Impact of changes in natural UV radiation on pigment composition, physiological and morphological characteristics of the Antarctic moss, Grimmia antarctici.

Sharon A. Robinson  
*University of Wollongong, sharonr@uow.edu.au*

J. D. Turnbull  
*University of Wollongong*

C. E. Lovelock  
*University of Queensland*

Publication Details  
This article was originally published as Robinson, SA, Turnbull, JD Lovelock, CE, Impact of changes in natural UV radiation on pigment composition, surface reflectance and photosynthetic function of the Antarctic moss, Grimmia antarctici, Global Change Biology, 11 (3), 2005, 476-489. Original journal available [here](#). Copyright Blackwell.
Impact of changes in natural UV radiation on pigment composition, physiological and morphological characteristics of the Antarctic moss, Grimmia antarctici.

Abstract
The impact of ambient UV-B radiation on the endemic bryophyte, Grimmia antarctici, was studied over 14 months in East Antarctica. Over recent decades, Antarctic plants have been exposed to the largest relative increase in UV-B exposure as a result of ozone depletion. We investigated the effect of reduced UV and visible radiation on the pigment concentrations, surface reflectance and physiological and morphological parameters of this moss. Plexiglass screens were used to provide both reduced UV levels (77%) and a 50% decrease in total radiation. The screen combinations were used to separate UV photoprotective from visible photoprotective strategies, since these bryophytes are growing in relatively high light environments compared to many mosses. G. antarctici was affected negatively by ambient levels of UV radiation. Chlorophyll content was significantly lower in plants grown under near ambient UV, whilst the relative proportions of photoprotective carotenoids, especially ß-carotene and zeaxanthin, increased. However, no evidence for the accumulation of UV-B absorbing pigments in response to UV radiation was observed. Although photosynthetic rates were not affected, there was evidence of UV effects on morphology. Plants that were shaded showed fewer treatment responses and these were similar to the natural variation observed between moss growing on exposed microtopographical ridges and in more sheltered valleys within the turf. Given that other Antarctic bryophytes possess UV-B absorbing pigments which should offer better protection under ambient UV-B radiation, these findings suggest that G. antarctici may be disadvantaged in some settings under a climate with continuing high levels of springtime UV-B radiation.

Keywords
Schistidium antarctici, anthocyanins, ß-carotene, chlorophyll, chlorophyll fluorescence, leaf morphology, surface reflectance, UV-B absorbing pigments, xanthophyll cycle pigments.

Disciplines
Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

Publication Details
This article was originally published as Robinson, SA, Turnbull, JD Lovelock, CE, Impact of changes in natural UV radiation on pigment composition, surface reflectance and photosynthetic function of the Antarctic moss, Grimmia antarctici, Global Change Biology, 11 (3), 2005, 476-489. Original journal available here. Copyright Blackwell.
Impact of changes in natural UV radiation on pigment composition, physiological and morphological characteristics of the Antarctic moss, *Grimmia antarctici*.

RUNNING TITLE: Impact of UV radiation on an Antarctic moss

Sharon A. Robinson¹, Johanna D. Turnbull¹ and Catherine E. Lovelock²,³

¹Institute for Conservation Biology, University of Wollongong, Northfields Avenue, Wollongong, NSW 2522, Australia

² Smithsonian Environmental Research Center, PO Box 28, Edgewater MD 21037, USA.

³Present address: The Centre for Marine Studies, University of Queensland, St Lucia, QLD 4072 Australia

Date of receipt

Correspondence about this manuscript to:

Dr Sharon Robinson, Institute for Conservation Biology, University of Wollongong, Northfields Avenue, Wollongong, NSW 2522, Australia

Tel (61) 242 21 5753

Fax (61) 242 21 4135

email sharonr@uow.edu.au

Keywords: anthocyanins, β-carotene, chlorophyll, chlorophyll fluorescence, leaf morphology, surface reflectance, UV-B absorbing pigments, xanthophyll cycle pigments.

Abbreviations: A, antheraxanthin; D1_re, 1st derivative of red edge; ETR, electron transport rate; NIR, near infrared; REP, red edge position; TWC, turf water content; UV-B, ultraviolet-B; V, Violaxanthin; WC, water content; Z, zeaxanthin.
Abstract

The impact of ambient UV-B radiation on the endemic bryophyte, *Grimmia antarctici*, was studied over 14 months in East Antarctica. Over recent decades, Antarctic plants have been exposed to the largest relative increase in UV-B exposure as a result of ozone depletion. We investigated the effect of reduced UV and visible radiation on the pigment concentrations, surface reflectance and physiological and morphological parameters of this moss. Plexiglass screens were used to provide both reduced UV levels (77%) and a 50% decrease in total radiation. The screen combinations were used to separate UV photoprotective from visible photoprotective strategies, since these bryophytes are growing in relatively high light environments compared to many mosses. *G. antarctici* was affected negatively by ambient levels of UV radiation. Chlorophyll content was significantly lower in plants grown under near ambient UV, whilst the relative proportions of photoprotective carotenoids, especially β-carotene and zeaxanthin, increased. However, no evidence for the accumulation of UV-B absorbing pigments in response to UV radiation was observed. Although photosynthetic rates were not affected, there was evidence of UV effects on morphology. Plants that were shaded showed fewer treatment responses and these were similar to the natural variation observed between moss growing on exposed microtopographical ridges and in more sheltered valleys within the turf. Given that other Antarctic bryophytes possess UV-B absorbing pigments which should offer better protection under ambient UV-B radiation, these findings suggest that *G. antarctici* may be disadvantaged in some settings under a climate with continuing high levels of springtime UV-B radiation.
Introduction

Depletion of stratospheric ozone, resulting from anthropogenic, atmospheric pollution has led to increased ultraviolet (UV) radiation at the Earth’s surface. The increase in UV-B is most pronounced and consistent over Antarctica, with record levels of ozone depletion reported recently and predicted to continue for several decades (NASA 2004). Increased UV-B levels as a result of the “ozone hole” have been reported as far north as New Zealand, with the most biologically damaging UV-B wavelengths (280—320 nm) increasing by 12% over the past decade (McKenzie et al. 1999).

