

Impacts of long-term enhanced UV-B radiation on bryophytes in two sub-Arctic heathland sites of contrasting water availability

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• **Background and Aims** Anthropogenic depletion of stratospheric ozone in Arctic latitudes has resulted in an increase of ultraviolet-B radiation (UV-B) reaching the biosphere. UV-B exposure is known to reduce above-ground biomass and plant height, to increase DNA damage and cause accumulation of UV-absorbing compounds in polar plants. However, many studies on Arctic mosses tended to be inconclusive. The importance of different water availability in influencing UV-B impacts on lower plants in the Arctic has been poorly explored and might partially explain the observed wide variation of responses, given the importance of water in controlling bryophyte physiology. This study aimed to assess the long-term responses of three common sub-Arctic bryophytes to enhanced UV-B radiation (+UV-B) and to elucidate the influence of water supply on those responses.

• **Methods** Responses of three sub-Arctic bryophytes (the mosses *Hylocomium splendens* and *Polytrichum commune* and the liverwort *Barbilophozia lycopodioides*) to +UV-B for 15 and 13 years were studied in two field experiments using lamps for UV-B enhancement with identical design and located in neighbouring areas with contrasting water availability (naturally mesic and drier sites). Responses evaluated included bryophyte abundance, growth, sporophyte production and sclerophylly; cellular protection by accumulation of UV-absorbing compounds, β -carotene, xanthophylls and development of non-photochemical quenching (NPQ); and impacts on photosynthesis performance by maximum quantum yield (F_v/F_m) and electron transport rate (ETR) through photosystem II (PSII) and chlorophyll concentrations.

• **Results** Responses were species specific: *H. splendens* responded most to +UV-B, with reduction in both annual growth (–22%) and sporophyte production (–44%), together with increased β -carotene, violaxanthin, total chlorophyll and NPQ, and decreased zeaxanthin and de-epoxidation of the xanthophyll cycle pool (DES). *Barbilophozia lycopodioides* responded less to +UV-B, showing increased β -carotene and sclerophylly and decreased UV-absorbing compounds. *Polytrichum commune* only showed small morphogenetic changes. No effect of UV-B on bryophyte cover was observed. Water availability had profound effects on bryophyte ecophysiology, and plants showed, in general, lower growth and ETR, together with a higher photoprotection in the drier site. Water availability also influenced bryophyte responses to +UV-B and, in particular, responses were less detectable in the drier site.

• **Conclusions** Impacts of UV-B exposure on Arctic bryophytes were significant, in contrast to modest or absent UV-B effects measured in previous studies. The impacts were more easily detectable in species with high plasticity such as *H. splendens* and less obvious, or more subtle, under drier conditions. Species biology and water supply greatly influences the impact of UV-B on at least some Arctic bryophytes and could contribute to the wide variation of responses observed previously.

Key words: Enhanced long-term UV-B, water availability, sub-Arctic bryophytes, xanthophylls, chlorophyll fluorescence, sporophytes.

INTRODUCTION

Anthropogenic activity has depleted stratospheric ozone by about 7% over the Arctic (Weatherhead *et al.*, 2005) with a consequential increase in solar ultraviolet-B radiation (UV-B: 280–315 nm) reaching the biosphere. Full recovery of the Arctic ozone layer is not expected until 2050 (World Meteorological Organization, 2007). This increase in UV-B

irradiance is of concern because it can reduce above-ground biomass and plant height and increase DNA damage and the accumulation of UV-absorbing compounds in polar plants (Newsham and Robinson, 2009) with possible ecosystem consequences (Caldwell *et al.*, 1995; Paul and Gwynn-Jones, 2003; Newsham and Robinson, 2009).

Among Arctic plants, bryophytes are particularly important determinants of Arctic ecosystem functioning due to their

abundance and contribution to above-ground biomass production, their importance in mediating ecosystem biogeochemical cycling, affecting water balance and regulating soil temperatures, as well as their value in creating microenvironments for vascular plants and microorganisms (Longton, 1997; Cornelissen *et al.*, 2007; Woodin *et al.*, 2009). UV-B impacts on bryophyte performance may, therefore, have further consequences for the whole ecosystem.

Studies investigating the effects of enhanced UV-B on Arctic bryophytes have so far shown a diversity of responses, with UV-B either stimulating, depressing or having no effect on growth or physiology (for reviews, see Callaghan *et al.*, 2004; Rozema *et al.*, 2005; Boelen *et al.*, 2006; Newsham and Robinson, 2009). This variety of responses is commonly explained by the diversity of species and different experimental approaches (e.g. filters vs. lamps) (Newsham and Robinson, 2009). Surprisingly, the influence of other environmental factors on species responses to UV-B has rarely been measured, but could play a key role in mediating responses. Sonesson *et al.* (2002), for instance, explained that the differing results for UV-B impacts on *Sphagnum fuscum* growth from similar experiments on similar mire sites were due to different weather conditions in the years when the studies were performed. Further, while Arctic moss responses to UV-B have been reported, no liverwort or hornwort has been studied.

Water availability might particularly influence UV-B impact on bryophytes because they are poikilohydric. When water is not available, their leaf cells dry out and metabolism can cease within a few minutes (Proctor, 2009). Many bryophytes have developed desiccation tolerance which is possibly assisted by the development of antioxidant and photo-protection mechanisms that can scavenge or minimize the generation of reactive oxygen species (ROS; Proctor, 2009). This cellular protection might confer an advantage during periods of UV-B exposure. Turnbull *et al.* (2009) found that differences in UV-B tolerance between three Antarctic species match their desiccation tolerance, with *Ceratodon purpureus* most tolerant of both water stress and UV-B, *Bryum pseudotriquetrum* intermediate and *Schistidium antarctici* the least tolerant to both stressors (more UV-B impact). UV-B impacts on bryophytes might therefore be related to species tolerance of moisture deficit.

