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Metabolic recovery of the Antarctic liverwort *Cephaloziella varians* during spring snowmelt

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Abstract We measured the responses of pigments and chlorophyll *a* fluorescence parameters of the Antarctic leafy liverwort *Cephaloziella varians* to snowmelt during austral spring 2005 at Rothera Point on the western Antarctic Peninsula. Although no changes to the concentrations of UV-B photoprotective pigments were detected during snowmelt, chlorophyll and carotenoid concentrations and maximum photosystem (PS)II yield (F_v/F_m) were respectively 88%, 60% and 144% higher in the tissues of the liverwort that had recently emerged from snow than in those under a 10 cm depth of snow. A laboratory experiment similarly showed that effective PSII yield increased rapidly within the first 45 min after plants sampled from under snow were removed to an illuminated growth cabinet. The pigmentation and PSII yields of plants during snowmelt were also compared with those of plants in January, during the middle of the growing season at Rothera Point. During snowmelt, plants had lower F_v/F_m values, chlorophyll *a* / *b* ratios and concentrations of UV-B photoprotective pigments and carotenoids than during mid-season, suggesting that although there is some recovery of PSII activity and increases in concentrations of photosynthetic pigments during snowmelt, the metabolism of *C. varians* is restricted during this period.

Introduction

Most terrestrial habitats in the Maritime Antarctic are snow- and ice-covered for the majority of the year. Periods of biological activity are thought to be restricted to austral late spring and summer, when mean air temperatures are marginally positive and snow and ice has melted (Convey 2001). Snowmelt in these habitats typically occurs between November and December, at the beginning of the summer. This is a challenging time for Antarctic plants. Metabolism must recover rapidly in order to maximise carbon acquisition during the short growing season, but has to do so under the stresses associated with the snowmelt period, notably high radiative doses, desiccation, exposure to freeze-thaw events, and low soil and air temperatures (Oberbauer and Starr 2002).

Initial biological activity occurs when snowmelt begins and plants become rehydrated, a process that can occur while plants are still covered with snow (Oberbauer and Starr 2002; Schlensog et al. 2004). The second stage in metabolic recovery occurs when the insulating layer of snow and ice above plants melts, exposing them to full solar irradiance. This includes not only photosynthetically active radiation (PAR; 400 – 700 nm) but also biologically damaging UV-B radiation (280 – 315 nm), both of which are absorbed by snow and ice. For example, a 10 cm depth of snow absorbs *c*. 80% of erythemally-weighted UV-B radiation (Cockell et al. 2002), but still allows up to *c*. 60% of PAR to penetrate, which is sufficient to drive subnivean photosynthesis of lichens in the sub-Arctic (Kappen et al. 1995).

Previous studies have investigated the photosynthetic responses to desiccation and subsequent hydration of poikilohydric plants, typically lichens (e.g. Kappen and Breuer 1991; Kappen et al. 1995; Schlensog et al. 2004) but also mosses (Wasley et al. 2006). These studies, which have usually been conducted in the laboratory, have

found that the water content of lichen thalli or moss shoots has a strong effect on gas exchange and chlorophyll *a* fluorescence yield, and have concluded that desiccated thalli or shoots under deep layers of snow and ice are most probably physiologically inactive (e.g. Kappen 1993). However little is known about the effects of snowmelt on the metabolism of poikilohydric plants in the field, owing to the difficulties of measuring photosynthetic parameters under ice and snow cover. An exception to this is the study of Pannewitz et al. (2003), who measured the chlorophyll fluorescence of undisturbed lichens in the continental Antarctic during snowmelt by leaving fibre optic cables in close proximity to thalli in the previous summer. They found that the lichens only became active when they began to emerge from snow and thallus temperatures approached the freezing point of water.

Most of the available data in the literature on the responses of plant pigmentation to snowmelt, caused by the altered microclimate as plants emerge from melting snow and ice, are derived from work on Arctic and alpine vascular plant species. Although the constantly-hydrated state of homoiohydrous vascular plant species hampers comparisons with poikilohydric plants (Kappen 1993), several changes to the pigmentation of poikilohydric species can be anticipated from the vascular plant literature. For example, concentrations of photosynthetic pigments are likely to increase in poikilohydric plant tissues as they emerge from snow (Kimball et al. 1973; Oberbauer and Starr 2002). Similarly, those of UV-B photoprotective pigments such as anthocyanins, pigments that attenuate UV-B radiation and which are also known to be associated with chilling and desiccation tolerance (Chalker-Scott 1999; Gould 2004), are likely to increase in plant tissues as they emerge from melting snow and ice (Oberbauer and Starr 2002).

