.0(5.2)	0.119
	2003	40.0(7.4)	38.8(10.7)	28.8(5.2)	28.8(7.5)	0.624
<i>Sanionia uncinata</i>	2002	7.7(1.4)	10.8(3.5)	10.8(5.7)	7.0(3.3)	0.837
	2003	13.3(3.6)	15.0(4.6)	16.3(6.3)	10.8(4.0)	0.892
<i>Equisetum arvense</i>	2002	7.8(3.5)	2.0(1.0)	9.8(9.0)	7.5(5.5)	0.792
<i>Luzula confusa</i>	2002	7.7(2.6)	4.3(5.3)	6.0(2.6)	2.3(1.9)	0.127
<i>Festuca rubra</i>	2002	0.0(0.0)	0.0(0.0)	3.7(2.3)	0.0(0.0)	0.113
<i>Peltigera aphthosa</i>	2002	0.75(0.75)	0.75(0.75)	0.50(0.28)	1.30(1.25)	0.932
<i>Bistorta vivipara</i>	2002	4.8(1.7)	4.5(0.6)	4.0(2.0)	2.5(1.5)	0.739
<i>Crustose lichen</i>	2002	35(5.4)	13.5(7.1)	17.5(6.0)	18.7(6.3)	0.129
Isdammen						
<i>Salix polaris</i>	2002	18.8(3.8)	22.0(7.3)	48.7(5.7)	33.1(2.7)	0.003
	2003	20.0(0.0)	22.5(6.0)	15.0(2.0)	28.8(3.1)	0.058
<i>Cassiope tetragona</i>	2002	26.3(6.6)	28.8(7.5)	20.8(8.3)	4.5(3.9)	0.100
	2003	41.3(12.5)	33.8(13.0)	47.5(20.3)	7.0(6.0)	0.018
<i>Polytrichum hyperboreum</i>	2002	0.25(0.25)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.426
	2003	0.8(0.8)	0.8(0.8)	0.0(0.0)	9.8(0.8)	
<i>Sanionia uncinata</i>	2002	35.8(6.4)	41.3(2.9)	21.0(3.0)	26.8(4.4)	0.032
	2003	13.8(2.4)	18.8(1.3)	11.3(2.4)	21.3(8.8)	0.264
<i>Dryas octopetala</i>	2002	5.5(2.2)	5.0(1.2)	8.3(7.2)	7.8(2.4)	0.377
	2003	6.0(3.0)	8.3(1.8)	19.5(13.6)	22.5(12.5)	0.307
<i>Stellaria crassipes</i>	2002	0.0(0.0)	0.0(0.0)	2.5(2.5)	12.5(12.5)	0.483
<i>Festuca rubra</i>	2002	6.7(6.4)	0.2(0.2)	23.9(13.2)	0.6(0.1)	0.150
<i>Oxyria digyna</i>	2002	1.0(1.0)	1.5(0.9)	0.0(0.0)	0.0(0.0)	0.360
<i>Peltigera aphthosa</i>	2002	0.0(0.0)	0.3(0.3)	1.25(0.5)	0.7(0.4)	0.006
<i>Bistorta vivipara</i>	2002	17.5(4.3)	4.3(2.0)	4.0(2.3)	29.3(6.9)	0.004
<i>Saxifraga hirculus</i>	2002	0.25(0.25)	0.25(0.25)	0.0(0.0)	0.25(0.25)	0.802
<i>Crustose lichen</i>	2002	10.5(5.1)	0.5(0.5)	3.3(1.9)	5.0(1.7)	0.147

Average values and standard error of the mean (based on all subsamples). The anova's were carried out with the average values of the subplots of the four lamp units per treatment.

plants, bearing a sporophyte or not, was measured with a ruler from the base to the tip of the longest leaf.

Ecophysiological parameters

UV-B absorbance acid methanol leaf extracts *Salix polaris*. About 5 mg dried leaf material of *Salix polaris* was ground with 0.5 ml methanol, then another 4.5 ml methanol was added and the suspension was transferred into a Pyrex tube filled with 4 ml of a methanol:H₂O:HCl (79:20:1) mixture, heated (90 °C) in a waterbath for 60 min, vortexed. The samples were centrifuged at 2500 rpm for 5 min. UV-B absorption (280–400 nm) was measured with a Shimadzu UV-160PC spectrophotometer.