The plant life on continental Antarctica is limited to bryophytes and other cryptogams. These organisms are desiccation and freezing tolerant, and able to survive frozen beneath snow during the long polar winter. The emergence from snow and the start of the short, growing season currently coincides with an extended period of elevated UV-B radiation due to ozone depletion. In general, organisms which are native to habitats with naturally high levels of UV-B exposure (e.g. alpine and tropical areas) tend to have better developed mechanisms for UV-B tolerance than natives of lower UV environments (Barnes et al. 1987; Caldwell et al. 1982; Ziska et al. 1992). Over recent decades, Antarctic plants have been exposed to the largest relative increase in UV-B exposure as a result of ozone depletion (Madronich et al. 1995). Given that they have historically been exposed to low background UV-B radiation, endemic Antarctic plants may be particularly sensitive to these relatively large increases.

Plant responses to elevated UV-B radiation have been well documented in recent years, especially in relation to agricultural and model plants and in response to elevated UV-B. More recently the results of long term studies of plants in high latitudes have considered the impact of natural increases in UV-B as a result of ozone depletion (Robson et al. 2003; Searles et al. 1999). These studies have demonstrated responses from the molecular to the ecosystem level (Caldwell et al. 2003; Frohnmeyer & Staiger 2003; Jansen et al. 1998).
the plant level UV-B appears to affect growth, morphology and secondary metabolism rather than processes such as photosynthesis (Allen et al. 1998; Pancotto et al. 2003; Searles et al. 2001). Modest reductions in herbaceous plant growth are a common impact of UV-B radiation at mid latitudes (Ballare 2003) and have also been shown for a number of species at high latitudes (Robson et al. 2003; Rousseaux et al. 2001; Searles et al. 1999; Searles et al. 2002). For Antarctic plants, most studies have found little effect on photosynthesis, but growth was affected by exposure to UV-B radiation especially in the two vascular species. In both Deschampsia antarctica and Colobanthus quitensis, shorter, thicker leaves, reduced branching and fewer leaves per shoot were observed with increasing exposure to UV-B radiation (Day et al. 2001; Xiong & Day 2001). In a study of the Antarctic moss Sanionia uncinita, shoot biomass and length were unaffected but shoots had less branching, after 2 years growth under reduced UV-B radiation (Lud et al. 2002).

Although the accumulation of UV-B absorbing compounds, such as flavonoids, is one of the best documented responses to solar UV-B (Caldwell & Flint 1994), it may not be as widespread in high latitude herbaceous plants. In D. antarctica and C. quitensis, although UV-B absorbing pigments were higher after 4 months under ambient rather than reduced UV-B radiation, this trend was not sustained in longer term studies (Lud et al. 2001; Ruhland & Day 2000; Xiong & Day 2001). Long term studies in Tierra del Fuego have also shown that for the majority of herbaceous species studied, solar UV-B does not regulate the accumulation of UV-absorbing compounds (Giordano et al. 2003; Phoenix et al. 2002; Rousseaux et al. 1998; Rousseaux et al. 2001). Mosses are generally assumed to have a low capacity to produce flavonoids (Gwynn-Jones et al. 1999). Two of the five Antarctic bryophytes studied, Grimmia antarctici and Ceratodon purpureus, support this observation, showing low levels of UV-B absorbing compounds and no evidence of stimulation in response to elevated UV-B levels (Dunn 2000; Lovelock & Robinson 2002). However, four Antarctic bryophytes Bryum pseudotriquetrum, S. uncinita,
Andreaea regularis and Cephaloziella varians showed positive correlations between concentrations of UV-B pigments and levels of natural solar UV-B (Dunn 2000; Lovelock & Robinson 2002; Newsham et al. in press; Newsham et al. 2002); confirming that some bryophytes can produce screening pigments (Markham & Given 1988).

Studies have also shown that the ratio of total carotenoids to chlorophyll increases in UV-B exposed Antarctic vascular plants and bryophytes (Newsham et al. 2002; Ruhland & Day 2000; Xiong & Day 2001). In particular, high levels of photoprotective and antioxidant carotenoids have been observed in some Antarctic mosses, and it appears that species with low levels of UV-B absorbing pigments accumulate higher levels of carotenoids, suggesting the possibility that bryophytes may use alternative mechanisms of UV protection (Lovelock & Robinson 2002).

The aim of this field study was to investigate the impact of ambient UV-B radiation on the Antarctic endemic bryophyte *G. antarcticci*. We predicted that this species might be less tolerant to the increasing UV-B radiation that has resulted from ozone depletion, by virtue of its historically low UV-B environment, and its apparent low levels of UV-B screening pigments (Lovelock & Robinson 2002). The study was performed in the Windmill Islands region of Antarctica where extensive beds of this species are found. We investigated the effect of reduced UV and visible radiation on the pigment concentrations, surface reflectance and physiological and morphological characteristics of the moss. Four screen combinations were used to investigate the impact of both a decrease in ambient UV flux and a 50% decrease in total radiation. The latter were used to separate UV photoprotective from visible photoprotective strategies, since these bryophytes are growing in relatively high light environments compared to many mosses.
Materials and methods

Study site and experimental treatments

The Windmill Islands region of East Antarctica (66˚17’S, 110˚32’E), consists of a series of low-lying peninsulas and islands, which become partially ice-free during the summer melt period. The ice-free habitat occurs in a 35 x 15 km area, supporting four bryophyte species including the endemic moss species Grimmia antarctici Card. (= Schistidium antarctici, Card.) used in this study. Moss turves have a distinctive undulating microtopography caused by cryo-perturbation of the moss beds.

Screening treatments were established on two peninsulas approximately 20 km apart. One site was directly adjacent to the accommodation building at the Australian Casey Station (Red Shed site, 66.283° S, 110.527° E), while the other site was 20 km west at Robinson Ridge (66.368° S, 110.587° E). These sites were chosen because they support extensive communities of G. antarctici, and they differ in moisture availability and exposure. Robinson Ridge is more xeric, with lower water availability, cooler, and greater exposure to both sunlight and wind, compared to the more mesic Red Shed site (Melick & Seppelt 1997). The Red Shed site was directly adjacent to a large summer melt lake and remains moist throughout the summer. The Robinson Ridge site was adjacent to a melt stream that flows early in the summer and provides intermittent water later in the season.