This study aimed to identify changes occurring to the metabolism of the poikilohydric leafy liverwort *Cephaloziella varians* during snowmelt in late spring at Rothera Point on the western Antarctic Peninsula. We measured chlorophyll *a* fluorescence parameters and concentrations of pigments in hydrated *C. varians* tissues to determine changes to the liverwort's physiology as it emerged from melting snow. We anticipated that chlorophyll fluorescence yield would increase during this period, and, because of the rapid response of photoprotective pigments to changes in UV-B radiation recorded in previous studies (Newsham et al. 2002, 2005), that concentrations of an anthocyanin-like pigment and UV-B screening pigments would increase in *C. varians* tissues during snowmelt. A growth cabinet experiment was also performed to simulate the effects of rapid snowmelt on the photosynthetic yield of *C. varians*. Finally, we compared the photosynthetic yield and pigmentation of plants measured during snowmelt with those of plants during the middle of the growing season at Rothera Point, to determine whether or not full recovery occurs immediately after emergence from snow.

Materials and methods

Site description

The population of *C. varians* that was studied forms an extensive (*c*. 10 m^2) mat in a low-lying (*c*. 5 m a.s.l.) gully at Rothera Point on the Wright Peninsula, Adelaide Island (67° 34' S, 68° 07' W), *c*. 100 m from the British Antarctic Survey's Rothera Research Station. Between March and November plants in the gully are normally permanently covered with snow to depths of 0.2 – 1.0 m. Snowmelt at the site normally begins in late October, when, under clear skies, a permanent ice cornice in the gully releases meltwater and hydrates the mat of *C. varians*, including that under

snow and ice, below it. During the austral summer the plants are exposed to direct solar radiation between *c.* 10:00 and 19:00 hrs (local time).

Snow cover, temperature, irradiance and ozone column depth measurements

Ambient air temperatures were recorded every 5 min by two platinum resistance thermometers (PT100; Labfacility Ltd., Teddington, UK), within a standard Stevenson screen situated 180 m from the gully. Broad-band UV-B and PAR sensors (model nos. SKU 430 and SKP 215, respectively; Skye Instruments Ltd, Llandrindod Wells, UK) monitored the irradiance received every 5 min at the surface of the *C. varians* mat in the gully. In addition, two of the same sensors installed close to the site synchronously measured irradiances of UV-B and PAR at 3 m above ground level. The depth of snow covering the broadband sensors at the study site was measured weekly using snow stakes from July 2005 until the snow ablated in spring. The outputs from the UV-B and PAR sensors were cross-calibrated with data from a double monochromator grating spectroradiometer (Bentham DM150; Bentham Instruments Ltd., Reading, UK) situated in a laboratory 340 m from the gully. The spectroradiometer recorded global spectral irradiance between 280 and 600 nm every 30 min throughout the study period. It was calibrated against a 1000 W quartz-halogen tungsten coil filament lamp that meets US National Institute of Standards and Technology standards. Spectral data were expressed as biologically effective UV-B ($UV\text{-}B_{BE}$) weighted with the generalized plant action spectrum (Caldwell 1971) and normalized to 1 at 300 nm, or as the flux of PAR. Overpass measurements of ozone column depths over Rothera Point were obtained from the Ozone Monitoring Instrument, situated aboard the NASA Aura satellite (http://toms.gsfc.nasa.gov).

Measurements during snowmelt

Plants were sampled as they emerged from melting snow in November 2005. In order to mark the positions of the plants prior to them being covered with snow in autumn, 2 m length bamboo canes were laid on the ground next to four areas of healthy *C. varians* mat in March 2005. In November 2005, during the spring thaw, each cane was marked at solar noon (13:30 hrs local time) to indicate the horizontal distance that the snow had melted back along it during the first day on which it became exposed, and subsequently every 24 h afterwards for 6 d. Two canes became exposed on 10 November and the other two on 15 November.