Total phenolic content *Salix polaris* leaves

About 25 mg of dried *Salix polaris* leaves was ground with 0.5 ml 50% methanol, put into pyrex tubes with 2 ml 50% methanol. The tubes were shaken (1 h) and centrifuged at 2500 rpm (5 min). 50 µl of the extract was mixed with 3.95 ml distilled water. About 250 µl of the Folin Ciocalteu reagent (Merck) was added and after exactly 8 min 750 µl Na₂CO₃ (20 g/100 ml) was added. Absorbance was measured after 2 h at 760 nm with a Shimadzu UV-160PC spectrophotometer.

DNA damage

Leaves of tips of *Salix polaris* and *Cassiope tetragona* branches were sampled August 8, 2002,

at the Adventdalen and Isdammen site, and stored at -85°C within 1 h after leaf sampling. DNA was extracted from three leaves (*Salix*) or one or two smaller pedicels (*Cassiope*) following a protocol described in de Bakker (in prep.). In short: DNA damage was assessed as cyclobutane thymine dimers, and was quantified using the H3 antibody (Roza et al. 1988; Boelen 2002) applying an immunoblot procedure, see van de Poll (2003) for methodological details.

Reproductive parameters

Male and female catkins Salix polaris. Male and female catkins of *Salix polaris* were counted within squares of $20 \times 20 \text{ cm}^2$ in the small UV plots at Adventdalen. The apparent sex ratio was calculated using the ratio of maximum numbers of female and male catkins counted. It is based on visible above ground male or female flowers. It was not possible to determine an absolute sex ratio based on the number of male and female plants which would require destructive sampling of aboveground and belowground plant parts.

Inflorescence length Bistorta vivipara. Length of all inflorescences of *Bistorta vivipara* was measured at August 4 and 5, 2003, in the plots of the small UV lamps irradiated for 2 years at Adventdalen and at the site of the large UV lamps at Isdammen. The *Bistorta vivipara* plants were randomly distributed in the plots.

Statistical analysis. Effects of enhanced UV-B on vegetation and plant parameters were tested with a one way anova (with the Bonferroni test), with four replicates per treatment for the large and small UV lamp systems. In addition to analysis of UV-B effects after 6 or 7 years (large UV lamp systems) and 1 or 2 years of irradiance (small UV lamps) plant cover changes from 2002 to 2003 as affected by UV-B were statistically analysed. Normality was tested with Shapiro-Wilk or Kolmogorov-Smirnoff. Homogeneity of variance was tested with the Levene statistic. In cases where variances were not homogeneous, and transformations did not deliver homogeneity the non-parametric Mann-Whitney (2 independent samples) or Kruskal and Wallis (k independent samples) tests were applied following procedures

described in SPSS 10.1 and background knowledge derived from Sokal and Rohlf (1995) and Quinn and Keough (2002).

Results

Plant cover, plant growth and plant density

Based on the vegetation cover estimated in the subplots of the large UV lamps there is a non significant decline in the cover of *Salix polaris* at Adventdalen in 2002, and at Isdammen in 2002 and 2003 (Table 2). Also, plant cover of *Cassiope tetragona*, *Sanionia uncinata* and *Polytrichum hyperboreum* and other tundra species was not significantly affected by enhanced UV-B after 6 and 7 years of irradiance (Table 2).

Vegetation cover of the tundra species in the small UV plots after 1 and 2 years of irradiation with UV-A, UV-B1 and UV-B2 radiation treatment is summarized in Table 3. Since the mini lamps were installed June 2002 the cover data for 2002 are regarded a test for homogeneity of the distribution of the cover of the tundra species per plot. Cover of species with p -values < 0.05 is not homogeneously distributed over the four treatments.

These plant cover data for separate plots may eventually allow year-to-year comparisons with elevated UV-B which could reveal UV-B effects. Since estimation of vegetation cover in 2002 and 2003 was differing two weeks for the plots with the small lamps, no proper year to year comparisons could be made as yet.

Overall, after 6 and 7 years of irradiance, UV-B has not significantly affected plant cover of any of the tundra plant species studied.