At each site, four sets of open sided, treatment screens were applied. The screens (30 x 30 cm) were composed of 4 mm plexiglass that either transmitted (near-ambient UV; Plexiglass GS 2458, Plastral Pty Ltd, Sydney, Australia) or attenuated (reduced UV; Plexiglass G 233) UV radiation, in addition 50% shade cloth was also applied to half the screens. The screens transmitted 90% of incident radiation from 400-700 nm. The UV-blocking screens then blocked transmittance of almost all wavelengths below 350 nm, whilst the UV-transmitting screens allowed all UV-B and UV-A wavelengths to pass (cutoff 255 nm; see Fig 1). Mean
transmittance of UV radiation in the field was 81 ± 3% of incident radiation for the near-ambient UV treatment and 16 ± 2% for the reduced UV treatment (measured using a compact radiometer; RM21, and IP65 UV-B sensor; 280 – 315 nm (Dr Grobel, UV-Electronic, Ettingen, Germany). The shade cloth treatment was uniform across all wavelengths measured. Four replicates of each of the four treatment screens (near-ambient UV, near-ambient UV+shade, reduced UV and reduced UV+shade) were arranged randomly, within aluminium frames placed over G. antarctici turf, at each of the two sites. Screens were oriented along an east-west axis and frames were angled down on the northern face so as to minimise direct, midday solar radiation bypassing the screens. The height of the screens was 5-20 cm from the moss on the northern face, and 10-25 cm on the southern face. Frames were secured using guy wires in early December 1997. Measurements of UV transmission of the plexiglass at the end of the experiment revealed no photodegradation had occurred. Since most of the water available to these moss beds occurs as melt water, screens had little effect on water availability. Observations over the 14 months of the study showed that snow accumulation under screens was also similar to surrounding areas (Robinson 1999). The absence of sides promoted blowing snow and also air movement thus reducing the potential for fungal contamination (Huiskes et al. 2001). Temperatures of the moss turf were assessed over several overcast to full sun days, using an infrared thermometer (Scotchtrack T Heat tracer IR1600L; 3M, Austin, Texas) held 15-20 cm from the surface. Moss temperatures were compared under UV and shade treatment screens, beside the screens and over microtopographic ridges and valleys formed through cycles of freezing and thawing (Kappen et al 1989). As expected, moss under shaded screens and in microtopographic valleys had lower temps than that under clear screens or on microtopographic ridges (3.5 °C and 1.5 °C respectively) but UV treatment screens did not
affect temperature compared with unscreened control turf. Temperature differences between shaded and clear screens were most pronounced on sunny days and least on overcast days. In January 1999, after 14 months growth under the screens, samples (2 cm$^2$) were collected from separate ridge and valley areas of turf beneath each screen (32 samples for each of the Robinson Ridge and Red shed sites). Additional samples were also collected from ridges and valleys adjacent to each frame in areas which were not impacted by the screens (8 samples per site). Samples were returned to the laboratory at Casey where each sample was split into two with one half used for measurement of surface reflectance and subsequently frozen for pigment analysis (chlorophylls, carotenoids and anthocyanins), whilst the other half was used for measurement of photosynthetic parameters and then oven dried for determination of UV absorbing pigments.

Measuring surface reflectance

Changes in surface reflectance characteristics reflect both morphological and physiological changes in plant communities (Field et al. 1994) and have been shown to change with altitude and UV-B exposure (Filella & Penuelas 1999). We used an integrating sphere fitted to a scanning spectrophotometer (GBC UV-Vis 918, GBC, Dandenong, VIC, Australia) to measure spectral reflectance of the turf surface between 200 – 900 nm as described in Lovelock and Robinson (2002). From the entire reflectance spectra we present reflectance at key wavelengths and also the first derivative of the reflectance change at the red-edge ($D_1$) and the position of the red-edge (REP) which has been found to differ between moss species (Lovelock & Robinson 2002).

Physiological characteristics (photosynthetic parameters and turf water content)

After dark adaptation for 20 mins, the chlorophyll fluorescence parameter $F_v/F_m$ was measured for all samples using a PAM 2000 chlorophyll fluorometer (H. Walz, Effeltrich, Germany). Electron transport rates (ETR) were then determined during the programmed light response
curve of the PAM 2000 with a maximum light level of 550 µmolms⁻¹s⁻¹ PAR. The ETR values shown are the maximum achieved during each light response curve, but may not necessarily be the same as maximum light saturated rates.

Turf water content (TWC) of these samples was then determined after oven drying at 80 °C to stable weight. Turf water content is expressed as gH₂O g⁻¹ dry weight as described in Robinson et al. (2000). In higher plants, where tissue is bound by an epidermis, water content (WC) of tissues can be expressed relative to the WC at full turgor. Determination of the WC at full turgor is difficult in intact mosses (Fowbert 1996) because mosses store much of their water externally, in capillary spaces, or in the cell wall apoplastic spaces. We have chosen to rename it as TWC to recognise both the inclusion of external water in these measurements and that this is a measure of the water holding capacity of the turf as a whole, rather than individual gametophytes.

Pigment content of moss samples

After the reflectance spectra were measured, the photosynthetically active apices of the moss were removed using a razor blade and the tissue was frozen in liquid nitrogen. Samples were returned to Australia in liquid nitrogen and then stored at −80 °C in a freezer prior to pigment analysis. For chlorophyll and carotenoid determination, samples (50-100 mg fresh weight) were ground with liquid nitrogen and sand in a mortar and pestle and then extracted in 100% acetone, followed by a second extraction in 80% acetone after Dunn et al. (2004). Chlorophylls and carotenoids were quantified by HPLC using a method adapted from Gilmore and Yamamoto (1991) as described in Dunn et al., (2004).

Anthocyanin concentrations were determined using the differential pH method (Francis 1982) as modified by Lovelock and Robinson (2002). UV-B absorbing pigments were extracted in 1.5 ml of acidified methanol (methanol-H₂O-HCl; 79:20:1) as described in Lovelock and Robinson (2002).
Morphological measurements

UV-B radiation can affect both plant growth and morphology (Barnes et al. 1990). Therefore, gametophyte leaf density and length of photosynthetic tissue were measured and the occurrence of malformed leaves within each sample was noted. In addition, qualitative determinations of gametophyte colour were made during these microscopic inspections. Samples were stored at –20 °C prior to measurement and were defrosted and rehydrated in water prior to measurement. Five single gametophytes were randomly selected from each sample for measurement, with juvenile, atypical and/or dead gametophytes excluded from the selection. Measurements were conducted using a binocular microscope (Leica Wild M3C4, Leica Microsystems, Gladesville, NSW, Australia). The mean value of the five gametophytes was used in subsequent analyses.