A pulse amplitude modulated fluorometer (Mini-PAM, Heinz Walz GmbH, Effeltrich, Germany) was used to measure chlorophyll *a* fluorescence parameters of plants at solar noon on 21 November 2005. Measurements were made on plant material that had emerged 1, 2, 3, 4, 5 and 6 d previously from snow. Control measurements were also made in four areas after removing the 10 cm depth of snow covering each sample. All plants, including those under snow, were hydrated (tissue moisture contents *c*. 88% of fresh weight) when the measurements were made. Minimal chlorophyll *a* fluorescence (F_o) and maximum fluorescence (F_m), induced by a 0.8 s saturating flash, were recorded after dark adaptation for 20 min, achieved by covering the plants with a thick, close-weave dark cloth. Maximum PSII yield (F_v/F_m) and the non-photosynthetic quenching coefficient qN, a measure of heat dissipation from PSII (Maxwell and Johnson 2000), were subsequently calculated.

On 21 November, a single sample (*c*. 10 mm × 10 mm) of mat was excised with a knife from adjacent to each of the six points marked along each cane. On two occasions, there had been no recession along a cane on a given day, in which case no sample was collected. Four samples on which control measurements had been made

were also excised. A total of 26 samples were hence collected. Each sample was placed into a sterile plastic bag and kept in the dark while being transferred to the laboratory at Rothera Research Station. Immediately after transfer to the laboratory, each sample was frozen at -80°C and was subsequently dried in a ModulyoD freeze drier (Thermo Electron Corp., Waltham, MA, USA). The uppermost 2-3 mm of tissue was then cut from each sample with a scalpel and two sub-samples of 25 mg were ground in liquid nitrogen. UV-B screening pigments and the anthocyanin-like pigment were extracted from one sub-sample into 4 ml of methanol, water and HCl (70:20:1), and chlorophylls and carotenoids were extracted from the second sub-sample into 3 ml of methanol, using the methods described by Newsham et al. (2002). Sample preparation and analyses were conducted in dim light and over ice in order to avoid pigment degradation.

Extracts were immediately diluted with the appropriate solvent, transferred to quartz semi-microcuvettes and absorbances were measured in a spectrophotometer (Helios γ, Thermo Electron Corp.). To estimate concentrations of UV-B screening pigments, the absorbance of each acidified methanol extract was measured between 280 and 315 nm (1 nm step). The concentration of the anthocyanin-like pigment was estimated by measuring the absorbance of acidified methanol extracts at 495 nm (Post and Vesk 1992). Concentrations of UV-B screening pigments were expressed as the area under the absorbance curve ($AUC_{280\text{-}315}$) per mg dry weight of tissue. Data for the anthocyanin-like pigment were expressed as A_{495} per mg dry weight. To estimate concentrations of chlorophylls *a* and *b* and carotenoids, absorbances of methanol extracts were measured at 470, 653 and 666 nm, and concentrations of pigments were calculated from standard formulae (Lichtenthaler and Wellburn 1983). Weights of

chlorophylls and carotenoids extracted per gram dry weight of tissue were subsequently calculated.

Growth cabinet experiment

A hydrated sample of *C. varians* mat was excised from under a 10 cm depth of snow on 16 November 2005. The sample was kept in the dark and transferred to a growth cabinet in a laboratory at Rothera Research Station within a few minutes. The growth cabinet (Fitotron, Sanyo Gallenkamp PLC, Loughborough, UK) was set to 4 ºC, with 25% humidity and UV-B, UV-A and PAR irradiances of 0.961, 2.100 and 181.74 W m^2, respectively. Effective quantum yield of photochemistry (Φ_{PSII}) was measured, as described above but without dark adaptation, at 2 min intervals for the first 10 min after transfer to the cabinet, at 5 min intervals for the following 50 min, at 30 min intervals for the following 5 h and then every hour for the following 4 h.

Mid-season measurements

Fully-hydrated samples of *C. varians* from the middle of the growing season were collected on seven consecutive days, beginning on 4 January 2006, from four plots (0.5 × 0.5 m) located in the gully. F_v/F_m measurements were made each day at solar noon in triplicate in each of the four plots, as described above. Concentrations of the anthocyanin-like pigment and UV-B screening pigments were measured in one sample of material from each plot on each of the seven days, also as described above. Owing to limited availability of plant material, concentrations of chlorophyll and carotenoids were measured in plants collected from each plot on 4, 5 and 6 January only.