The importance of water supply in influencing UV-B impacts in Arctic bryophytes was highlighted by Gehrke *et al.* (1996) and Phoenix *et al.* (2001), who found that negative effects of UV-B seen in *Hylocomium splendens* were removed by increased summer precipitation. Sonesson *et al.* (2002) found that increased UV-B had no significant overall effect on growth in length or chlorophyll and flavonoid contents of *Sphagnum fuscum* and *Dicranum elongatum*. However, the growth of *S. fuscum* – the species most sensitive to dehydration – responded negatively to increased UV-B under increased temperature at the peak of the growing season – a response considered to be driven by greater water limitation. While these studies have been very valuable, uncertainty continues, and the influence of water supply on UV-B impacts have yet to be specifically assessed in Arctic bryophytes.

In the present study, therefore, we investigated whether long-term enhanced UV-B exposure (+UV-B) changed the abundance and growth of three common bryophyte species in two sub-Arctic heathland sites of contrasting water

availability (naturally mesic and drier). We assessed the development of cellular protection mechanisms from UV-B exposure and/or water stress such as the accumulation of extractable UV-absorbing compounds, antioxidant carotenoids (e.g. β -carotene and zeaxanthin) together with the development of photoprotection by de-epoxidation of the xanthophyll cycle pool (DES) and non-photochemical quenching (NPQ) (Newsham and Robinson, 2009 for UV-B exposure; Oliver, 2009 for water stress). The impact of +UV-B on bryophyte photosynthetic activity was evaluated by measuring the maximum quantum yield of photosystem II (PSII; (F_v/F_m)), the electron transport rate through PSII (ETR) and chlorophyll concentrations. In addition, the 'sclerophylly index' (the quotient between the shoot mass and the surface area of the fresh prostrate apex) was measured as a proxy for changes in the proportion of non-photosynthetic tissue. We also studied – apparently for the first time in bryophytes – the influence of +UV-B on sporophyte production.

The objectives of the present study were to (1) explore further the influence of water supply and species biology on the impact of UV-B on Arctic bryophytes, and (2) seek an explanation of the published variable results on UV-B effects on Arctic bryophytes. Our hypothesis was that the magnitude of UV-B impacts on the abundance or physiology (growth, reproduction, photosynthetic activity or cellular protection) of bryophytes would be related to prevailing conditions of moisture availability and their tolerance of moisture deficit. To achieve these aims we evaluated UV-B impacts in neighbouring sites with contrasting water availability (naturally mesic and drier sites) that contained two long-term UV-B-enhanced experiments established in 1991 and 1993 (Johanson *et al.*, 1995; Gehrke *et al.*, 1996; Phoenix *et al.*, 2001). These sites represent a unique opportunity to test, in the long term and without the artefacts of disturbance due to the establishment of experimental treatments, the influence of species biology and water supply on the impact of UV-B on Arctic bryophytes.

MATERIALS AND METHODS

Study species

Three bryophyte species with contrasting biology were selected: the feather moss *Hylocomium splendens* (Hedw.) Schimp., the common haircap moss *Polytrichum commune* Hedw. and the foliose liverwort *Barbilophozia lycopodioides* (Wallr.) Loeske. The three species are widespread terrestrial bryophytes in the northern hemisphere. *Hylocomium splendens* is an ectohydric weft-forming pleurocarpous moss with a plagiotropic growth form, typical of dry to slightly damp heath, grasslands and forests. *Polytrichum commune* is an endohydric turf-forming acrocarpous moss with an orthotropic growth form, occurring in a wide range of acid habitats, usually in damp to wet situations. The biology and population ecology of *H. splendens* and *P. commune* from the study area are described in Callaghan *et al.* (1978). *Barbilophozia lycopodioides* is a circumboreal sub-arctic–sub-alpine liverwort growing in tufts on well-drained soils in forests, shrublands and grasslands (Damsholt, 2002). Differences in morphology, anatomy, habitat preference and physiology indicate varying

responses to water availability that we hypothesize will, to some extent, influence the bryophytes' responses to UV-B.

Experimental design

The study was undertaken in June 2006 in a sub-Arctic heathland at the Abisko Scientific Research Station, Abisko, Sweden (68°21'N, 18°49'E, 340–370 m a.s.l.) using two long-term UV-B enhancement experiments. The first experiment was established in 1991 in a drier area of the heath (Johanson *et al.*, 1995) and the second in 1993 in a neighbouring (<50 m away) mesic area (Gehrke *et al.*, 1996). This natural contrast in water availability between the two experimental set-ups allowed a unique long-term comparison of the influence of the water environment (mesic vs. drier) on UV-B impacts on Arctic bryophytes. The two sites have different durations of UV-B treatment (15 and 13 years) but the difference is relatively small in comparison with the duration of the experiments and is unlikely to cause differences in UV-B response, particularly in comparison with short-term experiments in which interannual weather and UV-B variability can be significant. The heathland community consists of an open birch canopy [*Betula pubescens* Ehrh. ssp. *czerepanovii* (N. I. Orlova) Hämet-Ahti] with a dense dwarf shrub understorey dominated by *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* L. (both evergreen), *V. myrtillus* L. and *V. uliginosum* L. (both deciduous).