The length of photosynthetic tissue (green-yellow section) was measured for each gametophyte, with the colour of the tip scored as either green or yellow (Plate 1). Where branching occurred the length of the thickest gametophyte was measured. To determine the density of leaves, each gametophyte was cut 3.5 mm from the tip and all leaves were carefully dissected from this section and counted. Entire samples were also scored for presence or absence of leaves with altered morphology at the gametophyte tip (see Plate 1).

Data analysis

Tests of the influence of UV-B exposure, shading, site and microtopography on reflectance parameters, pigments and photosynthetic and physiological characteristics were performed using analysis of variance (ANOVA; Data Desk 6.1, Data Descriptions. Ithaca, NY, USA). The adequacy of ANOVA models were assessed by inspecting residual plots. To achieve homogeneity of variance and normality the data were transformed as follows; chlorophyll, anthocyanin, chlorophyll a/b, Z/VAZ, TWC (square root); AZ/VAZ (arcsin); R320 (log); R850 (squared); D1az (cubed) transformation. Results for statistical tests are shown where
Results

Biochemical and physiological responses

Effect of reduced incident UV radiation. Grimmia antarctici growing under near ambient
UV radiation had lower concentrations of total chlorophyll and correspondingly higher
relative concentrations of carotenoids than moss growing under reduced UV radiation (Fig 2).

For the photoprotective pigments, the relative concentration of β-carotene was higher under
near ambient UV radiation (Fig 2C). Whilst the photoprotective zeaxanthin (Z) comprised a
larger fraction of the xanthophyll cycle (VAZ) pool in moss exposed to near ambient UV
radiation on unshaded ridges (Fig 2D, Table 1; UVscreen*shade interaction, P=0.03). The
total carotenoid and neoxanthin concentration relative to chlorophyll also tended to be higher
under near ambient UV radiation (Fig 2B, D). However, anthocyanin and UV-B absorbing
pigment concentrations were not affected by variation in UV exposure.

Despite little change in UV-B absorbing pigments, turf-surface reflectance in the UV region
declined under reduced UV radiation, whilst reflectance of green and near infrared (NIR)
wavelengths increased compared to moss exposed to near ambient UV radiation (Fig. 3). The
D1\textsubscript{\text{re}} increased by 12.5\% (F\textsubscript{1,31} = 6.10, P=0.017) and the REP shifted from 700.09 to 700.79
nm when UV radiation was reduced (Fig. 3 inset; F\textsubscript{1,31} = 6.10, P=0.017).

None of the physiological characteristics measured (Fv/Fm, ETR and TWC) were altered as a
result of reduced UV exposure.

Incident solar radiation. Shading of moss led to an increase in anthocyanins and UV-B
absorbing pigments (Fig 4H, I). In contrast there was a decrease in the xanthophyll cycle
pigments relative to chlorophyll and to the proportion of this pool present as antheraxanthin (A) and Z in shaded moss (Fig 4G). Lutein concentration relative to chlorophyll declined 4.5% under shade treatments. Often the effects of shading were dependent on the site (Table 1; shade*site interactions for TChl, P=0.007; VAZ/Tchl, P=0.02; L/Tchl, P=0.01) with shading having a more pronounced effect on moss at the Robinson Ridge than at the Red Shed site. The effects of shading were also dependent on both site and topography for several pigments (shade*site*topography interactions; Tcar/Tchl, P=0.001; β-carotene/Tchl P< 0.001; Z/VAZ; P=0.006). These pigments were all highest in moss on unshaded ridges at the Robinson Ridge site than under other screen treatments.

Reduction of total radiation through shading of moss had less effect on the individual reflectance parameters although visible reflectance was 10% lower (R526; F1,31 = 3.35, P=0.073) and the REP was 0.64 nm longer under shaded screens (F1,31 = 5.43, P=0.024). None of the physiological characteristics measured were altered as a result of shading treatments.

**Effects of microtopography.** Moss from valleys showed similar, but stronger, responses to those seen for shaded treatments (Fig 4A-F). Total chlorophyll, anthocyanin and UV-B absorbing pigments were all found in higher concentrations in moss growing in valleys than that found on ridges (Fig 4A, E-F). However, carotenoid concentrations were generally higher relative to chlorophyll in ridge moss, particularly the carotenoids involved in photoprotection. The relative size of the VAZ pool, and the proportion present in the photoprotective forms A and Z, were 24% and 42% higher respectively, whilst β-carotene was 113% higher on ridges than in valleys (Fig 4C-D). The relative concentration of lutein was also significantly higher on ridges but the difference was only 7% (P=0.002).

Although reflectance in the UV region was lower in valleys than ridges, reflectance across the visible and NIR wavelengths was similar across turf topography. The REP was over a nm longer for moss growing in valleys than ridges (Table 2).
Max ETR and Fv/Fm were higher in valleys than on ridges (Table 2). Shading by screens also increased the TWC of moss growing on ridges compared to that under unshaded screens (shade*topography interaction term; P=0.05).

Site differences. Site effects were common with moss pigment concentrations generally higher at Robinson Ridge than at the Red Shed (Table 3; Total chlorophyll, anthocyanins, UV-B absorbing pigments). The proportion of lutein and neoxanthin relative to chlorophyll and the chl a/b ratio were also higher in moss from the Robinson Ridge site. Conversely, the proportion of the VAZ pool present as A and Z was higher in moss from the Red Shed site.

Many of these site differences were complicated by interactions with shade treatments or topographical differences (Table 1). In general, differences over treatments were most pronounced at the Robinson Ridge site, particularly in unshaded moss.

Moss from Robinson Ridge showed higher visible and NIR reflectance than moss from the Red Shed site (Table 3). This site effect was not apparent in the UV region. The D1<sub>kn</sub> was greater in moss from the Robinson Ridge site.

Turf water content was twice as high at the Red Shed site whilst ETR was greater at the Robinson Ridge site (Table 3).