Statistical analyses

Rank correlations were used to determine changes to the PSII yield and pigmentation of plants as they emerged from melting snow. The Spearman's rank correlation coefficient (r_s) was calculated for the association between each of the response variates and time (number of days after emergence from snow) and the total doses of UV-B_{BE}, UV-A and PAR received since emergence. The same test was used to determine associations between time and Φ_{PSII} in the growth cabinet experiment. ANOVA was used to compare the PSII yield and pigmentation of plants during snowmelt and in mid-season, and at different times during snowmelt.

Results

Snow cover, temperature, irradiance and ozone column depth

C. varians in the gully at Rothera Point became covered with snow between late March and early April 2005. Snow accumulation continued throughout the autumn and winter until plants were covered with a *c*. 20 cm depth of snow in early October. The depth of snow covering the plants reduced by *c*. 5 cm wk^{-1} from early October until the plants adjacent to the canes started to emerge from snow on 10 and 15 November. The minimum, mean and maximum horizontal rates at which snow receded along the canes during this period were 0, 25 and 40 cm d^{-1}. Moderate snowfalls occurred between 10:00 and 13:00 hrs on 18 November. Areas that were previously uncovered accumulated no more than 1 cm depth of snow, which melted within 30 min. Slight, intermittent snowfall also occurred between 09:00 and 13:00 hrs on 12 November and 18:00 and 20:00 hrs on 14 November. This snow melted immediately after falling. There was no precipitation between 4 and 10 January, other than intermittent snow between 09:00 and 11:00 hrs on 10 January.

Air temperatures between 10 and 21 November ranged between –5.2˚C and +5.9˚C, and those between 4 and 10 January 2006 varied between –3.0˚C and +4.3˚C (Fig. 1a). There was a significant increase in mean daily air temperature of 0.26˚C d^{-1} between 10 and 21 November ($F_{1,10}$ = 5.37, P=0.043, r^2 = 34.9%) and a significant decrease of 0.48˚C d^{-1} between 4 and 10 January ($F_{1,6}$ = 13.54, P=0.010, r^2 = 69.3%). Daily mean air temperature did not differ between the study periods in November and January ($F_{1,17}$ = 0.19; P=0.668). The ranges of UV-B_{BE} and PAR fluxes received by plants between 10 and 21 November were 3.34×10^{-6} – 1.3×10^{-1} and 3.0×10^{-2} – 290 W m^2, respectively (Fig. 1b, c). Those received between 4 and 10 January were 7.36×10^{-5} - 1.8×10^{-1} and 7.0×10^{-2} - 200 W m^2, respectively (Fig. 1b, c). Mean daily flux of UV-B_{BE} was 33% higher between 4 and 10 January than between 10 and 21 November ($F_{1,17}$ = 8.82; P=0.009; Fig. 1b). In contrast, mean daily PAR flux was 25% lower in January than in November ($F_{1,17}$ = 11.04; P=0.004; Fig. 1c). Minimum, mean and maximum ozone column depths over the study site between 10 and 21 November were 310, 353 and 377 Dobson units and those between 4 and 10 January were 266, 279 and 291 Dobson units (data not shown). Mean ozone column depth over Rothera Point was 21% lower in January than in November ($F_{1,17}$ = 159.47, P<0.001). Data from the broadband sensors indicated that a 10 cm depth of snow absorbed 80% of both PAR and UV-B radiation.

Measurements during snowmelt

The maximum PSII yield of plants one day after emergence from snow was 144% higher (P<0.001) than that of plants sampled from under a 10 cm depth of snow (Fig. 2a). There was then no subsequent change in F_v/F_m over the six days after the plants had emerged from snow (Fig. 2a). The quenching coefficient qN remained constant at

0.26 (± 0.01) in plants under 10 cm of snow and in those that had emerged from snow (data not shown).

There were no significant associations between time since emergence from snow and any measures of pigmentation (Fig. 2b-e). The canes emerged from snow on two different days, and therefore plants adjacent to different canes would not have received the same doses of radiation following snowmelt. Doses of UV-B_{BE}, UV-A and PAR received since emergence were hence used as predictor variables, but again, no significant correlations were recorded between radiative doses and pigment concentrations (data not shown). However the coefficients were all positive, indicating an overall trend towards an increase in metabolites following melt out. Chlorophyll *a* / *b* ratio remained constant at 2.1 (± 0.1) in tissues under snow and in those that had emerged from snow (data not shown).