The length growth of male gametophyte moss plants of *Polytrichum hyperboreum*, measured from the last developed antheridium appeared to be reduced from 3.25 (s.e.m 0.06) mm to 2.20 (s.e.m 0.05) mm with elevated UV-B ($p=0.015$), length of other moss plants in the plots was not affected by the UV-B treatments.

The number of *Pedicularis hirsuta* plants per plot did significantly decrease with enhanced UV-B both at Isdammen ($p=0.047$) and at Adventdalen ($p=0.027$), (Figure 4)

Morphological and ecophysiological parameters

Leaf area of *Salix polaris* (per leaf) was not significantly decreased with enhanced UV-B for Adventdalen plants (Table 4), but increased with enhanced UV-B for Isdammen plants.

Leaf thickness was not affected by UV-B, neither was fresh and dry weight per leaf, leaf UV-B absorbance, total leaf phenolic content, and water content (Table 4).

Table 4. Effects of enhanced UV-B radiation on leaf thickness, leaf area, UV-B absorbance, total phenolic content, fresh and dry weight per leaf, water content of arctic tundra plant species *Salix polaris* and *Cassiope tetragona* sampled July 2002 at Isdammen en Adventdalen after 1 and 6 years of UV-B radiation simulating 15% ozone depletion or 30% ozone depletion.

	Isdammen	Adventalen
<i>Salix polaris</i>		
Leaf thickness (mm)		
6 year radiation	$p=0.098$ n.s.	$p=0.192$ n.s.
1 year radiation	$p=0.001$ sign.	$p=0.092$ n.s.
Leaf area (mm ²)		
6 year radiation	$p=0.001$ sign.	$p=0.651$ n.s.
1 year radiation	$p=0.121$ n.s.	$p=0.976$ n.s.
UV-B absorption leaves (absorbance area/mg dry weight)		
6 year radiation	$p=0.125$ n.s.	$p=0.912$ n.s.
1 year radiation	$p=0.626$ n.s.	$p=0.247$ n.s.
Total phenolic leaves (g tannic acid/g dry weight)		
6 year radiation	$p=0.968$ n.s.	$p=0.861$ n.s.
1 year radiation	$p=0.022$ sign.	$p=0.127$ n.s.
Fresh weight per leaf (g)		
6 year radiation	$p=0.182$ n.s.	$p=0.707$ n.s.
Dry weight per leaf (g)		
6 year radiation	$p=0.064$ n.s.	$p=0.720$ n.s.
Water content (% dry weight)		
6 year radiation	$p=0.202$ n.s.	$p=0.782$ n.s.
1 year radiation	$p=0.68$ n.s.	$p=0.444$ n.s.
<i>Cassiope tetragona</i>		
Water content		
6 year radiation	$p=0.236$ n.s.	
1 year radiation	$p=0.065$ n.s.	
Fresh weight per leaf (g)		
6 year radiation	$p=0.101$ n.s.	
Dry weight per leaf (g)		
6 year radiation	$p=0.172$ n.s.	

p -Values of one way anova.

DNA damage did not increase with exposure to enhanced UV-B in *Salix polaris* and *Cassiope tetragona* (Table 5). However DNA damage in *Salix* leaves was larger than in *C. tetragona* ($p=0.001$).

Reproductive parameters

The number of male and female catkins of *Salix polaris* per plot and the ratio of this under the small UV lamps was assessed in Adventdalen in 2002 and 2003 (Figure 3), there was no significant effect of enhanced UV-B on the apparent sex ratio (n female/ n male catkins) in 2002 ($p=0.338$), and in 2003 ($p=0.434$), but the apparent sex ratio was male biased, i.e. significantly smaller than 1.0 ($p=0.05$ and $p=0.00$ in 2003). The number of female catkins in 2002 and 2003 did not differ significantly ($p=0.101$), neither did the number of male catkins ($p=0.150$). The UV-B treatment did not affect the number of female or male catkins in 2002 and 2003 ($p=0.760$; $p=0.212$; $p=0.063$; $p=0.499$, respectively).

The inflorescence length of *Bistorta vivipara* was measured 4th and 5th of August 2003 both under the large (31.5–31.9 mm) and the small UV lamps (26.3–37.7 mm). There was no significant effect of the UV-B treatment on the inflorescence length ($p=0.877$ and $p=0.855$, respectively).