Morphological characteristics

The length of photosynthetic tissue was greater in moss growing in valleys than on ridges, and in moss growing at Robinson Ridge compared to the Red Shed site (Tables 2 & 3). Moss growing in valleys was visually entirely green whilst 54% of gametophytes scored from ridge-grown moss were classified as yellow (P<0.0001). Shading had a similar effect, with more than 80% of moss growing under shade screens scored as green, compared to 65% of moss growing under unshaded screens (P<0.01).

Density of leaves on individual gametophytes was 7% higher in gametophytes growing under near ambient UV compared with those growing under reduced UV radiation (8.83±0.51 and 8.34±0.42).
8.23±0.41 leaves mm⁻¹ respectively; $F_{1,31} = 3.82$, $P=0.056$). In addition, leaf density was 60%
higher on ridges than in valleys (Table 2). Leaf density was reduced by shading treatments at
Robinson Ridge but not at the Red Shed site (Table 1; shade*site interaction, $P=0.026$).

The proportion of leaves with blunt-tip morphology decreased from 26% under near ambient
UV, to 12% under reduced UV exposure (Plate 1; $P<0.01$). Leaves with atypical morphology
were more common on ridges than in valleys (30% compared to 8%, $P<0.0001$) and in moss
growing under unshaded rather than shaded screens (26% compared to 11%, $P<0.001$).

Effects of screening moss

Comparison of samples from outside the screened area with samples under the UV
transparent screens show enhanced reflectance at shorter wavelengths under screens
compared to unscreened moss (30% higher at R320; $P=0.005$ and 16% higher at R526;
$P=0.098$). Pigment concentrations were largely unaffected by the presence of screens with
the exception of a 40% decrease in anthocyanin concentration under screens ($P=0.08$). The
presence of screens affected maximum ETR but not Fv/Fm. Maximum ETR was reduced
from 81.5 ± 5.0 to 58.8 ± 5.5 µmol m⁻²s⁻¹ in moss under screens ($P = 0.014$) although this
effect was modified by topography (screen*topography interaction, $P=0.07$) with ETR
reduced only for mosses on ridges under screens, whilst moss in valleys had similar ETRs in
both screened and unscreened samples.
Discussion

Reduction in UV-B exposure

Since stratospheric ozone depletion has increased the UV-B radiation incident on mosses growing in Antarctica, this study compared near ambient UV (the current situation) with reduced UV radiation. Although the reduction (77%) imposed by the screening treatment is more extreme than the change which has occurred in recent decades, this study provides indications of the likely impact of natural changes in UV-B radiation on the Antarctic endemic *G. antarctici*.

Chlorophyll concentration increased by 27% in moss grown under reduced UV radiation whilst β-carotene/Tchl. and the proportion of the VAZ pool present as Z decreased by 25% and 21% respectively. Other significant changes to pigments, reflectance parameters or morphology were smaller in magnitude (2-15%). UV radiation therefore had a significant destructive effect on the main light absorbing pigments whilst increasing the relative proportions of pigments involved in photoprotection, such as β-carotene and zeaxanthin. Interestingly, there was no evidence of accumulation of screening pigments in moss exposed to near ambient UV radiation levels. The reflectance data support this, with moss exposed to near ambient UV having higher reflectance in the UV region and lower reflectance in the visible and NIR consistent with reductions in concentration of the dominant chlorophyll pigments. The shift of the REP to longer wavelengths under reduced UV radiation is also indicative of increased absorption by chlorophyll. These results show that protection from UV-B is unlikely to occur through screening or reflectance of UV-B radiation. However, increased levels of antioxidant carotenoids such as β-carotene and Z might ameliorate some of the damage associated with UV-B exposure. Increased ability to scavenge reactive oxygen species has been shown to improve plant tolerance to UV-B radiation (Fujibe *et al.* 2004; Mazza *et al.* 1999; Middleton & Teramura 1993).
Increased accumulation of UV-B screening pigments or epicuticular waxes is one of most
common effects of UV-B on temperate and tropical plants (Bornman & Vogelmann 1991;
Krause et al. 2003; Robberecht et al. 1980). However, recent studies suggest that
accumulation of UV-B absorbing pigments may be a less common response in high latitude
plants. Three out of five species studied in a long term experiment in Terra del Fuego,
showed no response of UV-B absorbing pigments to UV-B exposure whilst the results for the
remaining two species were inconclusive (Giordano et al. 2003; Rousseaux et al. 1998;
Rousseaux et al. 2001). In a similar sub arctic study, two out of the three species showed
increased UV-B absorbing pigments under reduced UV-B (Phoenix et al. 2002). Similarly
conflicting results have been observed for vascular plants on the Antarctic peninsula with
higher concentrations of UV-B absorbing pigments observed in short term but not in longer
term studies (Lud et al. 2001; Ruhland & Day 2000; Xiong & Day 2001).

Although mosses have been reported as generally lacking inducible UV-B screening pigments
(Gehrke 1998; Gehrke 1999; Gwynn-Jones et al. 1999; Niemi et al. 2002a; Niemi et al.
2002b; Searles et al. 1999) recent studies suggest that many Antarctic mosses do produce
UV-B screening pigments in response to natural exposure to UV-B radiation (Dunn 2000;
Interestingly, tests of sensitivity to UV-B responses in moss species to date have not involved
Antarctic endemics, and we believe that this study of G. antarctici represents the first
endemic species tested under variable UV radiation.

Changes to chlorophyll have been observed in some species but are not a consistent response
to natural variations in UV-B exposure, although they have previously been observed in
Arctic bryophytes in response to enhanced UV-B radiation (Caldwell et al. 2003; Gehrke
1999; Searles et al. 2001). No change in chlorophyll concentration was observed as a result
of seasonal changes in UV-B radiation in either the South American Sphagnum magellanicum
(Searles et al. 2002) or two Antarctic bryophytes studied by Newsham et al. (2002). This
destruction of pigments under ambient UV radiation is thus unusual and again may indicate
that *G. antarctici* is less tolerant of UV exposure than other moss species studied. UV-
induced increases in the carotenoid to chlorophyll ratio are however relatively common in
Antarctic plants and algae (Newsham 2003; Newsham *et al.* 2002; Post & Larkum 1993;
Ruhland & Day 2000).