Carotenoid and chlorophyll concentrations in plant tissues that had recently emerged from snow were higher than in those under a 10 cm depth of snow (Fig. 2d, e). The concentrations of total carotenoids were 60% higher in tissues that had emerged from snow 24 h earlier than in those under 10 cm of snow (Fig. 2d; $P<0.05$). Concentrations of chlorophylls *a* + *b* in tissues that had emerged from snow 24 h previously were 88% higher than in those under snow (Fig. 2e; $P<0.05$).

Growth cabinet experiment

The photosynthetic yield of *C. varians* recovered rapidly after transfer to the illuminated growth cabinet (Fig. 3). During the first 45 min of the experiment, Φ_{PSII} increased from 0.52 to 0.68 ($r_s = 0.784$, $P=0.002$). Over the following 9 h, Φ_{PSII} remained constant at *c.* 0.66 ($r_s = 0.335$, $P>0.05$).

Intra-seasonal comparison

F_v/F_m and foliar pigment concentrations differed between snowmelt and the middle of the growing season at Rothera Point. F_v/F_m and the concentrations of the anthocyanin-like pigment, UV-B screening pigments and total carotenoids were respectively 45%, 120%, 56% and 55% higher in January than in November (Fig. 4a - d). The concentration of chlorophyll *a* + *b* did not vary significantly between the two periods (Fig. 4e), and neither did those of chlorophyll *a* or *b*, but the chlorophyll *a* / *b* ratio was 10% higher in January than it was in November (Fig. 4f).

Discussion

The present study shows the rapid recovery of metabolic activity by hydrated plants of the leafy liverwort *Cephaloziella varians* during spring snowmelt in the natural Antarctic environment. F_v/F_m of plants under a 10 cm depth of snow, which would have taken up to two weeks to melt at the rate of ablation recorded in the present study, was 60% lower than that of plants which had emerged from snow. Previous studies have similarly reported the recovery of PSII of plants during snowmelt. For example, PSII activity of four lichen species studied by Pannewitz et al. (2003) at Granite Harbour in Victoria Land, continental Antarctica, only recovered when thalli had almost fully ablated from snow, corroborating data on Arctic and alpine vascular plant species (Oberbauer and Starr 2002; Hamerlynck and Smith 1994). Similarly, Schlensog et al. (2004) found that F_v/F_m of the mosses *Bryum subrotundifolium* and *Hennediella heimii* recovered to optimum levels four days after hydration following overwintering in a dehydrated state at Botany Bay, also in Victoria Land. However, in contrast, Schlensog et al. (2004) reported that F_v/F_m of the Antarctic lichens *Physcia caesia* and *Umbilicaria aprina* recovered almost completely within a few minutes of

hydration. They suggested that the rapid recovery of PSII activity of the lichens was owing to the reactivation of conserved photosystems, while the much slower recovery of F_v/F_m of the mosses indicated that repair had taken place to the photosystems. Given that in the current study the effective PSII yield of *C. varians* increased within 45 min of plants under snow being transferred to a growth cabinet, our data suggest that either PSII of this species is conserved over winter, or, perhaps more likely, that repair to the photosystems may occur before the species emerges from snow.

The rapid recovery of PSII by *C. varians* during snowmelt would permit rapid carbon assimilation following a prolonged winter of low light levels. This characteristic has similarly been suggested to be beneficial to Arctic and alpine plants and lichens with short growing seasons (Hamerlynck and Smith 1994; Kappen et al. 1995; Oberbauer and Starr 2002). Chlorophyll concentrations similar to those measured in the middle of the growing season were reached in *C. varians* tissues within 24 h after snowmelt, further facilitating the rapid fixation of carbon after emergence from snow. Concentrations of chlorophylls and carotenoids in emergent plants were approximately twice those in plants under snow, corroborating the data of Kimball et al. (1973), who found chlorophyll concentrations in the leaves of the montane herbs *Claytonia lanceolata* and *Nemophila breviflora* under 10 cm of snow to be one third of those in leaves above snow. Whether or not concentrations of photosynthetic pigments in the tissues of *C. varians* decrease with increasing depth of snow cover at present remains unknown. However, this is likely to occur, as chlorophyll and carotenoid concentrations in the foliage of subnivean vascular plants are known to be inversely associated with the depth of snow from which the plants are sampled (Kimball et al. 1973; Oberbauer and Starr 2002). Similarly, concentrations of UV-B photoprotective pigments, induced by exposure to low irradiances of UV

radiation whilst plants are still beneath snow and ice, might also increase in tissues of *C. varians* prior to emergence.