The experiments were established with the aim of exposing heath communities to an enhanced UV-B regime that simulated a 15% reduction in stratospheric ozone under clear sky conditions at Abisko. This enhancement was achieved from six parallel fluorescent tube lamps (Q-PANEL UVB-313, Cleveland, OH, USA) mounted on metal frames (2.5 × 1.3 m), 1.5 m above the soil level. The middle 70 cm of the two central lamps was covered in aluminium foil to allow even irradiance throughout the plot at canopy height. Either glass or UV transparent Plexiglass (Röhme GmbH, Darmstadt, Germany) with cellulose diacetate foil (0.13 mm, Courtaulds, Derby, UK) was placed directly below each lamp to expose heath vegetation to ambient UV-B (control) and enhanced UV-B (+UV-B), respectively. UV-B lamps were switched on progressively around noon by timers which controlled three of the six lamps per frame simultaneously to gain a step-wise 'square wave' increase and decrease in daily UV-B enhancement. Maximum biologically effective UV-B doses, which were calculated using the generalized plant damage action spectrum from Caldwell (1971) normalized at 300 nm, corresponded to 5.8 kJ m⁻² d⁻¹ for +UV-B plots and 4.6 kJ m⁻² d⁻¹ for control plots. Further information about the experimental designs can be found in Johanson *et al.* (1995), Gehrke *et al.* (1996) and Phoenix *et al.* (2001).

The physiognomy of the mesic and drier sites was visibly different, with the mesic site having much greater abundance of bryophytes than the drier site. Measurements of soil moisture (Delta-T probe, Cambridge, UK) during peak biomass (August) confirmed that the mean water contents of drier and mesic plots were significantly different (37.3 and 55.7%, respectively, $P < 0.01$).

Each radiation regime (control and +UV-B) was replicated four times in both the mesic and the drier sites (16 plots in total).

Species abundance and physiological measurements

Plant cover and sporophyte abundance. Percentage cover of each bryophyte and sporophyte abundance were estimated using a 50 × 50 cm quadrat with 25 squares of 10 × 10 cm placed centrally within each plot. The number of sporophytes (which were found only in *H. splendens*) was counted in each of the 25 squares.

Annual growth measurement. Both mosses have readily visible markers of annual growth (Callaghan *et al.*, 1978). For *H. splendens*, individuals with sympodial growth were selected and the length of the stem of the newest bud was measured. For *P. commune*, new growth was identified by changes in leaf colour (new tissue was light green compared with dark green old tissue) and leaf morphology (smaller leaves are produced at the beginning and end of the growing season: Callaghan *et al.*, 1978), and the length of the new stem was measured. In the case of the liverwort, a clear change in colour from brown to light green was used to recognize new growth, and the length of the new stem was measured. Fifteen individuals per species per plot were measured.

Sclerophylly index (SI). The SI was calculated as the ratio between the dry mass (oven dried at 80 °C for 24 h) and the surface area of the fresh prostrate apex (measured using an LI-3000 leaf area meter, LI-COR, Lincoln, NE, USA). In bryophytes this variable can indicate the proportion of non-photosynthetic tissue (Martínez-Abaigar *et al.*, 1994).

In vivo chlorophyll fluorescence. Chlorophyll fluorescence measurements were made using a MINIPAM portable pulse amplitude modulation fluorometer connected to a 2060-M micro quantum/temperature sensor (Walz, Effeltrich, Germany) following Schreiber *et al.* (1995). Minimal and maximal fluorescence (F_0 and F_m) were measured on specimens dark adapted overnight (around 15 h) and maintained fully hydrated to ensure recovery. White actinic light was then applied following a light curve (LC) with incremental PPFD (0, 30, 100, 200, 400, 600, 800, 1200, and 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) with 30 s duration, a 0.8 s saturating pulse (10 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) being applied between each interval. The maximum quantum yield of PSII (F_v/F_m), the ETR and the maximal quenching due to non-photochemical dissipation of absorbed light energy (NPQ_{max}) were recorded during the LC. LC measurements were made at a near constant temperature of 10 °C. Further information on the method can be found in Núñez-Olivera *et al.* (2004).

Photosynthetic pigment composition. Plant samples were collected at around 1400 h on a day with clear skies. Shoot apices (approx. 3–5 cm² of fresh tissue per sample depending on the species) were frozen in liquid nitrogen immediately after collection and stored in the dark at –80 °C. The content of chlorophylls *a* and *b*, and the chlorophyll *a/b* (Chl *a/b*) ratio, were measured by spectrophotometry and carotenoids by high-performance liquid chromatography (HPLC), following Arróniz-Crespo *et al.* (2008a). The content of individual carotenoids was expressed as a percentage of total carotenoids. The pool of xanthophylls of the xanthophyll cycle (XC) was calculated as (violaxanthin + antheraxanthin + zeaxanthin), and the extent of DES as (antheraxanthin + zeaxanthin)/(violaxanthin +

antheraxanthin + zeaxanthin) (Demmig-Adams and Adams, 1996). Digital pictures of each tissue sample were taken before freezing and the surface area of each sample was calculated using the program Sigma Scan Pro5 (Systat Software, Inc., Chicago, IL, USA).

Methanol-extractable UV-absorbing compounds (MEUVACs). Plant samples were collected immediately after the lamps were switched off (around 1500 h) and were air-dried at room temperature. From 10 to 20 mg dry mass (depending on the species) was used per sample for the analysis. After extraction in methanol:water:7 M HCl (70:29:1, v/v/v), the absorbance was measured spectrophotometrically and MEUVACs were expressed in arbitrary units as the area under the absorbance curve in the wavelength interval 280–400 nm ($AUC_{280-400}$) on a dry mass basis (Arróniz-Crespo et al., 2006).

