Photosynthetic responses of selected Antarctic plants to solar radiation in the southern maritime Antarctic

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The effects of UV-B exclusion and enhancement of solar radiation on photosynthesis of the two phanerogams which occur in the maritime Antarctic, *Deschampsia antarctica* and *Colobanthus quitensis*, and the moss *Sanionia uncinata* were investigated. Data on air temperature and solar radiation illustrate a drastic seasonal variation. Daily O_3 column mean values and UV-B measured at ground level document the occurrence of the O_3 "hole" in the spring of 1997, with a concomitant increase in UV-B. The grass, *D. antarctica*, exhibited a broad temperature optimum for photosynthesis between 10–25°C while photosynthesis did not saturate even at high irradiance. The high water use efficiencies measured in the grass may be one of the features explaining the presence of this species in the maritime Antarctic. The net photosynthesis response to intercellular CO_2 (A/c_i) for *D. antarctica* was typical of a C_3 plant. Exposure to a biologically effective UV-B irradiance of 0.74 W m^{-2} did not result in any significant change in either the maximum rate of photosynthesis at saturating CO_2 and light, or in the initial carboxylation efficiency of Rubisco. ($V_{c,max}$). Furthermore while ambient (or enhanced) solar UV-B did not affect photochemical yield, measured in the field, of *C. quitensis* and *D. antarctica*, UV-B enhancement did affect negatively photochemical yield in *S. uncinata*. In *D. antarctica* plants, exposure to UV-B at low irradiances elicited increased flavonoid synthesis. The observed effects of UV-B enhancement on the moss (decreased photochemical yield) and the grass (increase in flavonoids) require further, separate investigation.

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Summer climatic conditions in the Antarctic, together with the isolation from more northerly land-masses, restrict the vegetation in the maritime Antarctic to mosses, lichens, algae, cyanobacteria and to two vascular species: the pearlwort *Colobanthus quitensis* and the grass *Deschampsia antarctica* (Smith 1984). Evidence of climatic change in the Antarctic Peninsula includes an upward trend in summer air temperatures since the late 1940s (Smith 1994). Mean annual air temperatures have also increased by 0.022 to 0.067°C per year (King 1994). Since the mid-1970s there has been a marked thinning of the stratospheric ozone layer over the polar regions (Farman et al. 1985), which has continued throughout the 1980s and 1990s (Jones & Shanklin 1995). Climate change is likely to lead to shifts in species, communities and relative abundance of polar vegetation (McGraw & Fetcher 1992). Without detailed knowledge of species physiology and ecosystem properties, such shifts will be difficult to predict.

Monitoring populations of both Antarctic vascular species over a 27 year period has revealed a significant increase in numbers of individuals and populations at two separate localities in the maritime Antarctic (Fowbert & Smith 1994). In *D. antarctica* no specific adaptations to the Antarctic environment are evident in terms of reproductive strategies (Convey 1996), or the fatty acid composition of phospholipids and galacto-lipids in leaves and roots (Zuñiga et al. 1994). However, an inverse relationship of chloroplast to cell area index and temperature has been reported

for *D. antarctica* along a climatic and latitudinal gradient (Jellings et al. 1983). More significantly, one previous study (Edwards & Smith 1988) suggests that photosynthetic rates in both species approach 30% of their maximum at 0°C. A much larger number of studies on the cryptogamic vegetation of the region exist, including photosynthetic measurements in both lichens (reviewed by Schroeter et al. 1997) and mosses (e.g. Davey & Rothery 1996).

Cellular responses to extreme fluctuations in solar radiation, temperature and water status are likely to be critical to plant competitive balance (Larcher 1995). In Antarctic terrestrial biota these relationships remain largely unexplored. The biological effects of UV-B on vegetation can be direct or indirect; direct effects include DNA photodamage and physiological effects (reviewed by Caldwell et al. 1995). Although direct damage of Photosystem II has been widely documented (Bornman 1991; Nedunchezhian & Kulandaivelu 1997), inhibition of photosynthesis by UV-B is more likely to be linked to CO_2 fixation (Baker et al. 1997). Photoprotective responses to UVR include structural modifications and increased synthesis of UV-B absorbing compounds (Caldwell et al. 1995; Rozema et al. 1997).