Photoprotective pigments, notably the anthocyanin-like pigment and UV-B screening pigments, have been previously shown to increase in concentration in tissues of *C. varians* exposed to UV-B radiation. For example, Newsham et al. (2002) found that concentrations of UV-B screening pigments were associated with the dose of solar UV-B radiation received by plants at Rothera Point over two growing seasons. Similarly, Newsham et al. (2005) placed polyester screens over *C. varians* in order to attenuate UV-B radiation, and recorded reduced concentrations of the anthocyanin-like pigment in liverwort tissues. Subsequent removal of the screens leads to the rapid resynthesis of the pigment (K.R.S. Snell, unpubl. data). In the present study we found a 10 cm depth of snow to absorb 80% of UV-B radiation dose, corroborating the data of Cockell et al. (2002). We hence anticipated that concentrations of UV-B photoprotective pigments would increase as *C. varians* emerged from melting snow, in the same way that anthocyanins increase during snowmelt in the foliage of Arctic ericoid species (Oberbauer and Starr 2002). This response was not observed. Plants under snow and those that had melted out had the same qN values, corroborating the observation that concentrations of the anthocyanin-like pigment did not change, since qN is lower in tissues containing more of the pigment (K.R.S. Snell, unpubl. data). At present it is unclear why concentrations of UV-B photoprotective pigments did not respond to changes in UV-B exposure caused by snowmelt. We hypothesize that *C. varians* may prioritise pigment synthesis in favour of photosynthetic pigments in order to maximise carbon gain when resources are limited during snowmelt.

Data from the intra-seasonal comparison in the present study indicated that concentrations of the anthocyanin-like pigment, UV-B screening pigments and total carotenoids were all higher during the middle of the growing season at Rothera Point compared with during snowmelt. These increases in concentrations of photoprotective pigments in January, when UV-B fluxes were higher than in November owing to a significantly shallower ozone column over Rothera Point, corroborate previous studies showing that concentrations of UV-B screening pigments, the anthocyanin-like pigment and carotenoids increase in the tissues of *C. varians* exposed to UV-B radiation (Newsham et al. 2002, 2005). We also recorded significantly higher F_v/F_m values in the middle of the growing season, indicating that although there was some recovery of PSII activity during snowmelt, full recovery did not occur immediately. These data corroborate those of Oberbauer and Starr (2002), who found F_v/F_m of the vascular plant species *Cassiope tetragona*, *Ledum palustre* and *Vaccinium vitis-idaea* to reach optimum levels (*c*. 0.8) up to a month after snow had ablated. It is possible that the lower concentrations of UV-B photoprotective pigments in the tissues of *C. varians* during snowmelt may have predisposed plants to photoinhibition (Gould et al. 1995), accounting for the lower F_v/F_m of plants in November.

Data from the intra-seasonal comparison also indicated that chlorophyll *a / b* ratio, which was similar to the mean of 1.97 reported by Marschall and Proctor (2004) for 16 liverwort species, increased between November and January. This is attributable to more physiologically active tissues synthesizing more chlorophyll *a* compared with chlorophyll *b* in the middle of the growing season, or possibly to the higher irradiance of PAR received by plants during November, which may have decreased chlorophyll *a* / *b* ratio owing to the preferential destruction of chlorophyll *a* in reaction centres (Post 1990). Despite previous evidence indicating that chlorophyll

a / *b* ratio decreases in bryophytes grown under shade conditions (Martin and Churchill 1982), we found no change in this ratio as plants emerged from snow. Post and Vesk (1992) similarly found no difference between the chlorophyll *a* / *b* ratios of *C. varians* from shaded and sun-exposed habitats.

Changes to air temperatures, precipitation rates and radiative patterns arising from climate change processes in Antarctic ecosystems (Convey and Smith 2006) are likely to present new challenges to *Cephaloziella varians*. These include the loss of snow cover and earlier melt-out times in the habitats in which *C. varians* occurs. Earlier melt-out times will expose the species to additional UV-B radiation arising from springtime stratospheric ozone depletion, subjecting the liverwort to additional stress during this critical period. Early photosynthetic reactivation, in conjunction with the rapid synthesis of photosynthetic pigments, suggests that *C. varians* is well adapted to the changing microclimatic conditions that it experiences during snowmelt. This suggests that, at least while its habitat remains hydrated, the species is well placed to cope with these additional challenges.