Statistical analysis

Overall effects of UV-B (control vs. long-term enhanced UV-B) and site (water regime: mesic vs. drier) were determined separately for each species with two-way analysis of variance (ANOVA). To identify if water availability can affect the magnitude of UV-B impacts, a Student's *t*-test between radiation regime was run at each site separately within the ANOVA when an overall UV-B effect or interaction between both factors was detected. Bonferroni's correction was used to determine the level of significance of the *t*-test (Rice, 1989). For all variables, measurements were taken from several plants (6–15 depending on the variable) in each plot; hence mean values per plot were used in the analyses. All statistical procedures were performed with SPSS 17.0.1 for Windows (SPSS Inc., Chicago, IL, USA).

RESULTS

Bryophyte percentage cover and sporophyte abundance

Hylocomium splendens was the most abundant bryophyte at both sites, with *P. commune* and *B. lycopodioides* being the least abundant in the drier and mesic sites, respectively. Percentage cover of the individual species was unaffected by +UV-B at both the mesic and drier sites (Fig. 1A). Cover of *H. splendens* was not significantly different between mesic and drier sites, whereas *P. commune* and *B. lycopodioides* showed significantly more and less abundance, respectively, in the mesic compared with the drier site ($P < 0.001$ and $P < 0.01$, respectively; Fig. 1A). Sporophytes were only observed on *H. splendens* at the mesic site where +UV-B almost halved their abundance (83 ± 3.5 and 46 ± 8.0 % in control and +UV-B plots, respectively; $P < 0.025$ Bonferroni correction).

Annual growth and sclerophylly index

Enhanced UV-B did not have an overall significant effect on growth or SI for any of the three species (Fig. 1B, C), although a near significant UV-B effect on growth was observed in *H. splendens* (ANOVA; $P = 0.06$). Growth of *H. splendens* decreased by 22 % under +UV-B (*t*-test, $P < 0.025$ Bonferroni correction) in the mesic site (Fig. 1B). Significant UV-B \times site interactions were observed in

P. commune and *B. lycopodioides* SI (ANOVA; $P < 0.05$). At the mesic site, *P. commune* SI was reduced (*t*-test, $P < 0.025$ Bonferroni correction) and *B. lycopodioides* SI increased under +UV-B (*t*-test, $P < 0.025$ Bonferroni correction), whereas no UV-B effect was detected in any species at the drier site (Fig. 1C).

Site effects (water regime) generally showed a greater overall impact than UV-B enhancement on the bryophytes. Both *H. splendens* and *P. commune* showed significantly lower growth (–18 and –35 %, respectively) in the drier compared with the mesic site ($P < 0.05$ and $P < 0.01$, respectively; Fig. 1B), while SI of *P. commune* was greater in the drier site compared with the mesic site ($P < 0.05$; Fig. 1C).

Chlorophyll concentration

Enhanced UV-B increased total chlorophyll concentrations overall in *H. splendens* (ANOVA; $P < 0.05$), but a significant UV-B \times site interaction showed the increase to be greater at the drier site (Table 1; *t*-test, $P < 0.025$ Bonferroni correction). The mesic site had significantly lower total chlorophylls in *P. commune* and higher total chlorophylls in *B. lycopodioides* compared with the drier site (ANOVA: $P < 0.001$ and $P < 0.01$, respectively; Table 1).

The Chl *a/b* ratios remained unaffected by +UV-B in all species (Table 1). In contrast, both *H. splendens* and *B. lycopodioides* had significantly higher Chl *a/b* ratios in the drier site compared with the mesic site (ANOVA: $P < 0.001$ and $P < 0.01$, respectively; Table 1).

Impacts on PSII: F_v/F_m and ETR

Both F_v/F_m and ETR of all species were unaffected by long-term +UV-B exposure (Figs 1D and 2). In contrast, the water regime significantly impacted these parameters, with both *H. splendens* and *B. lycopodioides* having higher F_v/F_m and ETR values overall in the mesic site compared with the drier site (ANOVA: F_v/F_m $P < 0.01$ and $P < 0.05$, respectively, for each species; ETR $P < 0.01$ for both species; Figs 1D and 2).

Photoprotection mechanisms: carotenoids, NPQ_{max} and MEUVACs

Few overall effects of +UV-B on carotenoids were observed and only in *H. splendens* (Table 1). Overall across both sites, +UV-B increased violaxanthin and decreased zeaxanthin, XC and DES in *H. splendens* (ANOVA: $P < 0.05$ in each case). Significant UV-B \times site interactions ($P < 0.01$) revealed that in *H. splendens*, neoxanthin increased under +UV-B only in the drier site (*t*-test, $P < 0.025$ Bonferroni correction). UV-B \times site interactions were also observed for β -carotene in *H. splendens* ($P < 0.001$) and *B. lycopodioides* ($P < 0.05$) that showed that β -carotene increased in *H. splendens* under +UV-B in the mesic site (Table 1; *t*-test, $P < 0.025$ Bonferroni correction) and in *B. lycopodioides* in the drier site (Table 1; *t*-test, $P < 0.025$ Bonferroni correction). Neoxanthin in *P. commune* and lutein in *H. splendens* increased under +UV-B in the drier site but decreased under +UV-B in the mesic site, again

