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Abstract

We report a meta-analysis of data from 34 field studies into the effects of UV-B radiation on Arctic and Antarctic bryophytes and angiosperms. The studies measured plant responses to decreases in UV-B radiation under screens, natural fluctuations in UV-B irradiance, or increases in UV-B radiation applied from fluorescent UV lamps. Exposure to UV-B radiation was found to increase the concentrations of UV-B absorbing compounds in leaves or thalli by 7% and 25% (expressed on a mass or area basis, respectively). UV-B exposure also reduced aboveground biomass and plant height by 15% and 10%, respectively, and increased DNA damage by 90%. No effects of UV-B exposure were found on carotenoid or chlorophyll concentrations, net photosynthesis, Fv/Fm or ΦPSII, belowground or total biomass, leaf mass, leaf area or specific leaf area (SLA). The methodology adopted influenced the concentration of UV-B absorbing compounds, with screens and natural fluctuations promoting significant changes in the concentrations of these pigments, but lamps failing to elicit a response. Greater reductions in leaf area and SLA, and greater increases in concentrations of carotenoids, were found in experiments based in Antarctica than in those in the Arctic. Bryophytes typically responded in the same way as angiosperms to UV-B exposure. Regression analyses indicated that the percentage difference in UV-B dose between treatment and control plots was positively associated with concentrations of UV-B absorbing compounds and carotenoids, and negatively so with aboveground biomass and leaf area. We conclude that, despite being dominated by bryophytes, the vegetation of polar regions responds to UV-B exposure in a similar way to higher plant-dominated vegetation at lower latitudes. In broad terms, the exposure of plants in these regions to UV-B radiation elicits the synthesis of UV-B absorbing compounds, reduces aboveground biomass and height, and increases DNA damage.

Keywords

aboveground biomass, angiosperms, Antarctic, Arctic, bryophytes, DNA damage, flavonoids, height, methodology, UVB absorbing compounds

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Responses of plants in polar regions to UV-B exposure: a meta-analysis

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Running title: meta-analysis of polar plant response to UV-B

Abstract

We report a meta-analysis of data from 34 field studies into the effects of UV-B radiation on Arctic and Antarctic bryophytes and angiosperms. The studies measured plant responses to decreases in UV-B radiation under screens, natural fluctuations in UV-B irradiance, or increases in UV-B radiation applied from fluorescent UV lamps. Exposure to UV-B radiation was found to increase the concentrations of UV-B absorbing compounds in leaves or thalli by 7% and 25% (expressed on a mass or area basis, respectively). UV-B exposure also reduced aboveground biomass and plant height by 15% and 10%, respectively, and increased DNA damage by 90%. No effects of UV-B exposure were found on carotenoid or chlorophyll concentrations, net photosynthesis, F_v/F_m or Φ_{PSII}, belowground or total biomass, leaf mass, leaf area or specific leaf area (SLA). The methodology adopted influenced the concentration of UV-B absorbing compounds, with screens and natural fluctuations promoting significant changes in the concentrations of these pigments, but lamps failing to elicit a response. Greater reductions in leaf area and SLA, and greater increases in concentrations of carotenoids, were found in experiments based in Antarctica than in those in the Arctic. Bryophytes typically responded in the same way as angiosperms to UV-B exposure. Regression analyses indicated that the percentage difference in UV-B dose between treatment and control plots was positively associated with concentrations of UV-B absorbing compounds and carotenoids, and negatively so with aboveground biomass and leaf area. We conclude that, despite being dominated by bryophytes, the vegetation of polar regions responds to UV-B exposure in a similar way to higher plant-dominated vegetation at

lower latitudes. In broad terms, the exposure of plants in these regions to UV-B radiation elicits the synthesis of UV-B absorbing compounds, reduces aboveground biomass and height, and increases DNA damage.

Introduction

The depletion of ozone in the stratosphere over polar regions is particularly intense (Farman *et al*., 1985; Newman *et al*., 1997). Chemical reactions on the surfaces of polar stratospheric clouds, which form each winter in cold (< -78 °C) air masses over the Arctic and Antarctic, convert chlorine, derived from chlorofluorocarbons, into chlorine monoxide, which photocatalyses ozone to oxygen (World Meteorological Organization, 2007). Because ozone is the principal gas in the atmosphere that absorbs solar ultraviolet-B radiation (UV-B; 280-315 nm), its depletion exposes plants in polar regions to elevated irradiances of UV-B during boreal or austral spring, often as the plants emerge from melting snow and ice. Since UV-B is absorbed by DNA and biological membranes, these increased irradiances of UV-B have possible deleterious effects on plant physiology and growth, and consequences for the functioning of these ecosystems (Caldwell *et al*., 1995; Rozema *et al*., 1997; Paul & Gwynn-Jones, 2003).

In recent years, considerable effort has been invested in determining the responses of polar vegetation, which is dominated by bryophytes, to UV-B exposure. However, the UV-B responses of plants in polar regions are at present poorly defined, with wide variation in responses found between different studies. For example, negative effects on biomass accumulation have been recorded in some experiments (e.g. Xiong & Day, 2001; Xiong *et al*., 2002; Robinson *et al*., 2005) but not in others (e.g. Lappalainen *et al*., 2008). The responses of photosynthetic pigments to UV-B exposure also often differ between studies, with different experiments showing either increases (e.g. Niemi *et al*., 2002a), no change (e.g. Niemi *et al*., 2002b; Lappalainen *et al*., 2008) or decreases (e.g. Gehrke, 1998; 1999; Robinson *et al*., 2005) in the concentration of chlorophylls in leaves or thalli. Damage to DNA in aboveground plant parts also varies widely, with increases in damage in some studies (e.g. Lud *et al*., 2001a; Turnbull & Robinson, 2009) but no apparent effects in others (e.g. Lud *et al*., 2003; Boelen *et al*., 2006; Rozema *et al*., 2006). One of the most consistent responses of plants at lower latitudes to elevated UV-B exposure is the synthesis of UV-B absorbing compounds in foliage (Searles *et al*., 2001), but, even for this response, polar UV-B experiments have yielded conflicting results, with consistent positive effects on the concentrations of these pigments in some studies (e.g. Xiong & Day, 2001; Newsham *et al*., 2002; Newsham, 2003), but no effects in others (e.g. Gehrke, 1998; 1999; Boelen *et al*., 2006; Rozema *et al*., 2006).

The reasons for the disparate results from these studies are presently unclear. One potential factor is the differences between studies in the methodologies used to alter the dose of UV-B radiation received by plants. Three main approaches have been used in polar UV-B experiments. The first of these is to cover plants with screens made from materials that either absorb or transmit UV-B radiation, with Mylar polyester (cut off λ = 314 nm) typically being used to remove UV-B from solar radiation. The responses of plants under this material are compared with those of plants under materials such as Aclar, Teflon, or polymethylmethacrylate (PMMA), each of which transmit most or all of the

wavelengths of solar UV-B radiation that reach the Earth's surface (e.g. Xiong & Day, 2001; Newsham *et al*., 2005; Albert *et al*., 2008). The second approach is to use fluorescent UV lamps, suspended over plants from frames, to increase the flux of UV-B in solar radiation, typically simulating between 15% and 30% loss of ozone from the atmosphere, assuming cloudless skies over the study site (e.g. Gehrke, 1998; 1999; Björn *et al*., 1999; Rozema *et al*., 2006). In order to apply UV-B radiation to treatment plots and to remove wavelengths of UV-C (200-280 nm), which are not present in solar radiation reaching the Earth's surface, energised fluorescent UV lamps are wrapped in cellulose acetate (cut off λ = 292 nm). The responses of plants under cellulose acetate-filtered lamps are then compared with those in control plots, under energised lamps wrapped in Mylar polyester or encased in glass (cut off λ = 318 nm; Gehrke, 1999). The third, and much less commonly used approach, is to examine plant response to natural fluctuations in ambient UV-B irradiance. This non-manipulative approach samples plants repeatedly from the same location in the natural environment under varying ozone column depths, exposing plants to wide fluctuations in UV-B irradiance (e.g. Newsham *et al*., 2002; Dunn & Robinson, 2006).

