

Photosynthetic responses of three common mosses from continental Antarctica

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Abstract: Predicting the effects of climate change on Antarctic terrestrial vegetation requires a better knowledge of the ecophysiology of common moss species. In this paper we provide a comprehensive matrix for photosynthesis and major environmental parameters for three dominant Antarctic moss species (*Bryum subrotundifolium*, *B. pseudotriquetrum* and *Ceratodon purpureus*). Using locations in southern Victoria Land, (Granite Harbour, 77°S) and northern Victoria Land (Cape Hallett, 72°S) we determined the responses of net photosynthesis and dark respiration to thallus water content, thallus temperature, photosynthetic photon flux densities and CO₂ concentration over several summer seasons. The studies also included microclimate recordings at all sites where the research was carried out in field laboratories. Plant temperature was influenced predominantly by the water regime at the site with dry mosses being warmer. Optimal temperatures for net photosynthesis were 13.7°C, 12.0°C and 6.6°C for *B. subrotundifolium*, *B. pseudotriquetrum* and *C. purpureus*, respectively and fall within the known range for Antarctic mosses. Maximal net photosynthesis at 10°C ranked as *B. subrotundifolium* > *B. pseudotriquetrum* > *C. purpureus*. Net photosynthesis was strongly depressed at subzero temperatures but was substantial at 0°C. Net photosynthesis of the mosses was not saturated by light at optimal water content and thallus temperature. Response of net photosynthesis to increase in water content was as expected for mosses although *B. subrotundifolium* showed a large depression (60%) at the highest hydrations. Net photosynthesis of both *B. subrotundifolium* and *B. pseudotriquetrum* showed a large response to increase in CO₂ concentration and this rose with increase in temperature; saturation was not reached for *B. pseudotriquetrum* at 20°C. There was a high level of variability for species at the same sites in different years and between different locations. This was substantial enough to make prediction of the effects of climate change very difficult at the moment.

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Introduction

In Antarctica, vascular plants are confined to north-western parts of the Antarctic Peninsula so that the vegetation of the main continent is composed entirely of cryptogams (Smith 1984). Lichens dominate on rock surfaces, or within rocks (endolithic communities) but are also found on the surface of moss turfs. Liverworts are not extensive in continental Antarctica and reach their southern limit at Botany Bay, Granite Harbour, southern Victoria Land (77°S). In continental Antarctica mosses are common and occur at their greatest biomasses in areas with regular meltwater in summer, in combination with algae and cyanobacteria.

There is little doubt that mosses owe their presence in continental Antarctica to their poikilohydric lifestyle which gives them the ability to tolerate the extreme cold of the Antarctic winter (Kappen & Valledares 1999, Schlensoeg *et al.* 2004). Although regular desiccation has also been assumed to be part of this lifestyle it now appears that mosses in wet areas can remain moist and continuously active over long periods (Smith 1999, Schlensoeg & Schroeter 2000, Pannewitz *et al.* 2003a). Wetting and rehydration events seem to be scarce once the mosses have become rewetted in a meltwater site. The preconception that these plants are in a harsh, highly variable habitat may need to be revisited, especially for the productive summer season. It is also becoming clear that there are a variety of environments for mosses in Antarctica ranging from xeric,

This paper is dedicated to Professor Dr Ludger Kappen, pioneer of Antarctic ecology, on the occasion of his 70th birthday.

rock cracks and fellfield (feldmark) to mesic, regular meltwater sites (Longton 1988, Kappen *et al.* 1989, Smith 1999, Schlenzog & Schroeter 2000). The different environments appear to influence the rates at which organisms recover after desiccation (Schlenzog *et al.* 2004) with mosses from continuously wet sites recovering only slowly compared to xeric species.

A habitat in which the plants are continuously hydrated brings other potential stresses. There is the possibility of damage from the high irradiances that can occur for long periods of the day, freeze/thaw events and from increased ultraviolet radiation (UV) in the spring and early summer as a result of atmospheric ozone depletion (Robinson *et al.* 2003). The mosses, however, appear to be not only well protected against these stresses (Post 1990, Green *et al.* 2000b) but also to be able to respond rapidly to changes in UV (Newsham *et al.* 2003, Green *et al.* 2005) and freeze/thaw events (Lovell *et al.* 1995a, 1995b). It is possible that the ability of mosses to adapt themselves to environmental stress has been underestimated.