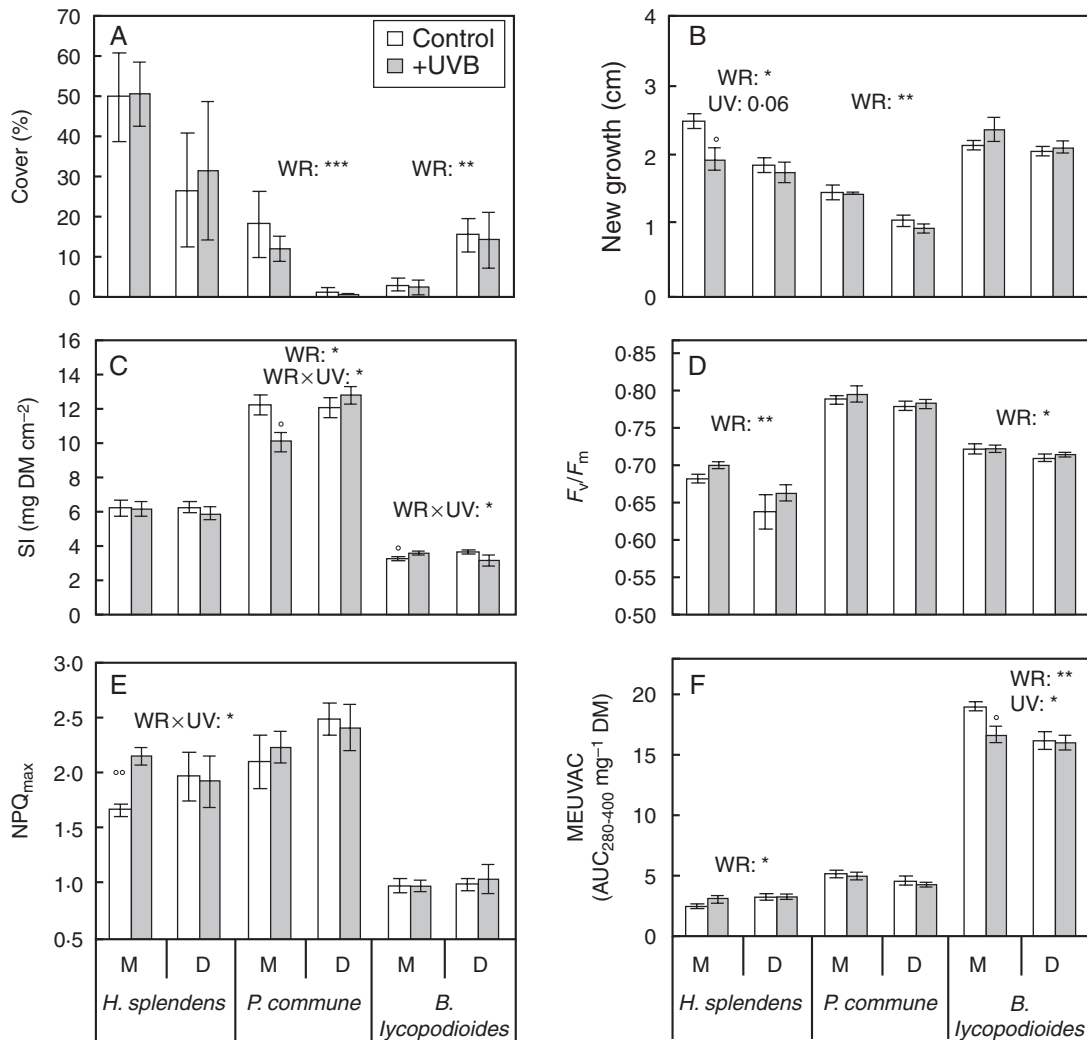


FIG. 1. (A) Percentage cover, (B) new growth, (C) sclerophylly index (SI; dry matter per surface area), (D) maximum quantum yield of PSII (F_v/F_m), (E) maximal non-photochemical quenching (NPQ_{max}) and (F) methanol-extractable UV-absorbing compounds (MEUVACs) of the three bryophytes (the mosses *Hylocomium splendens* and *Polytrichum commune*, and the foliose liverwort *Barbilophozia lycopodioides*), studied in plots exposed to two radiation regimes (control or enhanced UV-B, as indicated) under two different water regimes (M, mesic plots; D, drier plots). Means \pm s.e. are shown ($n = 4$). The main factor effects (two-way ANOVA) of water regime (WR) and UV-B radiation (UV), and the interactions between both (WR \times UV), are indicated for each species when significant (** $P < 0.001$; * $P < 0.01$; $P < 0.05$). Differences between control and +UV-B plots for each species and water regime separately are shown over the corresponding bars (Student's t -test adjusted with Bonferroni; $\circ P < 0.025$; $\circ\circ P < 0.005$).

showing interaction between both factors (ANOVA interaction: $P < 0.05$ for both).

In comparison with +UV-B effects, many more and clearer differences were observed between the sites (i.e. the effect of contrasting water regime; Table 1). Site significantly affected most carotenoid concentrations in the three species (Table 1). There were significantly greater XC and violaxanthin concentrations in all bryophyte species in the drier site compared with the mesic site (ANOVA: $P < 0.001$ in all cases except $P < 0.05$ for both parameters in *P. commune*) and greater antheraxanthin concentrations in *P. commune* ($P < 0.001$) and *H. splendens* ($P < 0.01$). β -Carotene was also higher in *H. splendens* plants growing in the drier site ($P < 0.001$). In contrast, the relative concentration of lutein was significantly lower in all species growing at the drier

site ($P < 0.05$ for *P. commune* and $P < 0.001$ for *H. splendens* and *B. lycopodioides*). Similarly, DES was significantly lower at the drier site in *H. splendens* and *B. lycopodioides* ($P < 0.01$ for both species).