A further explanation for the disparities that exist between studies is the wide variation in the doses of UV-B radiation received by plants in treatment and control plots. Such variation is often associated with the methodologies used in different experiments. For example, UV-B attenuating screens reduce incident UV-B dose by up to 86% (Xiong *et al*., 2002), whereas lamps, depending on which action spectrum the spectral irradiances are weighted with and the level of ozone depletion simulated, are typically used to increase the dose of UV-B radiation received by plants by *c*. 30% above that present in solar radiation (e.g. Gehrke, 1998; 1999; Björn *et al*., 1999; Niemi *et al*., 2002a). The substantial effect of UV-B attenuating screens on the dose of UV-B radiation received by plants has been put forward as the reason for the consistent, but as yet unquantified, effects of screens on plant performance, compared with the apparently less consistent effects of fluorescent UV lamps (Rozema *et al*., 2005). This is a difficult issue to address, since studies often do not report the absolute UV-B doses received by plants in treatment and control plots, or use different biological action spectra to weight the calculated UV-B doses, hampering the direct comparison of data from different studies.

Another potential factor that could account for the differences between studies in plant response to UV-B exposure is the taxa that are studied. Different plant forms are known to transmit different amounts of UV-B radiation to the mesophyll (Day *et al*., 1992; Day & Vogelmann, 1993), possibly because of the presence of hairs, cuticles and surface waxes on leaves (Day, 1993), which are more frequent in angiosperms and gymnosperms than in bryophytes (Gehrke, 1999). It has also been suggested that higher plants and bryophytes could differ in their abilities to synthesize UV-B absorbing compounds (Gwynn-Jones *et al*., 1999), although recent data do not support this argument (Newsham *et al*., 2002; Newsham, 2003; Dunn & Robinson, 2006; Clarke & Robinson, 2008). In addition, previous experiments may have underestimated the UV-B screening potential of bryophytes, since a recent study has demonstrated that UV-B absorbing compounds located in the cell walls of Antarctic mosses are not efficiently extracted with acidified methanol (Clarke & Robinson, 2008).

In order to resolve why these differences exist in plant response to UV-B exposure between studies, and to identify common effects of UV-B radiation on polar vegetation, a meta-analysis of data

from the literature on the UV-B responses of plants in polar regions was performed. Meta-analyses have been used in similar ways to clarify the responses of plants to warming (Arft *et al*., 1999), elevated concentrations of carbon dioxide and ozone in air (Curtis & Wang, 1998; Stiling and Cornelissen, 2007; Feng *et al*., 2008) and simulated ozone depletion (Searles *et al*., 2001). The latter study analysed data on higher plant responses to UV-B radiation applied from fluorescent UV lamps, typically at mid-latitudes, with data from only three polar field experiments included in the analyses. In the current study, we augment the analyses of Searles *et al*. (2001) by including data from screen and non-manipulative studies, the latter of which did not exist in the literature until 2002. We aimed to determine whether differences in plant response to UV-B exposure can be ascribed to variation in methodology, plant form, UV-B dosage or the duration of exposure to UV-B treatments. Given that a previous narrative review suggests that plant response to UV-B exposure varies between the Arctic and Antarctic (Rozema *et al*., 2005), we also tested for differences in plant response between polar regions.

Materials and methods

Data were extracted from peer-reviewed publications in primary research journals on angiosperm and bryophyte response to UV-B exposure in the Arctic, sub-Arctic, maritime Antarctic and continental Antarctic. Although lichens are a key component of the polar flora, data on the responses of the symbiosis to UV-B radiation were not included in the analysis, since it was centred on higher and lower plant response to UV-B exposure. It was deemed necessary to impose several selection criteria on the data before they were included in the meta-analysis. These limited the numbers of observations for certain responses in subsequent analyses, but increased the robustness of the conclusions that could be drawn from them. Data were included from studies that met the following criteria: (i) *Experimental location*. Data were only included from outdoor experiments. Those from laboratory and glasshouse studies, in which UV-B radiation is known to have anomalously large effects on plants (Rozema *et al*., 1997), were disregarded. (ii) *Screen methodology*. Screens affect both the temperature and humidity of vegetation (Kennedy, 1995), and hence have significant effects on plant growth and photosynthetic parameters (Huiskes *et al*., 2001). Data from studies using screens were hence only included when both control and treatment plots had been covered with screens. Those from studies comparing the responses of plants under screens with those of plants outside of screens were disregarded. It should be noted, however, that screens, because they warm vegetation and increase humidity, can alter plant response to UV-B exposure, and hence do not provide an accurate simulation of ozone depletion (Rozema *et al*., 2005). (iii) *UV-A exposure.* Data from screen studies that attenuated only UV-B radiation were included in the analyses. Those that attenuated both UV-A (315 - 400 nm) and UV-B radiation with screens were excluded, since UV-A radiation is known to have significant effects on plant growth (e.g. Flint & Caldwell, 2003). (iv) *Lamp methodology*. Energised Mylar-filtered fluorescent UV lamps are known to have effects on plant growth relative to unenergised lamps (Newsham *et al*., 1996), and so data from lamp studies were only included when comparisons had been made between cellulose acetate-filtered and glass- or Mylar-filtered lamps. Those from studies comparing the responses of plants under cellulose acetate-filtered lamps with those under unenergised lamps, or those in unirradiated plots, were disregarded. One study that did not use Mylar-filtered lamps as a control

(Niemi *et al*., 2002a) was included in the analysis since the authors explicitly state that no effects of Mylar-filtered fluorescent UV lamps were found on plant response in a previous study using the same irradiation facility.

Of the 46 publications that were considered for inclusion, 12 did not meet the above criteria and were hence excluded from the analyses. The 34 studies that met the criteria, and which were hence included, are listed in Appendix 1. Thirty two species of bryophyte and angiosperm were represented in the analysis (Appendix 1). In order to enable comparisons between studies, only commonly-measured parameters were analysed. These included acclimation responses, such as the synthesis of UV-B absorbing compounds (putative flavonoids) in leaves or thalli, measures of biomass and growth (above-, belowground and total biomass, height, individual leaf mass, total leaf area and specific leaf area) and indications of DNA damage, measured as the accumulation of cyclobutane pyrimidine dimers (CPDs). In addition to changes in the concentrations of photosynthetic pigments such as chlorophylls and carotenoids, three measures of photosynthetic physiology were included, *viz*., net photosynthetic gas exchange (P_n) and the two chlorophyll fluorescence parameters that measure phototosynthetic yield, Φ_{PSII} and F_v/F_m (Appendix 1).

In order to avoid bias towards studies that report multiple measurements of the same parameter, a mean value of each parameter was calculated for each plant species in each publication. The exceptions to this were when measurements had been made at more than one location in the same study or in different years. In cases where two levels of elevated UV-B radiation were applied, mean treatment plot response values were calculated and entered into the analyses. If the response to a factor other than UV-B radiation was reported (e.g. warming; Day *et al*., 2008), then only the data from the UV-B treatment plots were included. When specific leaf area (SLA) was reported (Xiong & Day, 2001; Xiong *et al*., 2002), then data for concentrations of UV-B absorbing compounds were expressed per unit of leaf mass and leaf area. Only chlorophyll and carotenoid concentrations that were expressed on a leaf mass basis were included, since few publications express the concentrations of these pigments per unit of leaf area. The length of the longest leaf of a grass and a forb species was used a proxy for height in three studies (Day *et al*., 2001; Ruhland & Day, 2000; Xiong *et al*., 2002).

The mean value of each parameter in treatment plots and control plots was determined, and the response ratio (ln *R*; Hedges *et al*., 1999) calculated:

$$\ln R = \ln(\text{treatment mean} / \text{control mean})$$

This enabled the expression of data as relative values, correcting for size differences between studies and plant species. Values for treatment means were derived from plots exposed to high doses of UV-B radiation, i.e., those from under cellulose acetate-filtered UV fluorescent lamps or from under Aclar, Teflon or PMMA screens. Those for control means were from plots exposed to low doses of UV-B radiation, under glass- or Mylar-filtered lamps or Mylar-filtered screens. For non-manipulative studies, data were regressed against daily UV-B dose and treatment and control means were respectively entered as the highest and lowest values on the *y*-axis, within the range of the data, along the line of best fit.

We then used a combination of weighted and unweighted meta-analyses in order to determine responses of ln *R* to UV-B exposure. For the weighted analyses, which used the reciprocal of the sampling variance to weight ln *R* (Rosenberg *et al*., 2000), *n* and standard deviations (s.d.) or standard errors (s.e.) values were extracted from the literature. Mean weighted effect sizes were calculated, and, because of the small sample size for most parameters, 95% bootstrap confidence intervals were calculated, using resampling tests generated from 999 iterations (Rosenberg *et al*., 2000). An effect size was considered to be significantly different at $P<0.05$ when its confidence intervals did not bracket zero (Curtis & Wang, 1998; Feng *et al*., 2008). The data from two reports using fluorescent UV lamps, in which the stated level of *n* is several times higher than that reported in previous studies using the same experimental facility, were excluded from the weighted analyses.