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Figure legends for Snell *et al*.

Fig. 1 (a) Air temperature and fluxes of (b) UV-B_{BE} and (c) PAR between 10 - 21 November 2005 and 4 - 10 January 2006. Data in (a) were recorded at 1 h intervals, those in (b) and (c) at 30 min intervals.

Fig. 2 (a) Maximum quantum yield of photochemistry (F_v/F_m) and concentrations of (b) the anthocyanin-like pigment, (c) UV-B screening pigments, (d) total carotenoids and (e) chlorophyll *a* + *b* in tissues of *C. varians* during snowmelt. Plants at day 0 were sampled from beneath a 10 cm depth of snow, approximately 14 d prior to emergence. Values are means (± S.E.M.) of four replicates, except at day 4, for which values are means of two replicates. Values that are distinctly superscripted differed at $P<0.001$ in (a) and at $P<0.05$ in (d) and (e).

Fig. 3 Response of Φ_{PSII} to simulated snowmelt in the growth cabinet experiment. Note that the *y*-axis does not extend to zero.

Fig. 4 (a) F_v/F_m and concentrations of (b) the anthocyanin-like pigment, (c) UV-B screening pigments, (d) total carotenoids and (e) chlorophyll *a* + *b*, and (f) chlorophyll *a* / *b* ratio during November and January. Values for November are means of 40 measurements in (a) and 25 in (b-f). Those for January are means of 24 in (a), 31 in (b-c) and 9 in (d-f). ** and *** denote differences at $P<0.01$ and $P<0.001$, respectively.

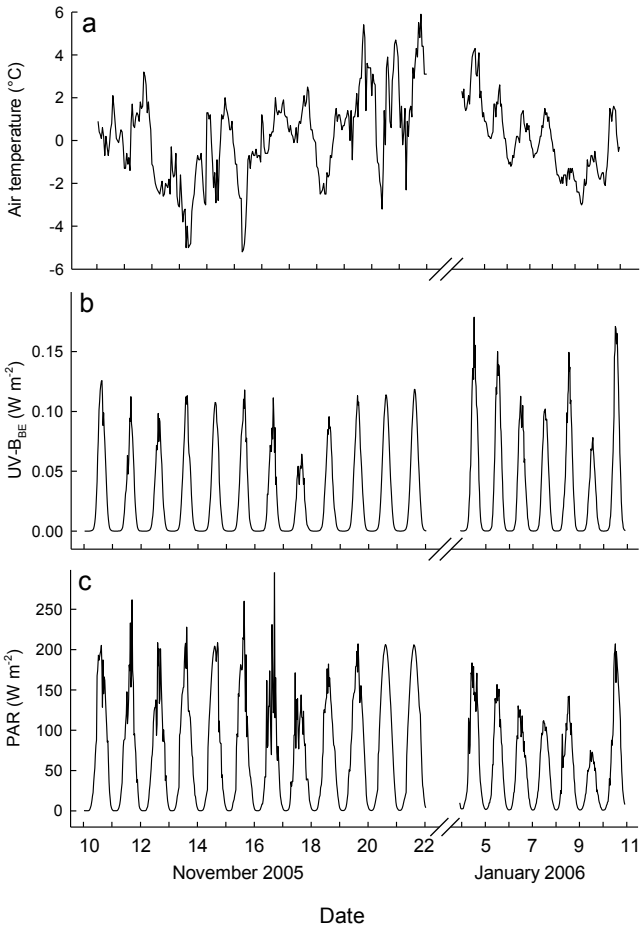

Fig. 1 Snell *et al*.