The performance of Antarctic mosses has been reviewed (Longton 1988, Green *et al.* 1999, Kappen & Schroeter 2002) but the existing knowledge is not extensive. Smith (1999) has reviewed the ecological situation of the three species studied in this paper and notes that all three are widespread in continental Antarctica. There is a growing interest in the use of changes in vegetation composition and performance along latitudinal gradients as a means to demonstrate and detect the effects of expected global climate change (Canadell *et al.* 2000), especially changes in temperature. However, there is a lack of studies comparing photosynthetic performance, as maximal net photosynthesis (NP) or optimal temperatures for NP (Smith 1999), for specimens of the same moss species either at a single location or at several locations. Further, little is known about year to year variability in NP or the factors that might produce such variability although this information is likely to be vital to the interpretation of any vegetation changes or the estimation of likelihood to change. There is also a lack of knowledge about the response of mosses to environmental factors such as low temperatures, especially at or below water freezing point, and to CO₂ concentration. The latter is of special interest because very high levels of CO₂ have been reported amongst mosses in Antarctica (Tarnawski *et al.* 1992, Green *et al.* 2000a). All of these factors could have major effects on the productivity of the plants.

In this paper we report results for three moss species (*Bryum subrotundifolium*, *B. pseudotriquetrum* and *Ceratodon purpureus*) at two locations (Victoria Land Granite Harbour, 77°S and Cape Hallett 72°S). The same species have also been studied at Edmonson Point (74°20'S) by Smith (1999). The results provide an initial insight into differences in NP response of continental Antarctic bryophytes to major environmental variables and to the level of variability in these responses.

Material and methods

Research sites

The research was carried out at Cape Hallett, northern Victoria Land (72°19'S, 170°13.5'E, January/February 1999) and Granite Harbour, southern Victoria Land (77°00'S 162°32'E, February 2000 (2000A), November/December 2000 (2000B) and January 2001).

Cape Hallett (an Antarctic Specially Protected Area 106, see Lewis Smith *et al.* 1994) rises steeply from sea level to about 300 m a.s.l. This scree slope protects the vegetation from strong winds and shades it at night. Cape Hallett is usually snow free during the late spring and summer season, precipitation, exclusively as snow, is low and the mean summer temperature is -2.4°C (Rudolph 1966a). High insolation during the summer season results in thawing of a local glacier, semi-permanent snow patches and the snow field at the top of the scree, so that meltwater flows often and forms numerous small meltwater channels through the vegetated areas. A high nutrient input is guaranteed by the rich bird life in the area (Green *et al.* 2000a).

Cape Geology and Botany Bay are situated in the ASPA 154 in Granite Harbour, an area with exceptional moss and lichen vegetation (Taylor 1913). During the summer season Cape Geology and Botany Bay are snow free. The area is protected from high winds and several small water flows occur in Botany Bay due to thawing of a snow field on the summit of the adjacent ridge.

Investigated species

Bryum subrotundifolium Jaeg., is a widely distributed species on banks and disturbed soils in moist or wet sites in continental Antarctica (Seppelt & Green 1998, Smith 1999). It represents a yellowish-green species close to *B. argenteum* Hedw., that appears to dominate in Victoria Land (Seppelt *et al.* 1995, Seppelt & Green 1998, Ochyra 1998). Samples were collected at Botany Bay as well as at Cape Hallett where *B. subrotundifolium* completely covers large areas.

The common, bipolar moss *B. pseudotriquetrum* (Hedw.) C.F. Gaertn., B. Meyer et Scherb., previously referred to in Antarctica as *B. algens* Card. (Seppelt 1984), grows as a dense turf in moist or wet places along meltwater channels and in low lying flush areas (Ochyra 1998, Smith 1999). Samples were collected from a closed turf area located outside the ASPA 106 in Cape Hallett where the moss grew on a small bench close to the bottom of the scree slope. The species is present at Botany Bay, Granite Harbour and this seems to be its southern limit for extensive growth. It is only a minor component in the McMurdo Dry Valleys.