The morphological changes also indicate that UV exposure may be having negative effects on
this species. The increased leaf density per gametophyte is likely due to reduced
gametophytic growth under ambient UV radiation, producing shorter internodes. Increased
leaf density was also observed in *Polytrichum splendens* under elevated UV-B radiation
(Gehrke 1999). Reductions in internode length and increases in leaf thickness are highly
correlated with reduced growth rates over a wide range of species (Saverimuttu & Westoby
1996), and thus it is likely that high levels of UV radiation are reducing growth in *G.
antarctici*. Similar morphological changes have been shown in response to water and
temperature stress in Arctic and Antarctic bryophytes (Dorrepaal *et al.* 2003; Fowbert 1996;
Heegard 1997; Wilson 1990). Increased numbers of leaves displaying atypical morphology in
the near ambient UV treatment could be the result of UV-B damage to tissues. Growth
measurements of Antarctic mosses are extremely difficult due to the slowness of growth
(estimate for this species 0.6 mm y\(^{-1}\); Melick & Seppelt 1997) and long term studies would be
needed to confirm any negative impact on growth.

Studies of the moss *S. uncinata*, performed over similar periods on the warmer Antarctic
peninsula, failed to detect alterations in growth rates by UV-B radiation but similar to this
study, moss also showed morphological alterations (Lud *et al.* 2002). Although the height of
*S. magellanicum* appeared unaffected by ambient UV-B in the first season of a study in Tierra
del Fuego, results after 3 and 6 years showed that growth was reduced by 9%. These studies
also demonstrate the need for long term experiments, since interannual variation was high,
and significant annual reductions were only observed in one of the six years of the study
(Robson et al. 2003; Searles et al. 1999; Searles et al. 2002). Effects of UV-B on plant growth may be evident within shorter time intervals where UV-B is elevated above ambient levels. Reductions in growth were observed in three subarctic bryophytes grown under supplemental UV-B lamp treatments for 3 years (Gehrke 1998; Gehrke 1999).

Similar to other plant species, changes in UV radiation altered pigment composition and morphology of *G. antarctici* while photosynthesis appears to be relatively robust to such changes (Allen et al. 1998; Searles et al. 2001). With UV-B radiation predicted to remain at elevated levels in the Antarctic, potential reductions in growth rates of *G. antarctici* with higher UV-B, particularly in exposed conditions, could lead to alterations in bryophyte community composition.

*Shading and Topographical differences*

The impact of shading on moss turves was also investigated in order to differentiate the effects of reduced UV radiation with light reduction in general. Shading did affect the pigment content and reflectance properties of the moss and, in many ways, reproduced the natural differences in light environment produced by topography (Table 1). However, the differences produced by shading were less pronounced than those found between moss growing on ridges and valleys and were also less significant than the changes induced by reducing UV radiation alone.

Topography had a significant effect on many of the parameters investigated. This study confirms our previous findings that topographical location is a key factor in determining the physiological and biochemical characteristics of this species (Lovelock & Robinson 2002). Lower chlorophyll and higher protective pigment concentrations on ridges compared to valleys confirm that ridges are stressful environments. However, increased photoprotection on ridges was not accompanied by increases in pigments that potentially screen UV-B, since the
levels of anthocyanins and UV-B absorbing pigments were higher in moss growing in valleys
than on ridges.

Although the changes in chlorophylls and carotenoids may reflect acclimation of
photosynthetic pigments to the light levels experienced by the moss, it is possible that these
results are in part explained by photooxidation of pigments and could explain the reduction in
anthocyanins and chlorophyll on ridges and under clear screens. In sub-arctic shrubs,
reductions in UV-B radiation resulted in increased levels of UV-B absorbing compounds
(Phoenix et al. 2002) which was attributed to either increased secondary metabolism in the
absence of UV-B radiation or UV photo-oxidation of these pigments. In this study, higher
levels of anthocyanins were observed when UV was reduced (albeit not significant), under
shade and most significantly in moss growing in valleys rather than on ridges. Taken together
this is supportive of photodestruction of pigments occurring in the higher radiation
environments. In addition, given that the shading treatment only increased chlorophyll
content by 13% (less than half that observed for the reduced UV treatment) we can be
confident that there is a UV radiation component to this photodestruction of photosynthetic
pigments.

Topographical changes in reflectance data are largely those associated with increases in
chlorophyll content, such as the shifting of the REP to longer wavelengths in moss growing in
valleys compared with ridges. The physiological parameters also indicate that moss in the
valleys is healthier and probably more productive with a higher Fv/Fm and an 18% increase
in ETR compared to moss growing on ridges. These differences are presumably mainly due
to the more benign light and exposure conditions associated with valleys since the water
content was slightly lower in valleys than on ridges. The increased length of photosynthetic
tissue in valley moss confirms that growth conditions are improved compared to that on
ridges. Moss growing in valleys also had a lower leaf density than moss on ridges, which is
consistent with leaf density being positively correlated with reduced growth.
Moss growing in the two sites varied considerably in reflectance parameters, pigment content, physiologically and morphologically. We initially chose the sites as representative of xeric (Robinson Ridge) and mesic (Red Shed) habitats. Our results indicate that despite the more xeric habitat at Robinson Ridge, pigment concentrations, ETR and length of photosynthetic tissue were generally greater than at the Red Shed site, and there were also only small differences in parameters associated with stress. The proportion of the VAZ pool present as AZ was higher at Red Shed but it is probable that this reflects the proximity of this site to the lab and therefore a faster freezing of samples after collection. Other photoprotective carotenoids such as β-carotene and the total VAZ pool did not differ between sites, and Fv/Fm did not change. Site strongly influenced the effects of the various screen treatments (Table 1). In particular shading was far more significant a treatment at Robinson Ridge than at the Red Shed, perhaps pointing to a strong effect of exposure at the latter site which was ameliorated by the screens. Moss at the Red Shed site is covered by water for most of the season whereas moss at the Robinson Ridge site is saturated for only a short period during snow melt and has a more seasonal water supply. The increased exposure at the Robinson Ridge site also leads to more frost heaving and hence more pronounced microtopographic differences. The combination of light stress with intermittent water stress could explain the stronger response to shading at Robinson Ridge. Due to its increased exposure and cooler temperatures we had assumed that the Robinson Ridge site is harsher and less favorable for moss growth. However, our results suggest that the Red Shed site is less favorable than previously thought, possibly due to anaerobic conditions when moss is submerged for long periods during the summer. It maybe that when water is available, the Robinson Ridge site is more favorable for growth but that increased exposure at this site increases the variability in this response and increases the probability of microtopography influencing treatment responses.
Conclusions

This study provides evidence that the endemic, Antarctic moss *G. antarctici* is negatively affected by UV radiation with reductions in light harvesting pigments and an increased reliance on photoprotective and antioxidant pigments when grown under near ambient UV. Although the physiological parameters were not affected there was evidence that the plants might be suffering morphological damage or reduced growth as a result of UV exposure. Levels of UV-B absorbing and anthocyanin pigments are known to be low in this species (Lovelock & Robinson 2002) and there is no indication from the current study that they change in response to natural UV flux.