The two-way ANOVA did not show any overall significant effect of +UV-B or site on NPQ_{max} , although a significant UV-B \times site interaction ($P < 0.05$) revealed a considerable increase in *H. splendens* under +UV-B (t -test, $P < 0.005$ Bonferroni correction) at the mesic site (Fig. 1E).

At the mesic site, +UV-B reduced MEUVACs by 12 % in *B. lycopodioides* (t -test, $P < 0.025$ Bonferroni correction) and slightly, although not significantly, increased it in *H. splendens* (Fig. 1F). Site also had significant effects on MEUVACs, with a 14 % increase in *H. splendens* ($P < 0.05$) and a 10 % decrease in *B. lycopodioides* ($P < 0.01$) in the drier site (Fig. 1F).

TABLE 1. Total chlorophyll concentration (Total Chl, mg m^{-2}), chlorophyll a/b ratio (Chl a/b), neoxanthin (Neo), lutein (Lut), β -carotene (β -car), violaxanthin (Vio), antheraxanthin (Ant), zeaxanthin (Zea), together with the sum of the xanthophylls involved in the xanthophyll cycle (XC, Vio + Ant + Zea) and the extent of de-epoxidation of the xanthophyll cycle pool (DES), species and treatment details as for Fig. 1

<i>Hylocomium splendens</i>											
Water regime	Radiation regime	Total Chl (mg m^{-2})	Chl a/b	Neo	Lut	β -car	Vio	Ant	Zea	XC	DES
M	Control	33.1 \pm 1.9	2.15 \pm 0.07	6.7 \pm 0.3	57.9 \pm 0.8	18.0 \pm 0.6	1.5 \pm 0.3	2.2 \pm 0.1	13.7 \pm 0.5	17.4 \pm 0.3	89.5 \pm 0.8
	+UVB	34.9 \pm 0.9	2.22 \pm 0.04	6.2 \pm 0.1	55.3 \pm 1.5	22.0 \pm 0.9 ^o	1.8 \pm 0.2	2.2 \pm 0.2	12.4 \pm 0.6	16.5 \pm 0.7	88.3 \pm 1.6
D	Control	26.3 \pm 0.6	2.61 \pm 0.01	5.6 \pm 0.5	48.7 \pm 0.9	24.7 \pm 0.9	3.2 \pm 0.3	2.9 \pm 0.1	14.8 \pm 1.0	21.0 \pm 0.8	84.5 \pm 2.5
	+UVB	37.7 \pm 3.8 ^o	2.50 \pm 0.05	7.6 \pm 0.3 ^o	51.0 \pm 0.6	22.3 \pm 0.5	4.0 \pm 0.2	2.7 \pm 0.2	12.2 \pm 0.8	19.0 \pm 0.7	77.2 \pm 1.6
		UV*, WR \times UV *	WR***	WR*, WR \times UV**	WR***, WR \times UV*	WR***, WR \times UV***	WR***, UV*	WR**	UV*	WR***, UV *	WR**, UV*
<i>Polytrichum commune</i>											
Water regime	Radiation regime	Total Chl (mg m^{-2})	Chl a/b	Neo	Lut	β -car	Vio	Ant	Zea	XC	DES
M	Control	84.4 \pm 6.1	2.50 \pm 0.08	9.3 \pm 0.2	54.7 \pm 0.4	23.1 \pm 0.3	6.3 \pm 0.2	1.2 \pm 0.1	5.3 \pm 0.3	12.8 \pm 0.7	50.2 \pm 0.8
	+UVB	65.1 \pm 7.1	2.53 \pm 0.04	8.8 \pm 0.3	55.1 \pm 0.9	23.6 \pm 0.7	7.0 \pm 0.1	1.3 \pm 0.1	4.0 \pm 0.6	12.3 \pm 0.5	42.5 \pm 3.3
D	Control	151.4 \pm 11.7	2.56 \pm 0.05	8.0 \pm 0.4	51.0 \pm 1.0	25.2 \pm 0.5	7.4 \pm 0.9	2.5 \pm 0.3	5.7 \pm 1.4	15.7 \pm 0.9	51.2 \pm 8.1
	+UVB	143.1 \pm 9.7	2.47 \pm 0.04	8.9 \pm 0.1	53.7 \pm 0.9	22.1 \pm 2.4	8.5 \pm 0.3	2.2 \pm 0.4	4.5 \pm 1.2	15.1 \pm 1.6	42.7 \pm 5.6
		WR***		WR \times UV*	WR*		WR*	WR***		WR*	
<i>Barbilophozia lycopodioides</i>											
Water regime	Radiation regime	Total Chl (mg m^{-2})	Chl a/b	Neo	Lut	β -car	Vio	Ant	Zea	XC	DES
M	Control	69.1 \pm 3.4	2.03 \pm 0.02	10.1 \pm 0.2	59.9 \pm 0.5	19.8 \pm 0.2	3.7 \pm 0.3	1.7 \pm 0.3	4.8 \pm 0.7	10.2 \pm 0.6	61.5 \pm 5.7
	+UVB	60.1 \pm 5.8	2.05 \pm 0.05	10.4 \pm 0.4	60.1 \pm 0.2	19.5 \pm 0.3	3.9 \pm 0.5	1.8 \pm 0.2	4.2 \pm 0.6	9.9 \pm 0.4	59.4 \pm 6.2
D	Control	48.2 \pm 11.7	2.19 \pm 0.07	10.0 \pm 0.9	56.6 \pm 0.5	18.4 \pm 0.2	8.1 \pm 0.5	2.2 \pm 0.4	4.6 \pm 1.4	15.0 \pm 1.4	43.4 \pm 7.1
	+UVB	42.3 \pm 9.7	2.26 \pm 0.03	10.6 \pm 0.3	55.7 \pm 0.2	19.5 \pm 0.3 ^o	8.1 \pm 0.3	1.9 \pm 0.1	4.1 \pm 0.4	14.0 \pm 0.3	41.2 \pm 2.2
		WR**	WR**		WR***	WR \times UV*	WR***			WR***	WR**