Research into the biological effects of increased UV-B in the Antarctic has focused mainly on marine ecosystems (see Goes et al. 1994; Karentz 1994; Riegger & Robinson 1997; Neale et al. 1998), with relatively few studies on photoprotective pigments of terrestrial macro-algae, mosses and cyanobacteria (e.g. Post 1990; Garcia-Pichel & Castenholz 1991; Post & Larkum 1993). The present study defined photosynthetic responses in *D. antarctica* and assessed whether the two vascular plants and the moss *Sanionia uncinata* were responsive to manipulation of the solar environment (chiefly UV-B exclusion and enhancement) under ambient conditions at Léonie Island.

Methods

Monitoring of solar radiation: At Rothera Station (67°34'07"S, 68°07'30"W), in the south-western Antarctic Peninsula, a Bentham DM 150 scanning spectroradiometer has measured spectral global irradiance since 1997. Measurements are made from 280 to 600 nm with a step size of 0.5 nm and a resolution of 1 nm. The same instrument is used to calibrate UV-A and UV-B sensors (Delta-T Devices Ltd., Cambridge, UK) and irradiance (Photosynthetically Active Radiation, PAR, 400–700 nm) quantum sensors (Skye Instruments Ltd., Powys, UK) which are part of a year-round, automated station at Léonie Island (67°36'S, 68°20'W), 9 km south-west of Rothera Station.

Field experimentation: All field experimentation was carried out on Léonie Island. The species selected included the two vascular plants (*D. antarctica*, *C. quitensis*) and the moss *S. uncinata*. These species are found co-existing in similar locations, are widespread along the Antarctic Peninsula and provide a representative contrast between vascular and cryptogamic life strategies. Plants were transplanted to a north-facing terrace, dominated by grass swards. Following acclimation (10 days), plastic screens were positioned to affect changes in solar UV radiation. The screens (Du Pont Polyesters Group, Middlesborough, UK) used included UV transparent (Perspex OXO-2), UV opaque (Perspex VE) and UV-B opaque but UV-A transparent (Melinex). UV-B enhancement (around 30% of background solar levels) was provided by a UV-B lamp (313 nm maximum, Cole-Palmer Instrument Company, London, UK) fitted with Sanalux glass panels to absorb UV radiation below 280 nm. The UV-B lamp was positioned in such a way so as to provide uniform UV-B enhancement over the test area, whilst not shading any plant material from sunlight. This enhancement (square-wave addition) was given for 5 h day^{-1} around solar noon (13.00 local time). The UV-B lamp (115 VAC, 60 Hz) was switched on only when irradiance exceeded 300 µmoles m^{-2} s^{-1}. Such an arrangement allowed a total of five contrasting treatments, namely ambient (direct sun), UV transparent, UV exclusion, UV-B exclusion only and UV-B enhancement.

Controlled environment experiments: Plants (*D. antarctica*) were collected at Signy (60°43'S, 45°38'W) and Léonie islands and transported to the BAS headquarters (Cambridge, UK) where they were acclimated in growth chambers prior to experiments. Chamber temperatures were 15°C/ 7°C for daily 16 h day/8 h night cycles, respectively. These conditions were used throughout, with plants kept inside growth incubators under modified covers made from the same UV

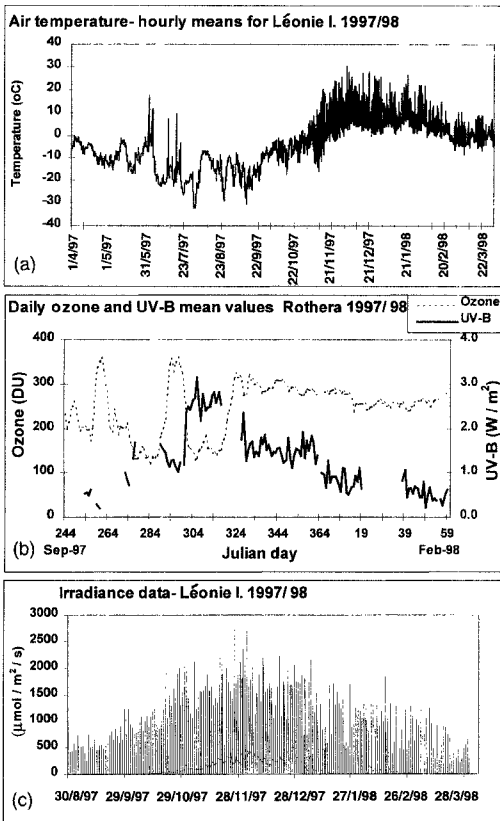Photosynthetic responses of selected Antarctic plants to solar radiation