Discussion

Plant cover, plant growth, plant density and plant morphology

There were no significant UV-B effects on plant cover and plant parameters of most of the tundra plants e.g. *Salix polaris*, *Cassiope tetragona*, *Sanionia uncinata* and *Polytrichum hyperboreum* after 7 and 2 years of UV radiation (Tables 3, 4). The evergreen ericaceous dwarf shrub *Cassiope tetragona* is considered to be rich in secondary compounds such as the flavonoids myricetin and quercetin (Björn et al. 1997) with a characteristic, apparent smell and is not grazed by the reindeer and appears to be tolerant to enhanced UV-B (Callaghan et al. 1989).

The compound responsible for the characteristic smell of *Cassiope* leaves has recently been identified as eudesmol (Blokker et al. 2005). Probably the smell of eudesmol acts as a deterrent and prevents reindeer grazing.

Table 5. DNA damage expressed as CPD's per megabase DNA.

Treatment	Control	UVA	UVB1	UVB2	<i>p</i> -value
<i>Salix polaris</i>					
Isdammen 2 years	5.4(3.5)	6.9(6.3)	3.1(1.1)	8.7(3.5)	0.31
Isdammen 6 years	7.7(3.1)	–	3.0(2.3)	–	0.05
<i>Cassiope tetragona</i> 2 years	1.1(0.8)	1.8(2.1)	2.6(3.4)	2.3(0.8)	0.27
<i>Cassiope tetragona</i> 6 years	0.7(0.6)	–	0.2(0.3)	–	0.28
<i>Salix polaris</i>					
Adventdalen 2 years	8.8(3.5)	7.0(6.0)	7.2(6.1)	7.0(5.3)	0.96
Adventdalen 6 years	7.5(5.7)	–	5.0(4.1)	–	0.69

Average values of 4 replicate samples and standard deviation. P values of 1 way anova's.



Figure 3. Male (a) and female (b) catkin of *Salix polaris*. Photograph Jelger Herder.

Cover of the moss *S. uncinata* was not affected by enhanced UV-B, which agrees with results of Lud et al. (2002), who regard the moss *S. uncinata* a UV-B tolerant Arctic and Antarctic moss species. We have not observed spore capsules of *S. uncinata* at Isdammen and Adventdalen and obviously this moss species is reproducing vegetatively at the Svalbard tundra. By contrast, *P. hyperboreum* is frequently sporulating in the arctic summers (Table 2). Measured plant parameters (Table 4) as well as quantification of DNA damage of *Salix polaris* cannot easily be related to other plant parameters. Leaf area is not significantly reduced, the leaf weight of high UV-B plants is not reduced, neither is leaf thickness significantly affected by enhanced UV-B.

Individual *Salix* leaves develop, grow and photosynthesize during one tundra summer season (June-end of August) and then senesce, and for the growth, morphological and ecophysiological parameters studied here effects of enhanced UV-B would

be similar for the 6 year and 1 year irradiated plots, assuming such effects to occur each summer in developing leaves. Leaf buds of *Salix polaris* for the forthcoming summer season are already developed at the end of the preceding growing season, and have been exposed to enhanced UV-B in that season.

Plant ecophysiological parameters

There were only few significant effects of enhanced UV-B on leaf water content, leaf UV-B absorption and leaf phenolic content measured in *S. polaris* and *C. tetragona* (Table 4).

Leaf phenolic content increased with enhanced UV-B at the small lamps at Isdammen, but not at Adventdalen and leaf UV-B absorbance was unaffected for *S. polaris* at the large and the small UV lamp systems.

DNA damage in *Salix* leaves did not increase with enhanced UV-B (Table 5), neither was there a

DNA damage increase in *Cassiope* leaves with enhanced UV-B. However leaf DNA damage in *Salix* was significantly greater than in *Cassiope*. Lud et al. (2002) found UV-B induced DNA damage in *S. uncinata*, combined with efficient photorepair and the circumbipolar moss was judged UV-B tolerant (cf Rouseaux et al. 1999; Boelen et al. 2005).