Since UV-B absorbing pigments showed variation in response to reduced total radiation (in shaded or valley moss) and were closely correlated with chlorophyll concentrations, this suggests that they may not act as UV specific screens in this species. Other photoprotective pigments would appear to be more important for survival of this endemic species under increased UV-B radiation. Current studies, similar to those described by Rousseaux et al. (1999), will investigate the relationship between capacity for UV-screening and photoprotection and DNA damage in this species.

Our results show that ambient UV radiation has the potential to adversely affect an endemic, Antarctic bryophyte and confirms that this species has low potential for UV-B photoprotection. Indications of slower growth under UV-B as well as in the more stressful environments (ridges) may suggest lowered competitive advantage under high UV-B, possibly leading to changes in the balance of species in these extreme environments. Since other cosmopolitan mosses that co-occur with this species possess greater potential for UV-B screening and appear to be more desiccation tolerant than this endemic species (Dunn 2000; Lovelock & Robinson; Robinson et al. 2000) *G. antarctici* may lose its dominant position within the Windmill bryoflora.
Acknowledgements

This research was supported by grants and logistic support from the Australian Antarctic Division. We are grateful for the generous loan of the reflectance sphere by John Rock, Chemical Engineering, Granville TAFE College. Jane Wasley, Christian Gallagher and other Casey Station expeditioners (1997-9) provided field assistance in Antarctica.

References


Middleton EM & Teramura AH (1993) The role of flavonol glycosides and carotenoids in


Newsham KK (2003) UV-B radiation arising from stratospheric ozone depletion influences

radiation in the field alters the pigmentation of an Antarctic leafy liverwort.
*Environmental and Experimental Botany* (in press).


of two *Sphagnum* moss species and *Eriophorum vaginatum* to enhanced UV-B in a

B radiation alters fluxes of methane and carbon dioxide in peatland microcosms.

Pancotto VA, Sala OE, Cabello Metal. (2003) Solar UV-B decreases decomposition in
herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered

Phoenix GK, Gwynn-Jones D, Lee JA & Callaghan TV (2002) Ecological importance of
ambient solar ultraviolet radiation to a sub-arctic heath community. *Plant Ecology*,
165, 263-273.

Post A & Larkum AWD (1993) UV-absorbing pigments, photosynthesis and UV exposure in

Robberecht R, Caldwell MM & Billings WD (1980) Leaf ultraviolet optical properties along a


Robinson SA, Wasley J & Tobin AK (2003) Living on the edge - plants and global change in


Table 1. ANOVA summary table showing significant effects of UV exposure, shading, site and microtopography on surface reflectance characteristics, pigment concentrations, physiological and morphological parameters of *Grimmia antarctici*. Interactions are described in the table footnote. “XX” and “X” indicate significant effect at p<0.05 and p<0.10 respectively.

<table>
<thead>
<tr>
<th>Reflectance parameters</th>
<th>UV</th>
<th>Shade</th>
<th>Topography</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>R&lt;sub&gt;320&lt;/sub&gt;</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R&lt;sup&gt;c&lt;/sup&gt;</td>
<td>X</td>
<td>X</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>R&lt;sub&gt;526&lt;/sub&gt;</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>REP</td>
<td>XX</td>
<td>XX</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>D1&lt;sub&gt;44&lt;/sub&gt;</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Pigment content</th>
<th>UV</th>
<th>Shade</th>
<th>Topography</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthocyanins</td>
<td>X</td>
<td>XX</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>UV-B absorbing pigments</td>
<td>XX</td>
<td>XX</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>Total Chl&lt;sup&gt;a&lt;/sup&gt;</td>
<td>XX</td>
<td>XX</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>Chl a:b</td>
<td>X</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tcar./Tchl&lt;sup&gt;e&lt;/sup&gt;</td>
<td>X</td>
<td>X</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>VAZ/TChl&lt;sup&gt;b&lt;/sup&gt;</td>
<td>XX</td>
<td>XX</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>% (AZ/VAZ)</td>
<td>XX</td>
<td>XX</td>
<td>XX</td>
<td></td>
</tr>
<tr>
<td>% (Z/VAZ)&lt;sup&gt;d,e&lt;/sup&gt;</td>
<td>XX</td>
<td>XX</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>L/Tchl&lt;sup&gt;c&lt;/sup&gt;</td>
<td>XX</td>
<td>XX</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>N/Tchl</td>
<td>X</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B-carotene/Tchl&lt;sup&gt;e&lt;/sup&gt;</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Physiological parameter | UV | Shade | Topography | Site |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>ETR</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fv/Fm</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TWC&lt;sup&gt;b&lt;/sup&gt;</td>
<td>X</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Morphological parameter | UV | Shade | Topography | Site |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of photosynthetic tissue</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf density&lt;sup&gt;a&lt;/sup&gt;</td>
<td>XX</td>
<td>XX</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Interaction terms:
- A Shade*site;
- B Shade*topography;
- C Topography*site;
- D UVscreen*shade;
- E Shade*site*topography.
Table 2. Comparison of surface reflectance, physiological and morphological parameters for *Grimmia antarctica* moss growing in ridges or valleys under the screen treatments. Data are mean values ± SEM (n=32).