Fig. 1. Seasonal fluctuation in temperature, ozone and solar radiation at Rothera Station and Léonie I., 1997–98. (a) Air temperatures (20 cm above ground) are hourly average of readings taken every 10 min (April 1997–March 1998). (b) Ozone column values and UV-B irradiance fluences (derived from scans from the Bentham spectroradiometer) are daily means (September 1997–March 1998). (c) Irradiance (photosynthetically active radiation, PAR) are values (10 min intervals) from a quantum sensor (400–700 nm) (September 1997–March 1998).

noted that in the Antarctic the high seasonal variation in irradiance (Fig 1; see also Davey & Rothery 1996) combines with daily variation; high UV-B irradiances can occur at low irradiances during ozone hole events in early Spring (Webb 1997).

Photosynthetic gas exchange for D. antarctica: A Ciras-1 infra-red gas analyser (PP Systems Ltd., Herts., UK) was used, together with a microprocessor controlled cuvette which allowed complete control of leaf micro-environment variables (CO_2, temperature, irradiance and humidity). The Ciras-1 system allows simultaneous recording of photosynthetic and transpiration rates. Only the grass proved suitable for the automated cuvette. Water use efficiency (WUE) was calculated from CO_2 and H_2O exchange rates (Nobel 1991). Steady-state photosynthetic rate (measured after 7–8 min. equilibration for temperature and light response curves) was determined at an air flow rate of 300 ml min^{-1}, 345 ppm CO_2, (unless A/c_i curves were collected) and 80% relative humidity (5–6 mB). Attached *D. antarctica* leaves were used throughout. Temperature response curves (expressed as % of maximum rate achieved per plant, so as to eliminate interplant variation caused by different leaf mass), were obtained (10–15 February 1998) from eight plants from three contrasting habitats: full sun (up to 1800 µmol m^{-2} s^{-1}), partial sun (up to 1200 µmol m^{-2} s^{-1}) and shade (up to 250 µmol m^{-2} s^{-1}). Irradiance was maintained at 1500 µmol m^{-2} s^{-1} while cuvette and leaf temperature was increased stepwise from 2°C to 30°C and decreased similarly from 30°C to 2°C. Light response curves were also measured using plants from the same contrasting environments; irradiance was increased stepwise from 0–1500 µmol m^{-2} s^{-1}, following a 15 min dark acclimation, whilst leaf temperature was maintained between 15°C and 20°C.

Photochemical efficiency: Chlorophyll fluorescence was used to monitor PSII photochemistry in undisturbed plants exposed to the different UV treatments. Measurements were made in the morning and again towards the end of the day period in order to evaluate any possible interaction between UV treatments and extended exposure to high irradiance. A portable OS100 modulated chlorophyll fluorometer (Opti-Sciences Inc, MA, USA) was used to obtain
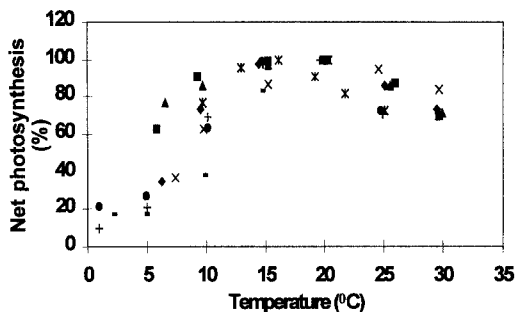
transparent and opaque acrylic plastics as employed in the field studies. Typical irradiance in the growth cabinets was 150 µmol m^{-2} s^{-1}, at plant level, while UV-B and UV-A was maintained at around 0.4 and 5.1 W m^{-2}, respectively, with a daily weighed ("generalized plant action spectrum" by Caldwell [1971]; parametrized by Thimijan et al. [1978]) dose of 4.89$_{BE}$ kJ m^{-2} day^{-1} for a 16 h day^{-1} cycle. Although the total irradiance in the growth cabinets was low compared to peak irradiance in the field (Fig. 1c), the ratio of UV-B/UV-A/PAR was similar to that measured in the field, in the absence of significant ozone depletion. It must be

Fig. 2. Temperature response curves for net photosynthesis (% of maximum rate achieved per plant;10–15 February 1998) in *D. antarctica* plants (N = 8) from contrasting habitats, i.e. full sun-exposed, partial sun-exposed and shade. Irradiance was kept at 1500 μmol m^{-2} s^{-1} while cuvette and leaf temperature was increased stepwise from 2°C to 30°C and decreased from 30°C down to 2°C. The different symbols represent measurements for replicate plants.