As in previous meta-analyses (e.g. Searles *et al*., 2001; Dormann & Woodin, 2002), we encountered several obstacles to extracting s.d. or s.e. values from the literature. For example, some of the selected publications report errors but do not stipulate whether they represent s.d. or s.e., whilst one publication does not report errors, reporting only mean values for treatment and control plots. In several publications, error bars associated with treatment means are obscured by those associated with control means, and *vice versa*. Therefore, as in previous studies (e.g. Dormann & Woodin, 2002), we also used unweighted meta-analyses in order to maximise the number of observations in our study. By using unweighted analyses, we were able include data that are not reported in the literature but which can be derived from the published data, such as total biomass when above- and belowground biomass are reported (e.g. Xiong & Day, 2001). Unweighted analyses also enabled us to determine the magnitude of response to UV-B exposure in non-manipulative experiments, which would not have been possible using weighted analyses. One-tailed *t*-tests were used in the unweighted analyses to determine significant differences between ln *R* and zero for each parameter, and general linear models, along with weighted analyses, were used to determine the effects of categorical variables (methodology, plant form or polar region) on ln *R*. Statistical analyses were made in MINITAB 15 (MINITAB inc., State College, PA, USA) and MetaWin 2.0 (Rosenberg *et al*., 2000).

Regression analyses

We used the percentage difference between treatment and control plots in UV-B dose weighted with the generalised plant action spectrum (Caldwell, 1971; UV-B_{PAS}) as a predictor variable for untransformed response ratios in regression analyses. The data from several studies (e.g. Niemi *et al*., 2002a, b; Lud *et al*., 2003) that report UV-B doses weighted with the DNA damage or CIE action spectra (Setlow, 1974; McKinlay & Diffey, 1987) were excluded from the regression analyses, since it is likely, owing to the different shapes of these action spectra from that of the generalised plant action spectrum (Holmes, 1997), that the percentage difference in UV-B exposure between treatment and control plots would have differed substantially from studies that used UV-B_{PAS} to weight irradiances. We did, however, include data from reports that used both formulations of the generalised plant action spectrum, either that of Green *et al*. (1974) or Thimijan *et al*. (1978), because the shapes of these two formulations are similar (McLeod, 1997) and, as in previous studies (e.g. Björn *et al*., 1997), we hence anticipated only minor effects of these differences on the analyses. For experiments based at Abisko in

northern Sweden, UV-B_{PAS} data were derived from Johanson *et al*. (1995b). For the non-manipulative studies, we calculated the difference between the maximum and minimum daily UV-B_{PAS} doses on the *x*-axes in the regression analyses referred to above, treating these as supplemental studies. To aid visualisation of the data, the inverses of the untransformed response ratios for screen studies were entered into these analyses. Data for two parameters (height and specific leaf area) were removed from the regression analyses, since, in each case, there were less than four levels of the predictor variable against which to regress the response ratios. In addition, the duration of the UV-B treatment (in days) was used as a predictor for untransformed response ratios in regression analyses. Linear and quadratic regressions were used to determine the associations between response ratios and UV-B_{PAS} exposure.

Results

Effects of UV-B exposure

Weighted and unweighted meta-analyses indicated a significant influence of UV-B exposure on ln *R* for concentrations of UV-B absorbing compounds, expressed on a mass basis, with a mean increase of 7.4% in plant tissues sampled from treatment plots, relative to those from control plots (Table 1; Fig. 1). Both methods of analysis also showed there to be a significant effect of UV-B exposure on ln *R* for concentrations of UV-B absorbing compounds expressed on an area basis (Table 1), with a mean increase of 24.6% in the concentrations of these pigments in plant tissues sampled from treatment plots, compared with those sampled from control plots (Fig. 1). Response ratios for photosynthetic parameters (F_v/F_m, Φ_{PSII} and P_n) and concentrations of associated pigments (total carotenoids and chlorophylls) were unaffected by UV-B exposure (Table 1; Fig. 1).

Both methods of analysis showed that UV-B exposure significantly decreased ln *R* for aboveground biomass (Table 1), with a 14.7% reduction in this parameter in treatment plots, relative to control plots (Fig. 1). Plant height was also significantly affected by UV-B exposure, with unweighted and weighted analyses both indicating a mean 10.0% reduction in height in treatment plots compared with control plots (Table 1; Fig. 1). Neither method of analysis showed an effect of UV-B exposure on ln *R* for belowground biomass, nor total biomass (Table 1; Fig. 1). The response ratio for total leaf area was unaffected by UV-B exposure in the unweighted analyses, but was significantly reduced by 6.1% in the weighted analyses (Table 1; Fig. 1). Neither method of analysis showed individual leaf mass or SLA to be affected by UV-B exposure (Table 1; Fig. 1), but both indicated that UV-B exposure significantly influenced ln *R* for DNA damage, with the formation of CPDs increasing by 90.2% in DNA from treatment plots, compared with that from control plots (Table 1; Fig. 1).

Effects of methodology

Methodology had a significant effect on the response ratio for concentrations of UV-B absorbing compounds expressed per unit of mass (Table 1). In unweighted analyses, studies that used screens to attenuate UV-B radiation, or recorded plant response to natural fluctuations in UV-B irradiance in non-manipulative experiments, showed significant 12.2% and 17.3% increases in the concentrations of UV-B absorbing compounds in response to UV-B exposure (both $n = 8$, $P<0.01$ and $P<0.05$, respectively; Fig. 2a). In contrast, ln *R* for concentrations of these compounds from studies that applied UV-B

radiation from fluorescent UV lamps was not significantly different from zero in unweighted analyses (n = 26, P>0.05; Fig. 2a). Weighted analyses similarly indicated no change in the concentrations of these pigments under fluorescent UV lamps (P>0.05), but a significant positive response to UV-B radiation under screens (P<0.05). Belowground biomass was also influenced by methodology (Table 1): unweighted analyses showed that the exposure of plants to UV-B radiation under screens led to a 16.9% reduction in this parameter (n = 5; Fig. 2b). In contrast, no effect was recorded on belowground biomass when plants had been exposed to UV-B radiation under fluorescent UV lamps (Fig. 2b). It should be noted, however, that the number of observations for this response was low (n = 2).

Effects of plant form

Unweighted and weighted analyses both indicated that the response ratios for UV-B absorbing compounds expressed per unit of leaf area differed between bryophytes and angiosperms (Table 1): ln R for concentrations of UV-B absorbing compounds expressed in this way was higher for angiosperms than for bryophytes, with both methods of analysis indicating a significant 34.5% increase in the concentrations of these pigments, relative to controls, in angiosperms (n = 8, Fig. 2c). A significant effect of UV-B exposure on ln R for concentrations of these pigments, relative to controls, was not found for bryophytes using either method of analysis (n = 6; Fig. 2c). It is important to note, however, that the latter data were all derived from one species of bryophyte sampled from a mixture of lamp and non-manipulative experiments in different years (Appendix 1). There was also a marginally significant effect of plant form on ln R for F_v/F_m in unweighted analyses (Table 1), with a reduction of 2.2% in this parameter in angiosperms, but an increase of 4.5% in bryophytes in response to UV-B exposure. However, neither response ratio was significantly different from zero (data not shown).

Effects of region

Unweighted analyses indicated different response ratios for carotenoid concentration in studies based in the Arctic and Antarctic (Table 1). There was no effect of UV-B treatment on ln R for carotenoid concentrations in plant tissues in the Arctic (n = 9, P>0.05), but ln R for concentrations of these pigments increased by 17.1% in Antarctic studies (n = 6; Fig. 2d). Unweighted and weighted analyses showed there to be an effect of region on ln R for SLA, with the former analyses also indicating an effect on total leaf area (Table 1). The response ratios for these parameters did not differ from zero in Arctic studies (n = 10 and 14, respectively, both P>0.05), but were respectively reduced by 25.3% and 21.4% in Antarctic experiments (n = 4 and 3, respectively; Fig. 2e, f). It should be noted, however, that the latter data were all derived from work by one research group on two plant species (Appendix 1). Unweighted analyses also showed there to be a marginally significant effect of region on ln R for total biomass (Table 1), with a mean increase of 8.5% in this parameter in Arctic studies, but a 10.4% decrease in Antarctic studies. However, neither response ratio was significantly different from zero (data not shown). Although there was no main effect of region on plant height (Table 1), separate analyses indicated that there was a significant 8.9% reduction in height when plants had been exposed to UV-B radiation applied from lamps simulating 15% ozone depletion in Arctic studies (n = 10; unweighted analyses P<0.01, weighted P<0.05; data not shown).