Even with more plant growth, morphological or physiological evidence, it may remain difficult to predict or explain unambiguously a change in plant cover. Often the effect of enhanced UV-B cannot be characterized as inhibition or damage, but rather as a photomorphogenetic effect. Shoot length growth of *Deschampsia antarctica* was decreased, but the number of tillers increased with enhanced UV-B (Rozema et al. 2001a) and the RGR remained unaffected. Also within one species parameters may respond differentially to enhanced UV-B. Male plants of *P. hyperboreum* growing after having developed antheridia, showed reduced length growth with enhanced UV-B, but no such effect was seen in *P. hyperboreum* moss plants bearing no sporophytes nor antheridia. We have no further evidence to support the assumption that the measured length growth of the last developed antheridium, started at the same time. Tagging other moss plants of *P. hyperboreum* with woollen threads indicated length growth of moss plants to be about 1 mm per summer season. This may imply that the measured length growth of male moss gametophyte plants may be the result of at least three summer seasons. This would indicate that antheridium formation in moss plants in the tundra will not take place every year, as occurs with *Polytrichum commune* in Dutch peat lands (Rozema et al. unpublished). It is unknown if sporophyte formation in the tundra occurs every year or less frequently.

Reproductive parameters

Salix polaris is a dioecious deciduous perennial woody tundra plant (Rønning 1996; Elvebakk 1994), with male and female catkins on separate plants and leaves rapidly developing when frost and snow disappear in June (Figure 3). Shining and hairy leaves of *Salix polaris* are in a more or less horizontal position, less than a few centimeters above the tundra soil, remain green until mid

August and then senesce. Individual male and female plants vary in size, but generally length of stems and rhizomes close to the tundra soil surface is less than 10–20 cm (Callaghan et al. 1989; Havstrom et al. 1995).

We found no effects of enhanced UV-B on the number of male and the number of female catkins of *Salix polaris*, neither there was a UV-B effect on the apparent sex ratio. More male catkins than female catkins were found. This male biased sex ratio is in contrast with female biased sex ratio's for arctic dwarf willows including *Salix polaris* reported by Crawford and Balfour (1983, 1990). Preferential herbivory by Svalbard reindeer has been suggested to explain female biased sex ratio's in *Salix polaris* (more female flowers than male flowers) (Dormann and Skarpe (2002). Exclusion of reindeer possibly preferring to graze on male *Salix* flowers led to an increase in male flowers. A fence surrounds the large UV lamp plots and there is no or very limited grazing by reindeer in our large (installed 1996) and small UV (installed 2002) lamp plots at Isdammen and Adventdalen. The small UV lamps are close to the large UV lamps and reindeer grazing has not been observed in 2002 and 2003. A male biased sex ratio in five wind pollinated gymnosperms and angiosperms has been attributed to dry conditions (Freeman et al. 1976). Male plants preferred dry sites to maximize pollen dispersal and female plants preferred moist sites maximizing seed set.

With the aim to determine UV-B absorbing compounds in pollen (Rozema et al. 2001b, c) male catkins have been collected in all UV plots. Collecting male flowers does not affect the sex ratio of *Salix polaris* since the number of male catkins per plot did not differ in 2002 and 2003. At the end of the summer season dried and senesced male flowers drop off the parental plant naturally.

Of the tundra species studied, the number of *Pedicularis hirsuta* plants per plot, both at Isdammen en Adventdalen reduced (Figure 4). *Pedicularis hirsuta* is a perennial hemiparasite with a taproot and root xylem bridges to neighbouring tundra plants, providing the hemiparasite with xylem water and nutrients. So far, clear ecophysiological causes of reduced numbers of *Pedicularis* plants in the UV-B plots remain unclear. Small seedlings of *Pedicularis* occur within the plots (personal observation), and if no root contact with host tundra plants occurs, these seedlings die.

Chlorophyll development is obviously impaired in this hemiparasite and one may speculate that a limited capacity of synthesizing protective UV-B absorbing compounds may cause *Pedicularis* to be sensitive to enhanced UV-B. Arctic hemiparasites often have nutrient-rich leaves with little phenolic or tannin content and therefore generally decompose faster than surrounding species (Qusted et al. 2003).

Inflorescences of *Bistorta vivipara* develop within one summer season, and will be exposed during this length growth to UV-B treatments. However unlike the density of *P. hirsuta* plants, the inflorescence length of *Bistorta* was not affected by UV-B.