Fig. 4. Water Use Efficiency (WUE) for *D. antarctica* at two irradiance levels (100 and 480 μmol m^{-2} s^{-1}) determined from net photosynthesis and transpiration data. Plants were collected from field locations and acclimated to growth cabinets. Growth cabinet conditions: temperatures of 15°C/7°C for daily 16 h day/ 8 h night cycles, respectively.

steady-state yield values from undisturbed plants under field conditions. The fluorometer was used with a modified, 65° open-body cuvette guide and an irradiance (PAR) sensor. Transplanted plants were "tagged" so that positioning of the fluorometer fiber optic tip on the same spots (4–5 per treatment) was reproducible throughout the experiments. Relative amplitude of the modulated light was set at 60 (vascular plants) and 70 (the moss) with a 0.8 s pulse duration.

Total flavonoid analysis by HPLC: Gradient HPLC analysis of flavonoids was performed on a Prodigy ODS3 column (Phenomenex, Cheshire, UK), at 30°C with diode array detection. Plant tissue was ground in a pestle and mortar with cold 50% aqueous methanol containing 0.5% (v/v)

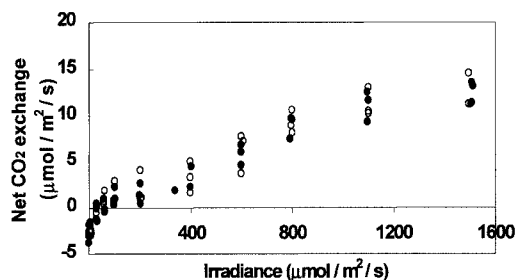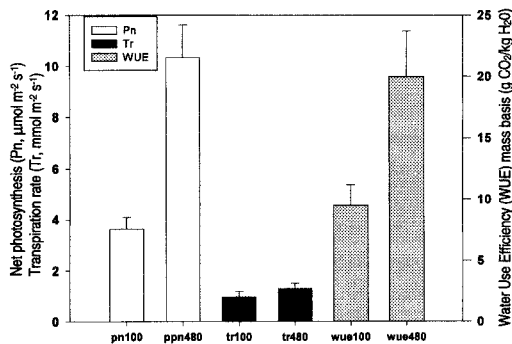
Fig 3. Light response curves for *D. antarctica* plants from contrasting habitats (open circles = full sun-exposed; filled circles = shade). Irradiance was increased stepwise from 0–1500 μmol m^{-2} s^{-1} (dark acclimation for 15 min). Leaf (and cuvette) temperature were kept between 15°C and 20°C.

glacial acetic acid, after which the extracts were centrifuged and passed through 0.45 μm filters. Mobile phases included ammonium dihydrogen phosphate (pH 2.5) and absolute acetonitrile (Lunte 1987).

Results

Data on air temperature (20 cm above ground) and solar radiation illustrate a drastic seasonal variation (Figs. 1a, c). Daily O_3 column mean values and UV-B (averaged from the Bentham scans) illustrate the occurrence of the O_3 "hole" in the spring of 1997, with a concomitant increase in UV-B during November 1997 (Fig. 1b).

Photosynthesis measurements showed that *D. antarctica* had a broad temperature optimum (approximately 90% of the maximum) between 10–25°C (Fig. 2).

Photosynthetic rate response to irradiance revealed no saturation at high irradiance even in plants from shaded environments. Similarly there was very little difference in light compensation points between plants collected from the contrasting habitats (Fig. 3).

Apparent water use efficiency (WUE) was very high, with values ranging between 62 and 123 mol H_2O per mol CO_2; typical values for C_3 species are between 300–500 mol H_2O per mol. Such efficiency, if confirmed in the natural environment, may partially explain the capacity of this species to

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Fig. 6. A/c_i response curves (net photosynthesis response to intercellular CO_2 concentration) for *D. antarctica* plants, maintained in controlled environment cabinets, and acclimated to UV-B exclusion or exposure (biologically effective irradiance of 0.74 W m^{-2} UV-B). Steady-state photosynthesis (measured after 7–8 min equilibration) was determined at an air flow rate of 300 ml min^{-1}, 345 µl l^{-1} CO_2, and 80% relative humidity (5–6 mB). Attached *D. antarctica* leaves were used throughout.