Associations between response ratios and predictor variables

The percentage difference in UV-B_{PAS} dose between treatment and control plots was a significant predictor for four untransformed response ratios (Table 2). The response ratio for concentrations of UV-B absorbing compounds, expressed per unit of mass, was positively associated with the difference in UV-B_{PAS} dose between control and treatment plots (Table 2). There were consistent increases and decreases in the response ratios for these pigments in non-manipulative and screen studies, respectively (Fig. 3a). The association between the two variables was best described by a quadratic function (Fig. 3a). In lamp experiments, the range in response ratios for UV-B absorbing compounds was considerable, varying between 0.7 and 1.2, compared with the ranges for screen and non-manipulative studies of 0.8 to 1.0 and 1.1 to 1.4, respectively (Fig. 3a). A linear association was found for concentrations of carotenoids: there was a positive association between the response ratios for the concentrations of these pigments and difference in UV-B_{PAS} dose, with unweighted analyses indicating significant 22.7% increases in the concentrations of these pigments in non-manipulative studies, but lamps and screens having no effect on carotenoid concentrations (Fig. 3b). Aboveground biomass was negatively and linearly associated with the difference in UV-B_{PAS} dose between treatment and control plots (Fig. 3c). Both unweighted and weighted analyses indicated that shielding plants from UV-B radiation under screens significantly increased aboveground biomass by 27.5%, while exposure to UV-B from lamps had no significant effect on this parameter (Fig. 3c). Leaf area was also negatively associated with difference in UV-B_{PAS} dose, with unweighted and weighted analyses both indicating a significant 34.5% increase in the response ratio for this parameter when UV-B was removed from solar radiation with screens, but no effect on the ratio when supplemental UV-B radiation had been applied from lamps (Fig. 3d).

One significant association between the duration of exposure to UV-B radiation and untransformed response ratios was recorded: the ratio for carotenoid concentration decreased linearly with the length of exposure to UV-B radiation (Fig. 3b, *inset*). The duration of exposure to UV-B was otherwise not associated with untransformed response ratios (r^2 adj. = 0.228 – 0.258; all P>0.05; data not shown).

Discussion

Here we show, using a combination of weighted and unweighted meta-analyses, that the exposure of polar bryophytes and angiosperms to UV-B radiation increases the concentration of UV-B absorbing compounds in leaves and thalli by 7% and 25% (expressed per unit of mass and area, respectively), and decreases the height and aboveground biomass of plants by 10% and 15%, respectively. These results are strikingly similar to those from a previous meta-analysis of plant response to simulated stratospheric ozone depletion (Searles *et al*., 2001). In the previous analysis, which used data from 62 studies, predominantly on temperate angiosperms and gymnosperms exposed to supplemental UV-B radiation from fluorescent UV lamps, UV-B absorbing compounds were found to be increased in concentration by 10% following UV-B exposure, height was diminished by 3% and shoot biomass was reduced by 16%, but only when studies simulated > 20% loss of ozone from the atmosphere (Searles *et al*., 2001). Furthermore, total leaf area, which the weighted analyses in the current study indicated was

reduced by 6% following UV-B exposure, was also reduced by 13% in the previous analysis (Searles *et al*., 2001). Other parameters common to the meta-analysis here and that of Searles *et al*. (2001), *viz*., chlorophyll and carotenoid concentrations, P_n and F_v/F_m, were each unaffected by UV-B exposure, supporting the view that photosynthesis and the concentrations of associated pigments are unaffected by UV-B radiation in field experiments (e.g. Fiscus & Booker, 1995; Allen *et al*., 1998; Sullivan & Rozema, 1999).

Although Searles *et al*. (2001) did not analyse data on DNA damage in plant foliage, the current study also recorded a significant 90% increase in the accumulation of CPDs in DNA following exposure to UV-B radiation. This substantial increase in DNA damage in the foliage of plants exposed to elevated UV-B radiation in treatment plots relative to that in control plots is apparently owing to unrealistically high doses of UV-B radiation having been applied to plants: two of the highest response ratios for this parameter were derived from lamp studies that applied Setlow (1974)-weighted doses of UV-B radiation to treatment plots at an order of magnitude higher than were received in control plots (Lud *et al*., 2002; 2003). However, even though the frequency of CPDs in DNA was tripled by exposure to elevated UV-B radiation in these studies, repair took place rapidly, with DNA damage in plants in treatment plots falling to the same level as in control plots within 12 h post irradiation (Lud *et al*., 2002; 2003). The recent finding that fewer DNA photoproducts accumulate in desiccated, compared with hydrated, mosses also suggests that screening and passive defence mechanisms are well developed in Antarctic bryophytes (Turnbull *et al*., 2009).

Bryophytes are thought to respond in the same way as vascular plants to UV-B exposure (Rozema *et al*., 2005). The analyses here support this view: although 60% of the plant species included in our analyses were bryophytes, similar results were found to those of Searles *et al*. (2001), who only analysed data from angiosperms and gymnosperms. Only one response ratio differed between these two plant forms in the current study. The higher response ratio of UV-B absorbing compounds expressed per unit of area for angiosperms than for bryophytes corroborates earlier suggestions that screening pigments in bryophytes are less responsive to UV-B exposure than those in angiosperms (Gwynn-Jones *et al*., 1999). However, this probably reflects a species-specific response, since data from only one study (Lappalainen *et al*., 2008) on a single bryophyte species were included in the analysis of these pigments. We did not anticipate finding this effect: since higher plants are able to attenuate UV-B radiation through the presence of epidermal hairs, cuticles and surface waxes on leaves (Day, 1993), they should not need to synthesize screening pigments to the same extent as bryophytes, which tend to lack these protective features (Gehrke, 1999).

Our study demonstrates that the method which is used to alter the dose of UV-B radiation received by plants has an effect on the synthesis of UV-B absorbing compounds in foliage. The analyses show that exposure to UV-B radiation in screen and non-manipulative studies increases the concentrations of UV-B absorbing compounds in leaves and thalli by 12% and 17%, respectively, but that UV-B applied from fluorescent UV lamps fails to elicit a change in the concentration of these compounds. These findings suggest that the use of fluorescent UV lamps in polar environments does not elicit the same response as at lower latitudes, since the exposure of plants to UV-B applied from fluorescent lamps, typically at mid-latitudes, significantly increases the concentrations of UV-B

absorbing compounds in foliage by 10% (Searles *et al*., 2001). It is unclear as to why this difference might exist. It is possible that it can be accounted for by higher doses of UV-B radiation having been applied to plants in the experiments analysed by Searles *et al*. (2001). Although the mean level of ozone depletion simulated in the lamp studies analysed here (18%) fell within the range of ozone depletion simulated in the majority of studies analysed in the previous meta-analysis (10-20%), the absolute doses of UV-B radiation applied to plants for a given level of ozone depletion in polar habitats will be less than at mid-latitudes because of lower solar elevation angles at higher latitudes. Another issue that might have contributed to the lack of effect of UV-B exposure on the concentrations of UV-B absorbing compounds in plant tissues could have been the application of inappropriate biological weighting functions. Recently, it has been suggested that the generalised plant action spectrum (Caldwell, 1971), which is often used to weight supplemental UV-B radiation, results in unrealistically low UV-B doses being applied from fluorescent UV lamps to vegetation (Flint & Caldwell, 2003; Caldwell *et al*., 2006). Our analyses also indicate that lamps introduce considerable heterogeneity into plant response to UV-B exposure in polar habitats, with a wider range in response ratios for UV-B absorbing compounds in lamp studies than in screen or non-manipulative studies, indicating positive responses in some lamp experiments and null, or negative, responses in others. We suspect that the difficulties of maintaining stable outputs from fluorescent UV lamps at low temperatures may be responsible for some of the heterogeneity in screening pigment response to UV-B exposure identified here (Johanson & Zeuthen, 1998; Rozema *et al*., 2001).