The content of individual carotenoids is expressed as a percentage of total carotenoids. Means \pm s.e. are shown ($n = 4$). The overall effects (two-way ANOVA) of the water regime (WR) and the radiation regime (UV, UV-B effect), and the interactions between both factors (WR \times UV), are indicated for each species when significant (** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$). Differences between control and +UV-B plots for each species and environment separately are shown beside the corresponding values (Student's t -test adjusted with Bonferroni; ^o $P < 0.025$).

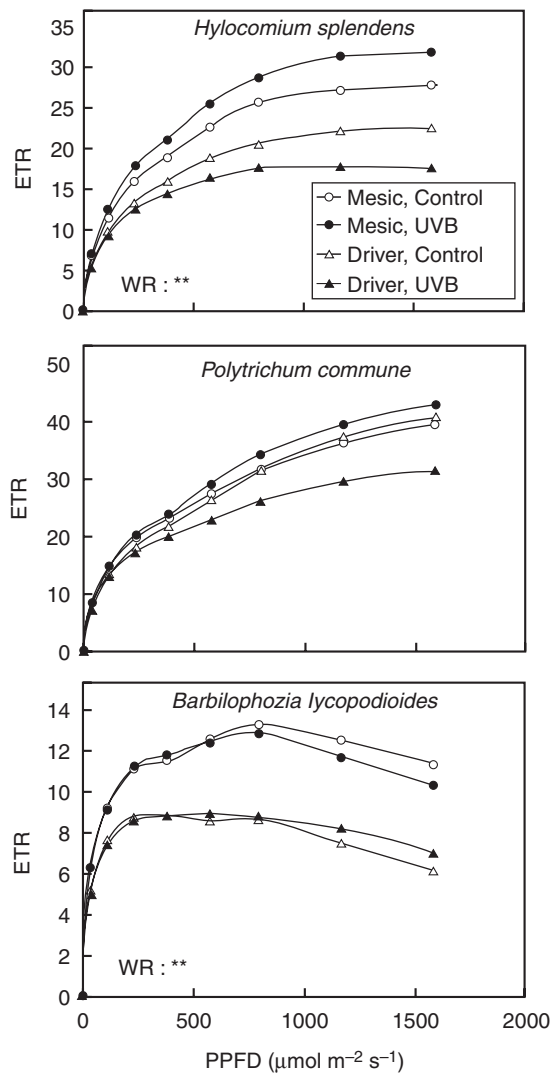


FIG. 2. Curves of the electron transport rate through PSII (ETR) against photosynthetic photon flux density (PPFD); species and treatment details as for Fig. 1. The s.e. are not shown for clarity. The overall effect (two-way ANOVA) of the water regime (WR) is indicated when significant (***) $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. The effect of the radiation regime (UV, UV-B effect) was not significant in any species.

DISCUSSION

This study, using essentially identical long-term +UV-B experiments located in neighbouring areas with contrasting water availability (mesic vs. drier), shows that species biology and water supply influenced UV-B impacts on Arctic bryophytes. In particular, *H. splendens* was the most sensitive species to +UV-B whereas UV-B impacts on *P. commune* and *B. lycopodioides* were significantly more subtle. Site differences in water availability, although relatively small, had a more profound effect on bryophyte ecophysiology than +UV-B. Water availability also influenced bryophyte responses to +UV-B as responses were less detectable in the drier site. The large influence of relatively small differences in water availability probably contributes

considerably to the wide variation of UV-B responses observed in other studies previously.

Bryophyte percentage cover and sporophyte abundance

Enhanced UV-B had no effect on the cover of the individual species in either the mesic or drier sites despite the considerable long-term +UV-B treatment. This agrees with other studies on sub-Arctic bryophytes (*H. splendens*, *Polytrichum hyperboreum* and *Sanionia uncinata*: Phoenix *et al.*, 2001; Rozema *et al.*, 2006). In contrast, bryophyte cover differed between sites (mesic vs. drier), reflecting their individual hydrological preferences. *Polytrichum commune* was less abundant in the drier site and *B. lycopodioides* in the wetter site. *Hylocomium splendens* showed no difference between sites (Callaghan *et al.*, 1978; Damsholt, 2002; see also species description).

There was a very large impact of UV-B on sporophyte production in *H. splendens* (44% reduction), but a much greater difference between sites as sporophytes were only produced at the mesic sites. Sporophyte production in this species is apparently very demanding of resources (Rydgren and Ökland, 2003) and the reduction may indicate that +UV-B causes some stress to this moss.

Annual growth and sclerophylly index

As found for sporophyte production, *H. splendens* also showed a considerable reduction in length growth under +UV-B (–22%) but again only at the mesic site. Nevertheless, this species appears to be the most sensitive to +UV-B as growth of the other two bryophytes was unaffected. Greater responsiveness of *H. splendens* has also been observed by Gehrke (1999) and might be related to the strong flexibility in life strategy shown by eurioic species such as *H. splendens* (Grime, 1979). UV-B exposure caused subtle morphogenetic changes in *P. commune* and *B. lycopodioides*, but again only in the mesic site. The SI was lower for *P. commune* under +UV-B – the shoots were visibly less dense – but was higher for the liverwort.