UV-B enhancement had little or no effect on the net assimilation response to intercellular CO_2 concentration (A/c_i) in *D. antarctica* (Fig. 6).

HPLC analysis of *D. antarctica* shoots kept in controlled environments at low irradiances showed that total flavonoid were increased by exposure to UV-B, with some flavonoid species showing marked increases (peaks 1, 2, 3 and 7 in the overlay chromatograms; Fig. 7). The identity of these flavonoids requires further investigation.
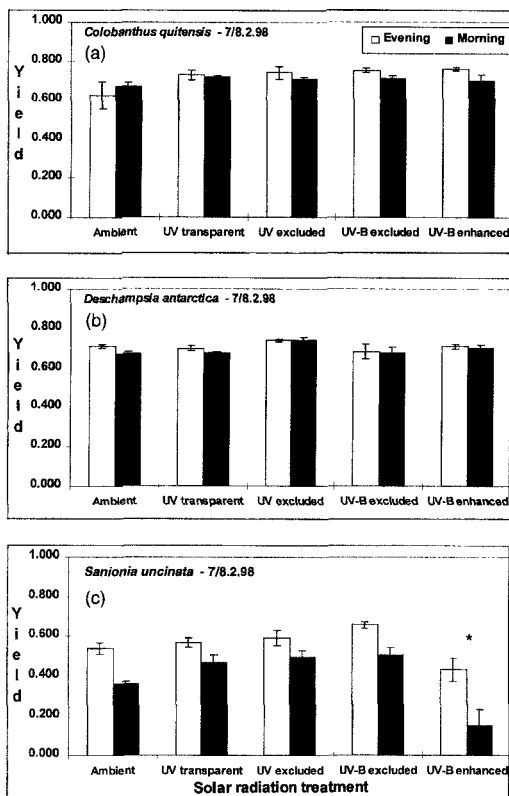
Fig. 5. Steady-state yield fluorescence parameter determined in the natural environment for (a) *C. quitensis*, (b) *D. antarctica* and (c) *S. uncinata*, following 7 days exposure to ambient conditions, total UV radiation exclusion, selective UV-B exclusion and UV-B enhancement (7–8 February 1998). Means ± 1 SE are given. Measurements were carried out in the morning (10.00 h, filled bars) and evening (19.30 h, open bars). Statistical significance (*t*-test, one-tail) is indicated (* P < 0.5) for the comparison of treatments vs ambient control.

survive in the cold semi-desert conditions of the maritime Antarctic (Fig. 4).

Chlorophyll fluorescence is used routinely as an intrinsic probe of photosynthetic function and as a screening tool for environmental stress tolerance, e.g. low temperatures (Öquist & Huner 1993), dehydration (Casper et al. 1993), and UV-B (Vassiliev et al. 1994). For both phanerogams the data suggest that following an initial transient reduction in PSII yield, induced by UV-B enhancement (data not shown), there was no significant change in PSII efficiency (Figs. 5a, b). In contrast, a significant and sustained decrease in photochemical yield was recorded for the moss *S. uncinata* when exposed to enhanced UV-B (Fig. 5c).
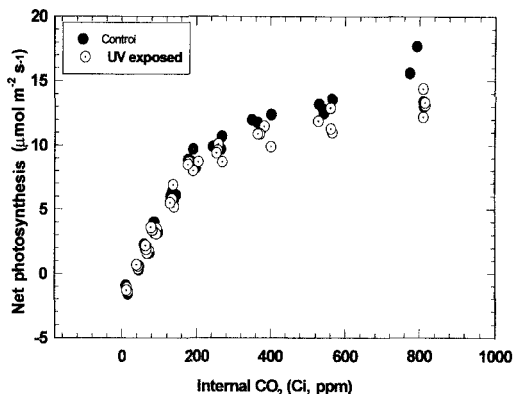
Discussion