In their narrative review of UV-B effects on polar vegetation, Rozema *et al*. (2005) conclude that plant response to UV-B exposure may differ between the Arctic and Antarctic. Our analyses suggest the same effect, showing that concentrations of carotenoids increase, and that leaf area and SLA decrease, in Antarctic experiments, but that no effects occur on these parameters in Arctic studies. However, these apparent differences in plant response between polar regions can largely be explained by the different methodological approaches used in the two regions: in the current study, the data for leaf area and SLA from Antarctic experiments were all derived from studies using screens (Ruhland & Day, 2001; Xiong & Day, 2001; Xiong *et al*., 2002), which have consistent effects on these leaf parameters. Most, but not all, of the Arctic studies from which leaf area and SLA were derived applied UV-B radiation from fluorescent UV lamps, with only two studies (Albert *et al*., 2005b; Albert *et al*., 2008) using screens. Our analyses thus suggest that the main reason plant response differs between the two polar regions is because screens, which have consistent effects on plant performance, are typically used in the Antarctic, and fluorescent UV lamps, which have less consistent effects, are more frequently used in the Arctic.

Rozema *et al*. (2005) surmise that, with the exception of studies close to Anvers Island in the maritime Antarctic (e.g. Day *et al*., 1999; 2001), most field-based lamp or screen studies indicate negligible effects of UV-B exposure on plants. Whilst our data support this view for lamp studies, they do not corroborate this view for screens, with analyses for screen studies showing effects on plant response irrespective of geographical location. For example, for UV-B absorbing compounds, in addition to data from screen studies from close to Anvers Island (Ruhland & Day, 2000; Ruhland & Day, 2001; Xiong & Day, 2001; Xiong *et al*., 2002), data from one Antarctic and three Arctic screen

studies (Newsham *et al*., 2005; Albert *et al*., 2005b; Albert *et al*., 2008; Kotilainen *et al*., 2008), were also included in the meta-analysis, all of which showed positive response ratios for concentrations of UV-B absorbing compounds expressed on a mass basis. It thus seems likely that the attenuation of UV-B radiation by screens does have consistent and generic effects on plant performance in polar field experiments.

Similar results were found in the current study when data were analysed using weighted or unweighted meta-analyses. This was most probably owing to the similar level of replication used in most of the lamp and screen experiments analysed here, which usually employed a modest level of replication, with typically three or four control or treatment plots used in each study. As in previous meta-analyses (e.g. Searles *et al*., 2001), we noted effects of data from apparently pseudoreplicated (Hurlbert, 1984) studies on the weighted analyses, with these data having anomalously large effects on the analyses because of the extra weight given to them, as a result of the large reciprocals of the sampling variances associated with their response ratios. These data were thus removed from the weighted analyses, constraining our ability to detect UV-B treatment effects on response ratios. Another factor that constrained our ability to detect effects on the response ratios was the low number of observations for certain parameters, which arose partly from the limited number of studies in the literature on the UV-B responses of polar vegetation, and partly from the selection criteria that we imposed on the data before they were included in the analysis. Caution is needed when interpreting the data for certain parameters because of the low number of observations, particularly those for photosynthetic parameters, belowground biomass, individual leaf mass and DNA damage. Our analyses do identify, however, that additional data are needed in the literature on the responses of these parameters to UV-B exposure in polar environments.

Although we found the percentage difference in $UV\text{-}B_{PAS}$ dose between treatment and control plots to be a predictor for four response ratios in the current study, the duration of exposure to UV-B treatment had little apparent influence on the response ratios. Only that for carotenoid concentration was associated with the duration of exposure, with the data indicating a reduction in the magnitude of response to UV-B exposure with increasing time. These data broadly indicate that the magnitude of effect of UV-B radiation on plant response does not increase or decrease with longer periods of exposure, corroborating the view that exposure to UV-B radiation does not have cumulative long-term effects on plant growth in polar regions (Rozema *et al*., 2006). For pigments, these data also broadly support the view that plants can rapidly acclimate to UV-B exposure, even in polar habitats at temperatures close to freezing point (Newsham *et al*., 2002; Newsham *et al*., 2005; Dunn & Robinson, 2006; Snell *et al*., 2009).

Given the responses shown here, then in broad terms, what will have been the likely consequences of increased UV-B exposure for polar vegetation in recent years? Assuming cloudless skies, then the mean 15% springtime loss of ozone from the stratosphere over the Arctic in the last two decades (World Meteorological Organization, 2007) will have led to a 30% increase at solar noon in $UV\text{-}B_{PAS}$ irradiance in late spring at 68° N (Johanson *et al*., 1995b), which, as reported here, reduces plant height by 9%. Data in Fig. 3 suggest that the 30% springtime loss of ozone from the stratosphere over the Antarctic in the last two decades (World Meteorological Organization, 2007), which has led to

an approximate doubling in UV-B_{PAS} exposure at solar noon in late spring at 64°-67° S, latitudes at which the majority of Antarctic UV-B studies have been made (Xiong *et al*., 2002; Newsham *et al*., 2002; Dunn & Robinson, 2006), might have reduced aboveground biomass by some 20%. The data in Fig. 3 also suggest that although there are unlikely to have been effects on the concentrations of UV-B absorbing compounds in plant tissues in the Arctic in recent years, the doubling in UV-B_{PAS} exposure in the Antarctic would have led to an approximate 5% increase in the concentrations of these compounds in leaves and thalli. Recent studies corroborate this view, with larger increases over the last three decades in the concentrations of UV-B absorbing compounds in clubmoss tissues sampled from South Georgia in the Scotia Sea than in those from Greenland (Lomax *et al*., 2008). Such increases will most probably have had effects on decomposition and herbivory (Caldwell *et al*., 1995; Paul & Gwynn-Jones, 2003), as well as subtle negative effects on plant growth, owing to the carbon drain associated with synthesizing flavonoids in leaves and thalli (Snell *et al*., 2009).

Conclusions

In broad terms, this meta-analysis indicates that vegetation in polar regions responds to UV-B radiation exposure in a similar way to that at lower latitudes, often by increasing the synthesis of UV-B absorbing compounds in leaves and thalli. Photosynthetic parameters show little consistent response to UV-B exposure, but there is evidence of negative effects on aboveground biomass, plant height and DNA. Given that a recovery of the ozone layer is not expected for several decades (World Meteorological Organization, 2007), we advocate further studies, preferably using the same methodologies in the Arctic and Antarctic, to assess the broader influence of UV-B radiation on overall ecosystem functioning in polar regions.

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Figure legends

Fig. 1 Untransformed response ratios for the effects of UV-B exposure on measures of pigmentation, photosynthesis, growth, biomass and DNA damage in polar vegetation. Where 95% confidence interval bars do not cross the horizontal dotted line, natural logarithm-transformed response ratios were significantly different from zero in unweighted analyses (* P<0.05, ** P <0.01 and *** P<0.001). All response ratios indicated as significantly different from zero were also significant at P<0.05 in weighted analyses, including that for leaf area. Numbers of observations for each parameter are shown in Table 1. *Abbreviations*: UV-B_{ac} mass and UV-B_{ac} area, UV-B absorbing compounds expressed per unit of mass and area, respectively; carots, carotenoids; chl, chlorophyll; F_v/F_m, maximum quantum yield of PSII; Φ_{PSII}, actual quantum yield of PSII; P_n, net photosynthesis; AGB, BGB and TB; above-, belowground and total biomass, respectively; SLA, specific leaf area; CPDs, cyclobutane pyrimidine dimers.

Fig. 2 The influence of categorical variables on untransformed response ratios for (a) UV-B absorbing compounds expressed per unit of mass, (b) belowground biomass, (c) UV-B absorbing compounds expressed per unit of area, (d) carotenoids, (e) leaf area and (f) specific leaf area. Where 95% confidence interval bars do not cross the horizontal dotted lines, natural logarithm-transformed response ratios were significantly different from zero in unweighted analyses (* P<0.05, ** P <0.01 and *** P<0.001). All response ratios indicated as significantly different from zero were also significant at P<0.05 in weighted analyses. See Table 1 for P values from unweighted analyses, indicating effects of categorical variables on response ratios. *Abbreviation*: non-manip, non-manipulative studies.