Overall, the results highlight that the impacts of +UV-B on bryophyte growth and sclerophylly are species specific and less likely to be detected under drier conditions. This might well explain the variability in other studies of UV-B impacts on bryophyte growth where reductions (Gehrke 1998, 1999; Rozema *et al.*, 2006), no effect (Björn *et al.*, 1998; Sonesson *et al.*, 2002; Lappalainen *et al.*, 2008) or increases (Phoenix *et al.*, 2001) have been reported. Similarly, for sclerophylly, Lappalainen *et al.* (2008) reported a decrease in *Pleurozium schreberi* while Gehrke (1999) found the opposite for *P. commune*.

Chlorophyll concentration

The impact of +UV-B on chlorophyll concentration was again species specific. There was no effect on *P. commune* and *B. lycopodioides*, a common result for polar bryophytes under field conditions (Boelen *et al.*, 2006; Newsham and Robinson, 2009). However, chlorophyll concentration increased in *H. splendens* and, surprisingly, the increment

was stronger in the drier site. Increased chlorophyll content under +UV-B was also previously observed in *Sphagnum* (Gehrke, 1998; Niemi *et al.*, 2002a). The Chl *a/b* ratio was not affected by +UV-B in any species, in line with previous field studies (Gehrke, 1998, 1999).

The influence of water availability on chlorophyll concentration depended on the species considered and did not show an overall trend. However, the Chl *a/b* ratio was higher in *H. splendens* and *B. lycopodioides* at the drier site, possibly indicating a smaller antenna size to reduce the rate of light absorption and photodamage (Baroli and Melis, 1998).

Impacts on PSII: F_v/F_m and ETR

The F_v/F_m and ETR were not affected by +UV-B in any of the species, and this is typical for polar bryophytes (Boelen *et al.*, 2006; Newsham and Robinson, 2009), with rapid adaptation to increased UV radiation being reported (Green *et al.*, 2005). These results, taken together with other previous studies, suggest that photosynthetic performance is unlikely to be affected by +UV-B in Arctic bryophytes.

In contrast to this unresponsiveness to +UV-B, moderate photoinhibition (F_v/F_m decrease) was observed in *H. splendens* and *B. lycopodioides* growing in the drier site. Full recovery of hydrated plants was possibly achieved overnight and thus the reduction in F_v/F_m might represent an active photoprotection mechanism by increased protective energy dissipation (Horton *et al.*, 1996). In this respect, the ETR was also significantly lower in the drier site in these two species, but no signs of full PSII closure (full reduction of PSII) at high light were detected, again suggesting that efficient dissipation mechanisms existed to avoid photodamage. In relation to these results, Proctor and Smirnov (2011) recently showed that desiccation-tolerant moss species can maintain high rates of photosynthetic electron transport (high quantum efficiency of PSII) at high irradiance by oxygen photoreduction that is associated with a high capacity to dissipate excess energy (photoprotection) and ROS tolerance.

Photoprotection mechanisms: carotenoids, NPQ_{max} and MEUVACs

Enhanced UV-B caused different changes in the carotenoid concentrations, especially in the most UV-B-sensitive species (*H. splendens*), with zeaxanthin tending to decrease and violaxanthin increasing, which is consistent with the results obtained in Antarctic bryophytes during periods of ozone depletion (Newsham *et al.*, 2002). This may be related to the inhibition of violaxanthin de-epoxidation by UV-B radiation (Pfundel *et al.*, 1992). Enhanced UV-B also increased the concentration of β -carotene in *H. splendens* as previously observed in Antarctic bryophytes (Robinson *et al.*, 2005) but only at the mesic site, whereas there was a general increase in the drier site – possibly reflecting the importance of its antioxidant capacity to counteract stress in general in this moss.

Site (water regime) had a stronger effect on carotenoids than +UV-B. Species in the drier site had higher concentrations of violaxanthin and the XC pool, and reduced lutein, suggesting that these are important changes for tolerance of water stress in these bryophytes. This might be linked to xanthophylls,

especially violaxanthin, being the major abscisic acid (ABA) precursors in water-stressed plants (Li and Walton, 1987), and ABA is an important molecule for desiccation tolerance in some bryophytes (Proctor *et al.*, 2007). In addition, zeaxanthin and antheraxanthin are also required for constitutive thermal energy dissipation in plants under long-term environmental stress (Demmig-Adams and Adams, 2002).

NPQ_{max} was unresponsive to both +UV-B and water availability, except for *H. splendens* in the mesic site which continued the trend that UV-B impacts were more common in *H. splendens* and less likely under drier conditions.

There were no clear effects of +UV-B on MEUVAC concentration. Published results are highly variable, with concentration increases, decreases or no change reported (Newsham *et al.*, 2002; Niemi *et al.*, 2002b; Newsham, 2003; Arróniz-Crespo *et al.*, 2008b). These diverse responses may reflect not only interspecific differences and interaction with other environmental factors as shown in our study but also the lack of extraction of cell wall-bound compounds (Clarke and Robinson, 2008). Overall, measurements of MEUVACs do not necessarily provide a good indicator of long-term UV-B tolerance in the species studied here.

In conclusion, our study shows that impacts of UV-B exposure on Arctic bryophytes were significant, compared with previously published modest or absent UV-B effects, and were more readily detectable in species with high plasticity such as *H. splendens* and less likely, or more subtle, under drier conditions. Overall, species biology and even small differences in water supply can greatly influence the impact of UV-B on Arctic bryophytes.

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