D. antarctica exhibited a typical C_3-type response to temperature with a broad optimum. Optimal temperatures for net CO_2 uptake are usually between 20°C to 35°C for C_3 plants (Nobel 1991); thus the lower optimum for *D. antarctica* could be regarded as a specific adaptation. A wide optimum has the advantage that large daily fluctuations in temperature result in only small changes in photosynthetic rate (Larcher 1995). The data also confirmed that *D. antarctica* can sustain net photosynthesis (15–25% of maximum rate) at temperatures approaching 0°C (Edwards & Smith 1988). The response of net photosynthesis to irradiance indicate that light saturation did not occur at high irradiance even when using plants
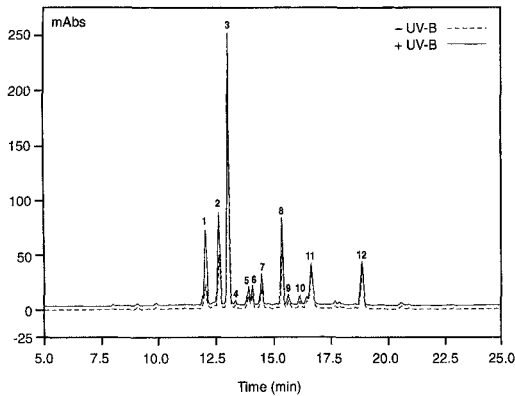
Fig. 7. Deschampsia antarctica. Overlay of chromatograms from two flavonoid extracts from tillers grown under conditions of low irradiances and where UV-B was excluded (−UV-B) or allowed through (+UV-B) for 17 days. Plants were grown at 15°C/7°C for 16 h day/8 h dark daily cycles. Extracts were prepared using similar amounts of leaf material (around 20 mg fresh weight) and injection of 60 μl from equal dilution volumes.

from shade habitats. A high saturation point may allow fuller exploitation of the high irradiance levels experienced in the region during the growing season (Fig. 1c), and may also serve as a protective mechanism against photoinhibition (Long & Humpries 1994).

The gas exchange data, A/c_i response curves in particular (Figs. 2, 6), confirm that *D. antarctica* uses C_3-type photosynthesis (Sage 1994). However instantaneous water use efficiency (WUE) values were markedly higher than expected for a C_3 grass. Comparable WUE values have been reported in both C_3 and CAM succulents, from the Southern Namib desert, suggesting that some C_3 plants can achieve high WUE values (Eller & Ferrari 1997). It is hypothesized that the high WUE of the hair-grass may play an important role in the successful performance of the plant in an environment where free water is restricted.

The finding that UV-B exposure did not effect PSII photochemical yield in either vascular species (Fig. 5a and Fig. 5b) concurs with the emerging consensus that PSII damage is only manifested at high and unrealistic UV-B exposures (Allen, McKee et al. 1997; Allen, Nogués et al. 1998). Similarly, exposure to a biologically effective UV-B irradiance of 0.74 W m^{-2} (Caldwell-weighted), at a relatively low irradiance in growth cabinets, did not result in any significant change in either the maximum rate of photosynthesis at saturating CO_2 and light (J_{max}), or in $V_{c,max}$. In contrast, Baker et

al. (1997) reported significant reductions in both these parameters at UV-B irradiances of 0.63 W m^{-2}. The responses of the vascular plants, in terms of photosynthesis and photoprotective pigments, to exclusion/enhancement of solar UV-B, indicates that current UV-B levels, experienced by *C. quitensis* and *D. antarctica* during the growing season, may not constitute a direct threat to photosynthetic activity. Furthermore, because of snow cover these species are unlikely to experience the elevated UV-B levels occurring during the spring O_3 depletion event (Fig. 1c). The negative effect of UV-B enhancement on photochemical yield in the green moss *S. uncinata* requires further evaluation (Fig. 5c).

This study has shown that exposure to enhanced solar UV-B irradiance elicited increased flavonoid production in *D. antarctica* (Fig. 7), thus sequestering energetic resources. Vegetation of the maritime Antarctic are slow growing, and subjected to numerous abiotic stresses, thus photoassimilate allocation may prove critical to survival. In Antarctic ecosystems particular attention should be paid to indirect plant responses to enhanced solar UV-B radiation; these are likely to affect competitive balance in species at the limits of their survival, with possible implications to biodiversity within ecosystems (Caldwell et al. 1995). It has been suggested that the current trend towards warmer growing seasons in the region will result in increased colonization by vascular plants (Fowbert & Smith 1994). The results of this study support this hypothesis, as photosynthesis in these species appears to be well-adapted to current levels of solar irradiance and UV radiation.

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