Fig. 3 Untransformed response ratios for (a) UV-B absorbing compounds expressed per unit of mass, (b) carotenoid concentration, (c) aboveground biomass and (d) leaf area as a function of percentage difference in UV-B_{PAS} dose between treatment and control plots in (○) screen, (●) lamp and (●) non-manipulative studies. Note that the inverses of response ratios are shown for screen studies. Dashed lines indicate lines of best fit. Line in (a) is a quadratic function. See Table 2 for details of regression analyses. Significant differences, from unweighted analyses, between the natural logarithm-transformed response ratios for each method and zero are indicated by * P<0.05, ** P <0.01 and *** P<0.001 in (b)-(d). All significant effects were also significant at P<0.05 in weighted analyses, except that in (b), which could not be analysed in this way. See Fig. 2a for the significance of effects of UV-B exposure on the response ratios shown in (a). *Inset* in (b) is association between untransformed response ratios for carotenoid concentration and duration of exposure to UV-B radiation.

Table 1. Results from unweighted and weighted meta-analyses testing for the effects of UV-B exposure and categorical variables (methodology, plant form and polar region) on the pigmentation, photosynthesis, biomass, growth and DNA damage of polar vegetation. *P* values from unweighted analyses are shown, with significant values in bold. Those significant at $P<0.05$ and below in weighted analyses are indicated by (*). All data were natural logarithm-transformed prior to analysis. Number of observations (*n*) for unweighted analyses are shown, with those for weighted analyses in parentheses.

	pigmentation				photosynthesis			biomass, growth and DNA damage							
	UV-B_{ac} mass	UV-B_{ac} area	carotenoids	chlorophyll *a* + *b*	F_v/F_m	Φ_{PSII}	P_n	above-ground biomass	below-ground biomass	total biomass	height	leaf area	leaf mass	SLA	CPDs
n	42 (30)	14 (10)	15 (12)	17 (14)	14 (14)	7 (7)	9 (9)	18 (15)	7 (7)	14 (9)	19 (19)	14 (13)	10 (9)	17 (12)	12 (10)
UV-B exposure	**0.015** (*)	**<0.001** (*)	0.713	0.396	0.543	0.956	0.125	**0.003** (*)	0.440	0.817	**<0.001** (*)	0.165 (*)	0.914	0.503	**0.030** (*)
methodology[1]	**0.043**[†]	0.377[†]	0.220[†]	0.536	0.735	0.879	0.126	0.893	**0.043**	0.117	0.719	0.128	-	0.359	0.174[†]
plant form[2]	0.420	**0.015** (*)	0.626	0.621	0.054	0.196	0.082	0.709	-	0.934	0.719	-	0.887	0.462	0.220
region[3]	0.847	0.234	**0.039**	0.664	0.438	0.709	0.989	0.534	0.515	0.051	0.719	**0.020**	-	**<0.001** (*)	0.400

[1]lamp, screen or non-manipulative studies; [2]bryophyte or angiosperm; [3]Arctic or Antarctic. Dashes indicate that analyses were not possible owing to insufficient replication, [†]indicate that weighted analyses were not possible since data from non-manipulative studies could not be included. See Fig. 1 for abbreviations.

Table 2. Number of observations (*n*), adjusted r^2 and *P* values from regressions between untransformed response ratios and percentage difference in UV-B_{PAS} between treatment and control plots. Significant *P* values are marked in bold. Analyses were not made on photosynthetic parameters, height, leaf mass or SLA because of insufficient replication.

	response	*n*	adj. r^2 (%)	*P*
pigmentation	UV-B_{ac} mass	29	30.7*	**0.001**
	UV-B_{ac} area	10	21.4	0.100
	carotenoids	8	55.4	**0.021**
	chlorophyll *a* + *b*	9	0.0	0.368
biomass, growth and DNA damage	aboveground biomass	13	43.9	**0.008**
	belowground biomass	5	0.0	0.887
	total biomass	10	0.0	0.399
	leaf area	13	45.8	**0.007**
	CPDs	7	0.0	0.679

* best fit provided by a quadratic function. Abbreviations as in Fig. 1.

Appendix 1. Literature from which the data for the meta-analysis were taken

				pigmentation				photosynthesis			biomass, growth and DNA damage							
reference	method	species (plant form)	region	UV-B_{ac} mass	UV-B_{ac} area	carots	chl $a + b$	F_v/F_m	Φ_{PSII}	P_n	AGB	BGB	TB	ht	leaf area	leaf mass	SLA	CPDs
Albert *et al*. (2005a)	S	*Salix arctica* (A)	Arc					x										
Albert *et al*. (2005b)	S	*Salix arctica* (A)	Arc	x				x								x	x	
Albert *et al*. (2008)†	S	*Vaccinium uliginosum* (A)	Arc	x				x		x	x	x	x		x	x	x	
Bredahl *et al*. (2004)	S	*Salix arctica* (A)	Arc					x		x								
		Vaccinium uliginosum (A)						x										
Kotilainen *et al*. (2008)	S	*Alnus incana* (A)	Arc	x														
		Betula pubescens (A)		x														
Rinnan *et al*. (2005)	S	*Vaccinium uliginosum* (A)	Arc									x						
Day *et al*. (2001)	S	*Colobanthus quitensis* (A)	Ant								x			x				
		Deschampsia antarctica (A)									x			x				
Day *et al*. (2008)	S	*Colobanthus quitensis* (A)	Ant								x							
		Deschampsia antarctica (A)									x							
Smith (1999)†	S	*Bryum argenteum* (B)	Ant										x					
		B. pseudotriquetrum (B)											x					
		Ceratodon purpureus (B)											x					
Newsham *et al*. (2005)	S	*Cephaloziella varians* (B)	Ant	x			x											
Ruhland & Day (2000)	S	*Colobanthus quitensis* (A)	Ant		x									x				
		Deschampsia antarctica (A)			x									x				
Ruhland & Day (2001)	S	*Colobanthus quitensis* (A)	Ant		x		x								x			
Xiong & Day (2001)	S	*Colobanthus quitensis* (A)	Ant	x	x	x	x	x	x	x	x	x	x		x		x	
		Deschampsia antarctica (A)		x	x	x	x	x	x	x	x	x	x		x		x	
Xiong *et al*. (2002)†	S	*Colobanthus quitensis* (A)	Ant	x	x		x				x	x	x	x	x			
Newsham *et al*. (2002)	NM	*Cephaloziella varians* (B)	Ant	x		x												
		Sanionia uncinata (B)		x		x												
Newsham (2003)	NM	*Andreaea regularis* (B)	Ant	x		x												
Dunn & Robinson (2006)	NM	*Bryum pseudotriquetrum* (B)	Ant	x														
		Ceratodon purpureus (B)		x														

		Schistidium antarctici (B)		x																					
Turnbull & Robinson (2009)	NM	*Bryum pseudotriquetrum* (B)	Ant																						x
		Ceratodon purpureus (B)																							x
Gehrke (1998)	L	*Sphagnum fuscum* (B)	Arc	x			x		x					x			x								
Gehrke (1999)	L	*Hylocomium splendens* (B)	Arc	x			x		x					x					x						
		Polytrichum commune (B)		x			x		x										x			x			
Gwynn-Jones (2001)	L	*Calamagrostis purpurea* (A)	Arc	x										x		x		x							
Johanson *et al*. (1995a)	L	*Empetrum hermaphroditum* (A)	Arc																				x		
		Vaccinium vitis-idaea (A)																		x			x		
		V. myrtillus (A)																		x			x		
		V. uliginosum (A)																		x			x		
Johanson (1997)[‡]	L	*Vaccinium vitis-idaea* (A)	Arc		x																				
		V. myrtillus (A)			x																				
Lappalainen *et al*. (2008)[†]	L, NM	*Pleurozium schreberi* (B)	Arc	x	x		x		x					x					x				x		
Mendez *et al*. (1999)	L	*Pinguicula vulgaris* (A)	Arc	x										x		x		x			x				
Niemi *et al*. (2002a)	L	*Sphagnum balticum* (B)	Arc				x		x																
		S. papillosum (B)					x		x																
		Eriophorum vaginatum (A)									x		x												
Niemi *et al*. (2002b)	L	*Sphagnum papillosum* (B)	Arc	x			x		x																
		S. angustifolium (B)		x			x		x																
		S. magellanicum (B)		x			x		x																
Phoenix *et al*. (2000)	L	*Vaccinium vitis-idaea* (A)	Arc											x						x			x		
		V. myrtillus (A)												x						x			x		
		V. uliginosum (A)												x						x			x		
		Calamagrostis lapponica (A)												x						x			x		
Rozema *et al*. (2006)[†]	L	*Salix polaris* (A)	Arc	x																x					x
Semerdjieva *et al*. (2003)	L	*Vaccinium vitis-idaea* (A)	Arc	x																					
		V. myrtillus (A)		x																					
		V. uliginosum (A)		x																					
Boelen *et al*. (2006)[†]	L	*Chorisodontium aciphyllum* (B)	Ant	x																					x
		Polytrichum strictum (B)		x																					x
		Sanionia uncinata (B)		x																					x

		Warnstorfia sarmentosa (B)		x								x
Lud *et al*. (2001b)	L	*Deschampsia antarctica* (A)	Ant					x	x			
Lud *et al*. (2002)	L	*Sanionia uncinata* (B)	both					x	x	x		x
Lud *et al*. (2003)	L, S	*Sanionia uncinata* (B)	Ant		x	x		x	x	x		x

'x' indicates that a parameter was included in the meta-analysis. †Additional data provided by the authors as pers. comm.. ‡Cited in Björn *et al*. (1999). *Abbreviations*: Arc, Arctic; Ant, Antarctic; B, bryophyte; A, angiosperm; S, screen; NM, non-manipulative; L, lamp; ht, height. See Fig. 1 for other abbreviations.