<table>
<thead>
<tr>
<th></th>
<th>Ridge</th>
<th>Valley</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reflectance parameter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R_{320}$</td>
<td>0.0085 ± 0.0006</td>
<td>0.0066 ± 0.0004</td>
<td>13.15</td>
<td>0.001</td>
</tr>
<tr>
<td>REP (nm)</td>
<td>699.79 ± 0.216</td>
<td>701.09 ± 0.192</td>
<td>22.6</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Physiological parameters</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ETR max (µmol m$^{-2}$s$^{-1}$)</td>
<td>68.42 ± 3.87</td>
<td>80.91 ± 4.61</td>
<td>5.24</td>
<td>0.027</td>
</tr>
<tr>
<td>Fv/Fm</td>
<td>0.691 ± 0.004</td>
<td>0.714 ± 0.004</td>
<td>10.82</td>
<td>0.002</td>
</tr>
<tr>
<td>TWC (g$^{-1}$H$_2$O g$^{-1}$dwt, n=26,28)</td>
<td>5.71 ± 0.62</td>
<td>4.8 ± 0.73</td>
<td>3.26</td>
<td>0.079</td>
</tr>
<tr>
<td><strong>Morphological characteristics</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of photosynthetic tissue (mm)</td>
<td>1.95 ± 0.12</td>
<td>4.05 ± 0.36</td>
<td>42.15</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Leaf density (leaves mm$^{-1}$)</td>
<td>10.6 ± 0.36</td>
<td>6.52 ± 0.18</td>
<td>135.34</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Table 3. Comparison of surface reflectance parameters, pigment concentrations, physiological and morphological parameters for *Grimmia antarctica* moss growing under screen treatments at the Robinson Ridge and Red Shed sites. Data are mean values ± SEM (n=32).

<table>
<thead>
<tr>
<th>Reflectance parameter</th>
<th>Robinson Ridge</th>
<th>Redshed</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{526}$</td>
<td>0.0305 ± 0.0014</td>
<td>0.0261 ± 0.0014</td>
<td>5.64</td>
<td>0.022</td>
</tr>
<tr>
<td>$R_{850}$</td>
<td>0.4097 ± 0.0158</td>
<td>0.3309 ± 0.0189</td>
<td>10.48</td>
<td>0.002</td>
</tr>
<tr>
<td>$D1_{RE}$</td>
<td>0.0092 ± 0.0004</td>
<td>0.0074 ± 0.0005</td>
<td>6.66</td>
<td>0.013</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Pigments</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>UV-B absorbing pigments</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthocyanins (A$_{520}$ diff g$^{-1}$ fwt)</td>
<td>1.82 ± 0.20</td>
<td>1.07 ± 0.20</td>
<td>7.61</td>
<td>0.008</td>
</tr>
<tr>
<td>Total Chlorophyll (nmol g$^{-1}$ fwt)</td>
<td>622 ± 52</td>
<td>469 ± 50</td>
<td>4.65</td>
<td>0.036</td>
</tr>
<tr>
<td>Chlorophyll a/b</td>
<td>3.32 ± 0.09</td>
<td>2.98 ± 0.09</td>
<td>7.86</td>
<td>0.007</td>
</tr>
<tr>
<td>AZ/VAZ (%)</td>
<td>24.1 ± 1.66</td>
<td>31.1 ± 1.60</td>
<td>19.26</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Z/VAZ (%)</td>
<td>21.4 ± 1.79</td>
<td>23.8 ± 1.70</td>
<td>6.28</td>
<td>0.016</td>
</tr>
<tr>
<td>L/Tchl (mmol mol$^{-1}$)</td>
<td>179 ± 3.17</td>
<td>172 ± 3.07</td>
<td>3.48</td>
<td>0.069</td>
</tr>
<tr>
<td>N/Tchl (mmol mol$^{-1}$)</td>
<td>74.1 ± 2.32</td>
<td>60.8 ± 2.28</td>
<td>17.51</td>
<td>0.000</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Physiological parameters</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>ETR max (µmol m$^{-2}$s$^{-1}$)</td>
<td>88.2 ± 4.04</td>
<td>61.1 ± 3.26</td>
<td>25.032</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>TWC (g$^{-1}$H$_2$O g$^{-1}$dwt, n=28, 26)</td>
<td>3.47 ± 0.24</td>
<td>7.15 ± 0.82</td>
<td>29.19</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Morphological characteristics</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of photosynthetic tissue (mm)</td>
<td>3.61 ± 0.385</td>
<td>2.39 ± 0.22</td>
<td>13.58</td>
<td>0.006</td>
</tr>
<tr>
<td>Leaf density (leaves mm$^{-3}$)</td>
<td>8.09 ± 0.42</td>
<td>8.97 ± 0.49</td>
<td>7.7079</td>
<td>0.008</td>
</tr>
</tbody>
</table>

Comment [SR2]: This is italicised incorrectly in the proofs.
Figure Legends

Figure 1. Transmittance spectra of near-ambient (solid line, Plexiglass GS 2458) or reduced (dotted line, Plexiglass G 233) UV-B screens measured in a spectrophotometer.

Figure 2. The effect of reducing UV radiation on pigment concentrations of *Grimmia antarctici*. Total chlorophyll (A), total carotenoid/chlorophyll (B), β-carotene/chlorophyll (C), neoxanthin/chlorophyll (D) and xanthophyll cycle pigments, violaxanthin, antheraxanthin, zeaxanthin (E). Data are means ± SEM, n=32.

Figure 3. The effect of reducing UV radiation on reflectance spectra of turf of *Grimmia antarctici*. Turf exposed to near-ambient (solid line) or reduced (dotted line) UV radiation. Reflectance 280-850 nm (main graph) and 280-700 nm (inset). Data are means ± SEM (n=32). Mean reflectance levels are significantly different at R_{220} (P<0.01***), R_{526} & R_{850} (P<0.05**), R_{720} (P=0.06).

Figure 4. The effect of shading by screens (G-I) or topographical position within the turf (A-F) on pigment concentrations of *Grimmia antarctici*. Total chlorophyll (A), total carotenoid/chlorophyll (B), β-carotene/chlorophyll (C), xanthophyll cycle pigments, violaxanthin, antheraxanthin, zeaxanthin (D, G), anthocyanins (E, H) and UV-B absorbing pigments (F, I). Data are means ± SEM, n=32.

Plate 1. Comparison of gametophytes of *Grimmia antarctici* showing the normal leaf morphology and green colouration (c-d) and atypical leaf morphology and yellow colouration (a-b), enlarged (e). Atypical leaves were characterized by short length and blunted leaf tips.
Figure 4