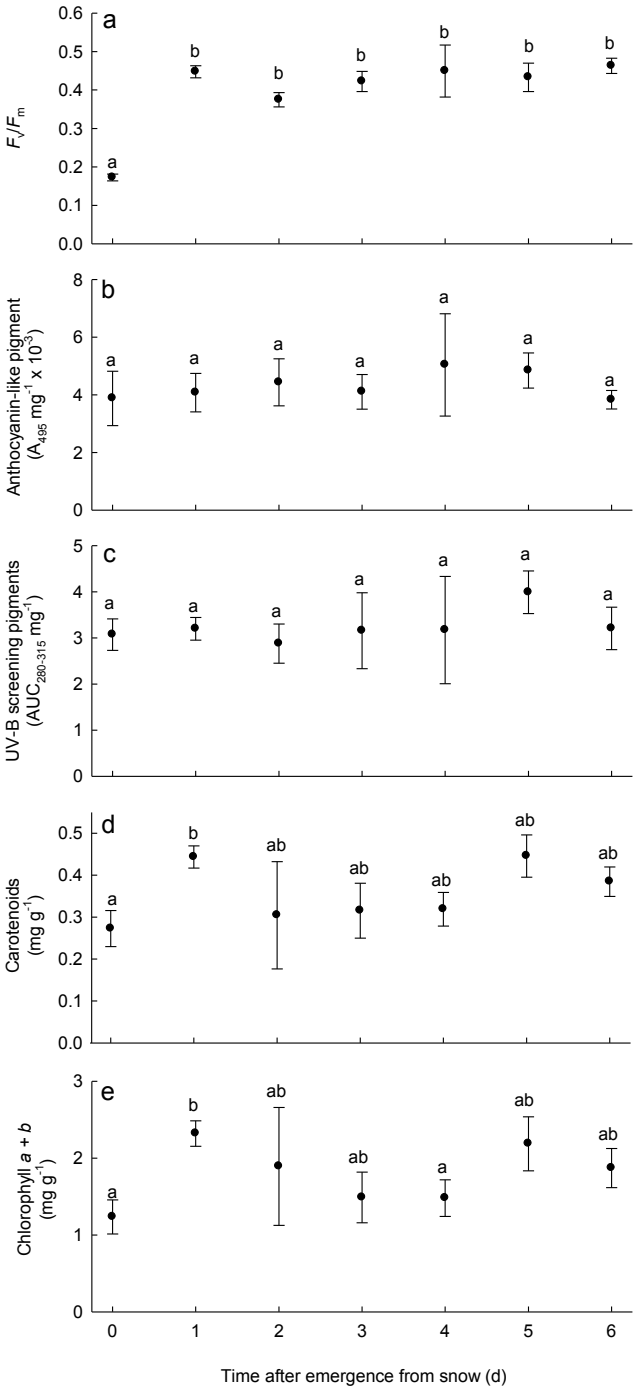

Fig. 2 Snell *et al*.

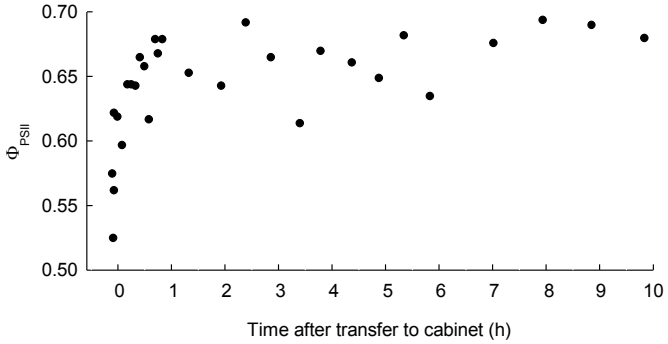

Fig. 3 Snell *et al*.

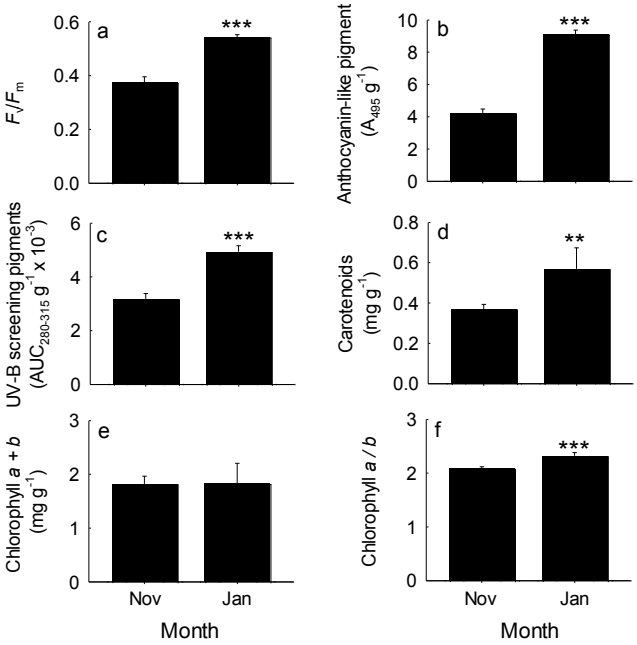

Fig. 4 Snell *et al*.