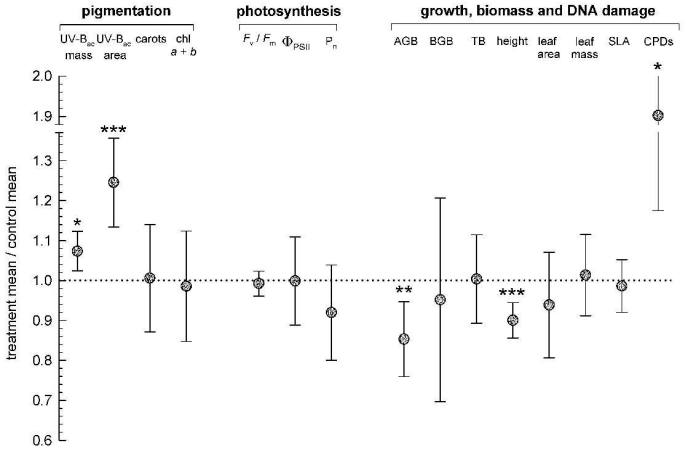

Fig. 1 Untransformed response ratios for the effects of UV-B exposure on measures of pigmentation, photosynthesis, growth, biomass and DNA damage in polar vegetation. Where 95% confidence interval bars do not cross the horizontal dotted line, natural logarithm-transformed response ratios were significantly different from zero in unweighted analyses (* P<0.05, ** P <0.01 and *** P<0.001). All response ratios indicated as significantly different from zero were also significant at P<0.05 in weighted analyses, including that for leaf area. Numbers of observations for each parameter are shown in Table 1. Abbreviations: UV-Bac mass and UV-Bac area, UV-B absorbing compounds expressed per unit of mass and area, respectively; carots, carotenoids; chl, chlorophyll; Fv/Fm, maximum quantum yield of PSII; ΦPSII, actual quantum yield of PSII; Pn, net photosynthesis; AGB, BGB and TB; above-, belowground and total biomass, respectively; SLA, specific leaf area; CPDs, cyclobutane pyrimidine dimers.
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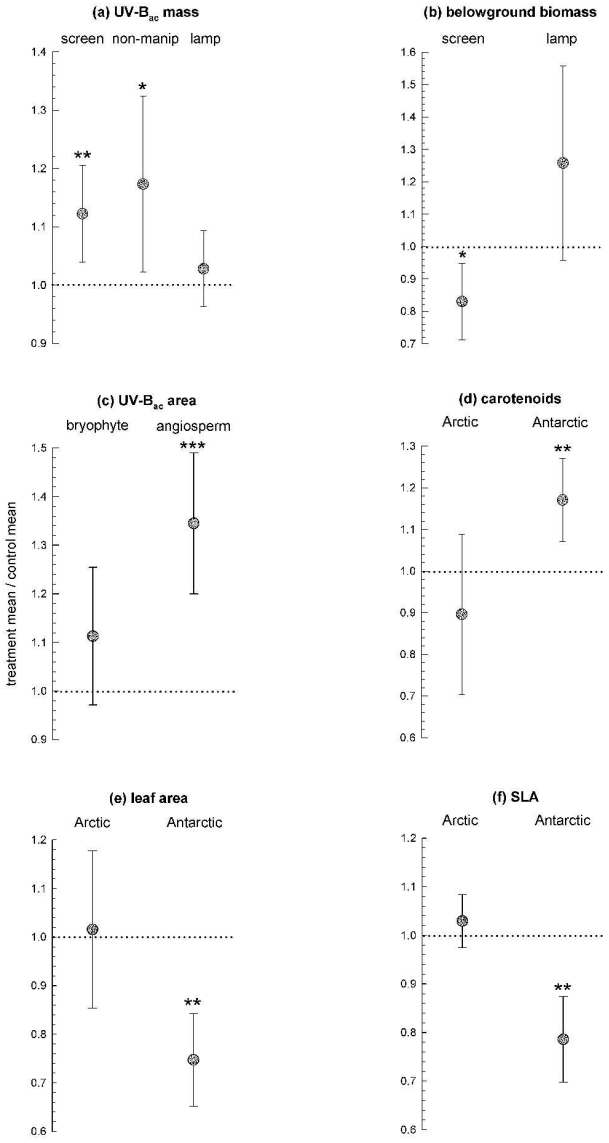

Fig. 2 The influence of categorical variables on untransformed response ratios for (a) UV-B absorbing compounds expressed per unit of mass, (b) belowground biomass, (c) UV-B absorbing compounds expressed per unit of area, (d) carotenoids, (e) leaf area and (f) specific leaf area. Where 95% confidence interval bars do not cross the horizontal dotted lines, natural logarithm-transformed response ratios were significantly different from zero in unweighted analyses (* P<0.05, ** P <0.01 and *** P<0.001). All response ratios indicated as significantly different from zero were also significant at P<0.05 in weighted analyses. See Table 1 for P values from unweighted analyses, indicating effects of categorical variables on response ratios. Abbreviation: non-manip, non-manipulative studies.
209x296mm (500 x 500 DPI)

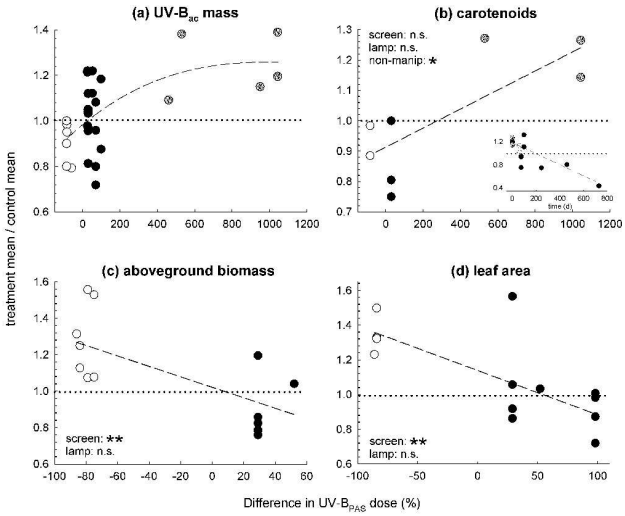

Fig. 3 Untransformed response ratios for (a) UV-B absorbing compounds expressed per unit of mass, (b) carotenoid concentration, (c) aboveground biomass and (d) leaf area as a function of percentage difference in UV-BPAS dose between treatment and control plots in (□) screen, (□) lamp and (□) non-manipulative studies. Note that the inverses of response ratios are shown for screen studies. Dashed lines indicate lines of best fit. Line in (a) is a quadratic function. See Table 2 for details of regression analyses. Significant differences, from unweighted analyses, between the natural logarithm-transformed response ratios for each method and zero are indicated by * P<0.05, ** P <0.01 and *** P<0.001 in (b)-(d). All significant effects were also significant at P<0.05 in weighted analyses, except that in (b), which could not be analysed in this way. See Fig. 2a for the significance of effects of UV-B exposure on the response ratios shown in (a). Inset in (b) is association between untransformed response ratios for carotenoid concentration and duration of exposure to UV-B radiation.