Enhanced UV-B does not affect tundra plant growth

The absence of UV-B effects in many plant growth, morphological and ecophysiological

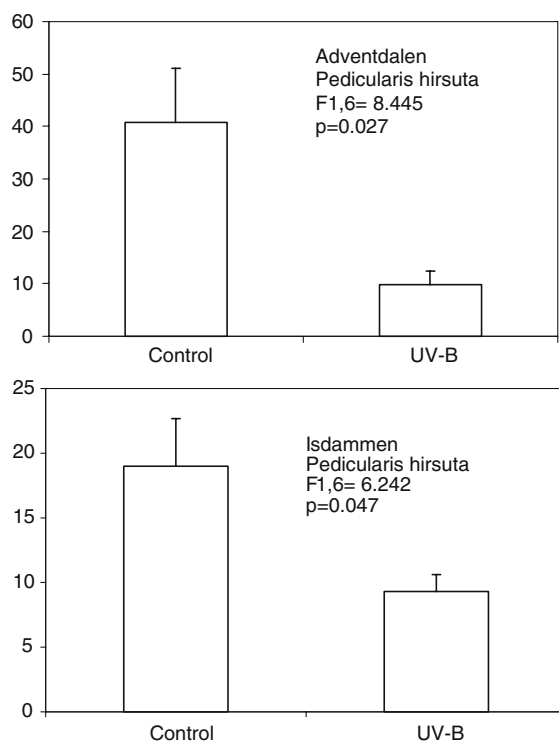


Figure 4. Effect of 6 year exposure (1996–2002) to enhanced UV-B, simulating 15% ozone depletion, on the number of *Pedicularis hirsuta* plants per plot. Mean values with standard error of the mean.

parameters for these tundra plants, as well as the lack of reduction of plant cover or numbers per plot (except for plant density *Pedicularis hirsuta* in Isdammen and Adventdalen, and the length growth of male gametophytes of *P. hyperboreum*) indicates that many tundra species are tolerant to enhanced UV-B. This would indicate that many plants species of tundra ecosystems do not differ in their response to enhanced UV-B from species of other terrestrial ecosystems of other climate zones (Rozema et al. 1997; Caldwell et al. 1998; Sullivan and Rozema 1999; Searles et al. 2001, 2002; Paul 2001; Aphalo 2003; Paul and Gwynn Jones 2003). However other causes may also explain absence of UV-B effects, which we discuss below.

Spatial variation and statistical power

Obvious spatial variation in nitrogen fixation by terrestrial cyanobacteria homogeneously irradiated by the UV lamps at Adventdalen and Isdammen has also been recognized by Solheim et al. 2006 (this volume). Similar spatial variation in the distribution of tundra plants may prevent detection of UV-B treatment effects on for example percentage cover of *Salix polaris* (Table 2).

An experimental design with a larger number of replicated UV plots than the current four replications per treatment would improve statistical power, though logistically it would be more complicated and expensive. Limited power of the current experimental design may obstruct detection of (small) UV-B effects.

UV-B supplementation and UV-B exclusion experiments in polar regions

Only few UV-B enhancement field experiments or UV-B field manipulations experiments in high arctic or antarctic regions are known to us (Arctic Svalbard: Björn 2002; Solheim et al. 2002; Bjerke et al. 2003; Zielke et al. 2003; Zielke 2004; Rozema et al. 2005; Antarctic: Day et al. 1999, 2001; Ruhland and Day 2000; Rozema 1999; Rozema et al. 2001a; Lud et al. 2002; Newsham 2003). There are some more similar studies in the sub-arctic (e.g. Johanson et al. 1995a, b; Björn et al. 1997; Gehrke 1998, 1999; Phoenix et al. 2001, 2003; Sonesson et al. 2002; Semerdjieva et al.

2003) and subantarctic (Rousseaux et al. 1999; Ballaré et al. 2001; Searles et al. 2001, 2002; Robson et al. 2003a,b,c) which are partially comparable to the polar studies. Most of these reports indicate small, subtle or no UV-B effects (see Rozema et al. 2005). UV-B exclusion experiments with UV-B absorbing foils in the field indicate length growth reduction of *Deschampsia antarctica* with UV-B levels varied from below ambient UV-B to near ambient UV-B (Day et al. 1999; Ruhland and Day 2000). Such UV-B exclusion manipulations may be relevant from an ecological point of view, but they do not demonstrate that growth of Antarctic flowering plants is reduced with enhanced UV-B as may be shown with UV-B supplementation in the field (Figure 5). With UV-B supplementation, UV-B is varied from ambient levels to above ambient levels, e.g. from 2.5 kJ UV-B_{be} m⁻² day⁻¹ to 5.0 kJ UV-B_{be} m⁻² day⁻¹. Because of different UV-B levels involved the outcome of UV-B exclusion field studies cannot be compared with those of UV-B supplementation field studies. In addition, the UV-B plant growth response curve (Figure 5) shows that growth reduction related with UV-B varied from ambient to above ambient is much less (18%) than from below ambient to near ambient UV-B (78%).

Based on the above, growth reduction with enhanced UV-B as in the Isdammen and Adventdalen UV lamp supplementation experiment is expected to be limited and not easy to detect.

In case absence of UV-B effects reflects real tolerance of tundra plants to enhanced UV-B, adaptations to UV-B may be expected such as effective UV-B absorbing pigments.

In a recent meta-analysis of about 100 reports of field studies of enhanced UV-B effects Searles et al. (2001) indicate a 10% increase of UV-B absorbing compounds with 15% ozone depletion in plant species of terrestrial ecosystems from various climate zones.

UV-B absorbing compounds may be induced by UV-B, e.g. the flavonoid quercetin however constitutively high levels of other UV-B pigments of tundra plants will also prevent UV-B damage, and may explain absence of UV-B induced UV-B damage.

Tolerance of polar plants to enhanced UV-B also implies that there is no apparent vulnerability of polar plants to frost, cold, short summer season

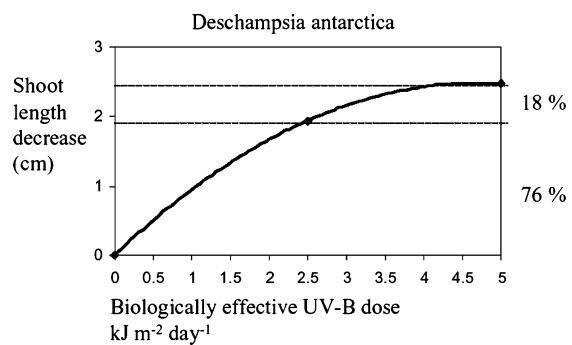


Figure 5. Shoot length decrease (cm) of *Deschampsia antarctica* relative to shoot length at 0 kJ m⁻² day⁻¹ of plants exposed to 0, 2.5 or 5.0 kJ m⁻² day⁻¹ biologically effective UV-B for 78 days. Plants were grown in a climate room (4 °C, PAR 150 μmol m⁻² s⁻¹, 75% Relative Humidity). Recalculated after Rozema et al. (2001a).

and that low temperatures do not markedly inhibit repair of DNA damage.

From a historical and biogeographical point of view, the tundra biome and ecosystems at Svalbard are relatively young and recent tundra vegetation of the northern hemisphere will have developed since the last glacial period, i.e. the Younger Dryas some 11,000 years ago (Isarin 1997) from northward migrating plants originating from lower than polar latitudes with higher natural solar UV-B fluxes and associated tolerance to UV-B.

Perspective

Although the use of CFC's has been phased out, recovery of stratospheric ozone may last until 2050–2060 (World Meteorological Organization 2002) and enhanced UV-B levels may occur several decades.

Ozone depletion is most severe in the Antarctic and Arctic spring and UV-B levels at ground level in polar regions are increased accordingly (Rozema et al. 2005; McKenzie et al. 2003; Rex et al. 2004). While terrestrial Antarctic ecosystems have only two species of higher plants: *Deschampsia antarctica* and *Colobanthus quitensis* (Smith 1994; Convey et al. 2005), more than 160 higher plant species occur in the high arctic tundra ecosystem of Svalbard (Elvebakk 1994; Rønning 1996), allowing more species interactions and feedbacks and perhaps providing a more general, representative ecosystem response to enhanced UV-B than the

more simple two-species Antarctic ecosystem (Rozema et al. 2005).

The world-wide unique longterm (1996–2004) UV-B supplementation field experiment at the Adventdalen and Isdammen high arctic tundra ecosystem should therefore be continued.

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