209x296mm (500 x 500 DPI)

Table 1. Results from unweighted and weighted meta-analyses testing for the effects of UV-B exposure and categorical variables (methodology, plant form and polar region) on the pigmentation, photosynthesis, biomass, growth and DNA damage of polar vegetation. *P* values from unweighted analyses are shown, with significant values in bold. Those significant at $P<0.05$ and below in weighted analyses are indicated by (*). All data were natural logarithm-transformed prior to analysis. Number of observations (*n*) for unweighted analyses are shown, with those for weighted analyses in parentheses.

	pigmentation				photosynthesis			biomass, growth and DNA damage							
	UV-B_{ac} mass	UV-B_{ac} area	carotenoids	chlorophyll *a* + *b*	F_v/F_m	Φ_{PSII}	P_n	above-ground biomass	below-ground biomass	total biomass	height	leaf area	leaf mass	SLA	CPDs
n	42 (30)	14 (10)	15 (12)	17 (14)	14 (14)	7 (7)	9 (9)	18 (15)	7 (7)	14 (9)	19 (19)	14 (13)	10 (9)	17 (12)	12 (10)
UV-B exposure	**0.015** (*)	**<0.001** (*)	0.713	0.396	0.543	0.956	0.125	**0.003** (*)	0.440	0.817	**<0.001** (*)	0.165 (*)	0.914	0.503	**0.030** (*)
methodology[1]	**0.043**[†]	0.377[†]	0.220[†]	0.536	0.735	0.879	0.126	0.893	**0.043**	0.117	0.719	0.128	-	0.359	0.174[†]
plant form[2]	0.420	**0.015** (*)	0.626	0.621	0.054	0.196	0.082	0.709	-	0.934	0.719	-	0.887	0.462	0.220
region[3]	0.847	0.234	**0.039**	0.664	0.438	0.709	0.989	0.534	0.515	0.051	0.719	**0.020**	-	**<0.001** (*)	0.400

[1]lamp, screen or non-manipulative studies; [2]bryophyte or angiosperm; [3]Arctic or Antarctic. Dashes indicate that analyses were not possible owing to insufficient replication, [†]indicate that weighted analyses were not possible since data from non-manipulative studies could not be included. See Fig. 1 for abbreviations.

Table 2. Number of observations (*n*), adjusted r^2 and *P* values from regressions between untransformed response ratios and percentage difference in UV-B_{PAS} between treatment and control plots. Significant *P* values are marked in bold. Analyses were not made on photosynthetic parameters, height, leaf mass or SLA because of insufficient replication.

	response	*n*	adj. r^2 (%)	*P*
pigmentation	UV-B_{ac} mass	29	30.7*	**0.001**
	UV-B_{ac} area	10	21.4	0.100
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	CPDs	7	0.0	0.679

* best fit provided by a quadratic function. Abbreviations as in Fig. 1.

Appendix 1. Literature from which the data for the meta-analysis were taken

reference	method	species (plant form)	region	pigmentation				photosynthesis			biomass, growth and DNA damage							
				UV-B_{ac} mass	UV-B_{ac} area	carots	chl $a + b$	F_v/F_m	Φ_{PSII}	P_n	AGB	BGB	TB	ht	leaf area	leaf mass	SLA	CPDs
Albert *et al*. (2005a)	S	*Salix arctica* (A)	Arc					x										
Albert *et al*. (2005b)	S	*Salix arctica* (A)	Arc	x				x								x	x	
Albert *et al*. (2008)†	S	*Vaccinium uliginosum* (A)	Arc	x				x		x	x	x	x		x	x	x	
Bredahl *et al*. (2004)	S	*Salix arctica* (A)	Arc					x		x								
		Vaccinium uliginosum (A)						x										
Kotilainen *et al*. (2008)	S	*Alnus incana* (A)	Arc	x														
		Betula pubescens (A)		x														
Rinnan *et al*. (2005)	S	*Vaccinium uliginosum* (A)	Arc									x						
Day *et al*. (2001)	S	*Colobanthus quitensis* (A)	Ant								x			x				
		Deschampsia antarctica (A)									x			x				
Day *et al*. (2008)	S	*Colobanthus quitensis* (A)	Ant								x							
		Deschampsia antarctica (A)									x							
Smith (1999)†	S	*Bryum argenteum* (B)	Ant										x					
		B. pseudotriquetrum (B)											x					
		Ceratodon purpureus (B)											x					
Newsham *et al*. (2005)	S	*Cephaloziella varians* (B)	Ant	x			x											
Ruhland & Day (2000)	S	*Colobanthus quitensis* (A)	Ant		x									x				
		Deschampsia antarctica (A)			x									x				
Ruhland & Day (2001)	S	*Colobanthus quitensis* (A)	Ant		x		x								x			
Xiong & Day (2001)	S	*Colobanthus quitensis* (A)	Ant	x	x	x	x	x	x	x	x	x	x		x		x	
		Deschampsia antarctica (A)		x	x	x	x	x	x	x	x	x	x		x		x	
Xiong *et al*. (2002)†	S	*Colobanthus quitensis* (A)	Ant	x	x		x				x	x	x	x	x			
Newsham *et al*. (2002)	NM	*Cephaloziella varians* (B)	Ant	x		x												
		Sanionia uncinata (B)		x		x												
Newsham (2003)	NM	*Andreaea regularis* (B)	Ant	x		x												
Dunn & Robinson (2006)	NM	*Bryum pseudotriquetrum* (B)	Ant	x														
		Ceratodon purpureus (B)		x														

		Schistidium antarctici (B)		x																			
Turnbull & Robinson (2009)	NM	*Bryum pseudotriquetrum* (B)	Ant																				x
		Ceratodon purpureus (B)																					x
Gehrke (1998)	L	*Sphagnum fuscum* (B)	Arc	x			x		x				x		x		x						
Gehrke (1999)	L	*Hylocomium splendens* (B)	Arc	x			x		x					x									
		Polytrichum commune (B)		x			x		x					x				x					
Gwynn-Jones (2001)	L	*Calamagrostis purpurea* (A)	Arc	x									x		x		x						
Johanson *et al*. (1995a)	L	*Empetrum hermaphroditum* (A)	Arc																		x		
		Vaccinium vitis-idaea (A)															x				x		
		V. myrtillus (A)															x				x		
		V. uliginosum (A)															x				x		
Johanson (1997)[‡]	L	*Vaccinium vitis-idaea* (A)	Arc		x																		
		V. myrtillus (A)			x																		
Lappalainen *et al*. (2008)[†]	L, NM	*Pleurozium schreberi* (B)	Arc	x	x		x		x				x				x				x		
Mendez *et al*. (1999)	L	*Pinguicula vulgaris* (A)	Arc	x									x		x		x		x				
Niemi *et al*. (2002a)	L	*Sphagnum balticum* (B)	Arc				x		x														
		S. papillosum (B)					x		x														
		Eriophorum vaginatum (A)								x		x											
Niemi *et al*. (2002b)	L	*Sphagnum papillosum* (B)	Arc	x			x		x														
		S. angustifolium (B)		x			x		x														
		S. magellanicum (B)		x			x		x														
Phoenix *et al*. (2000)	L	*Vaccinium vitis-idaea* (A)	Arc										x				x				x		
		V. myrtillus (A)											x				x				x		
		V. uliginosum (A)											x				x				x		
		Calamagrostis lapponica (A)											x				x				x		
Rozema *et al*. (2006)[†]	L	*Salix polaris* (A)	Arc	x													x						x
Semerdjieva *et al*. (2003)	L	*Vaccinium vitis-idaea* (A)	Arc	x																			
		V. myrtillus (A)		x																			
		V. uliginosum (A)		x																			
Boelen *et al*. (2006)[†]	L	*Chorisodontium aciphyllum* (B)	Ant	x																			x
		Polytrichum strictum (B)		x																			x
		Sanionia uncinata (B)		x																			x

		Warnstorfia sarmentosa (B)		x								x
Lud *et al*. (2001b)	L	*Deschampsia antarctica* (A)	Ant					x	x			
Lud *et al*. (2002)	L	*Sanionia uncinata* (B)	both					x	x	x		x
Lud *et al*. (2003)	L, S	*Sanionia uncinata* (B)	Ant		x	x		x	x	x		x

'x' indicates that a parameter was included in the meta-analysis. †Additional data provided by the authors as pers. comm.. ‡Cited in Björn *et al*. (1999). *Abbreviations*: Arc, Arctic; Ant, Antarctic; B, bryophyte; A, angiosperm; S, screen; NM, non-manipulative; L, lamp; ht, height. See Fig. 1 for other abbreviations.