Ceratodon purpureus (Hedw.) Brid., also known as *C. antarcticus* Card., is a cosmopolitan moss which is common in the maritime Antarctic and widely distributed on the continent (Ochyra 1998, Smith 1999). It forms dense

brownish turfs in a variety of habitats. Samples were collected at Botany Bay where it forms extended turfs on rocky terraces and on disturbed soils in areas of consistent water flow which contrasts to the drier sites reported by Smith (1999). It appears not to be present at Cape Hallett although it has been reported close by (Crater Cirque, 72°38'S 169°22'E).

Climatic conditions

Local climatic conditions were continuously recorded at both sites during the research using data loggers (SQ1021, Grant Instruments, UK). PPFD (photosynthetic photon flux density in the 400–700 nm waveband, $\leq 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$) was measured with GaAsP photodiodes (Hamasutu, J.) equipped with cosine correction according to Pontaillier (1990). The sensors were calibrated using an optical radiation calibrator (1800-02, LiCor, USA). The photodiodes were mounted on the ground both horizontally and with a similar exposure as the moss. The temperatures of the moss turfs (TT°C) were measured with microthermistors (\emptyset 0.3 mm, Grant, UK) placed in the top layer (5 mm). Air temperature (thermistors, \emptyset 0.3 mm, Grant, UK) and relative air humidity (capacitance humidity probes, HMP35, Vaisala, SF) were recorded in a ventilated screen at 1 m above the ground.

CO₂ gas exchange

NP and dark respiration (DR) of the mosses were measured using compact mini-cuvette systems (CMS4P, Walz GmbH, FRG) operated in the differential mode (see Schroeter *et al.* 1994). The open flow system was combined with a cooling trap in order to remove water from the gas stream before entering the non-dispersive infrared gas analyser (Binos 100, Rosemount, FRG). When required, light was provided by an incandescent halogen lamp (FL 400, 400F, Walz GmbH, FRG). The CO₂ concentration (c_a) of the gas stream was normally that of ambient air but, when required, was altered using a CO₂ mixer (Walz GmbH, FRG). The measurement systems were installed at the field camps in Cape Hallett and Granite Harbour. Photosynthetic response to ambient climatic conditions were performed using the same system but with the CMS4P in tracking mode.

The moss was collected in pieces of *c.* 8 cm² and immediately transported to the field laboratory. Debris and dead moss material was removed and the sample trimmed to a thickness of about 8 mm. CO₂ gas exchange measurements took place immediately after collection. NP and DR rates were expressed on an area base and gross photosynthetic rate (GP) calculated as (NP + DR).

The dependence of NP and DR on water content (WC) was measured for both *B. subrotundifolium* and *B. pseudotriquetrum* collected fresh from the field. The prepared moss samples were sprayed and then submerged in water.

Adherent water was shaken off and the maximally hydrated sample weighed on a precision balance (Bp310S, Sartorius, FRG, accuracy: 1 mg) before it was enclosed in the minicuvette. Samples were removed every 30 min and reweighed for later determination of WC (d.wt., 24 h 105°C). Between weighings, net CO₂ exchange was first recorded at 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (NP) and then at 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (DR) with TT always maintained at 10°C.

Photosynthetic response to PPFD and TT was determined for each sample by measuring NP from 0 to about 1300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 5K intervals from -5 to +30°C. Ambient air was used with c_a of 350–370 ppm. WC of the samples was regularly checked by weighing the sample and adjusted to, or close to, optimal levels because a certain amount of evaporative water loss could not be avoided.

The photosynthetic responses of *B. subrotundifolium* and *B. pseudotriquetrum* to c_a (100, 200, 360, 620, 800, 1000, 1500, 2000 ppm) were determined only at Cape Hallett. NP were first measured at near ambient c_a (360 ppm) at PPFD between 0 and 1350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and at 0, 10 and 20°C TT. Measurements were repeated stepwise to 2000 ppm CO₂, the measurement at near ambient was then repeated and, finally, c_a reduced stepwise to 100 ppm. A repetition of the individual experiments with a statistically relevant number of samples was impossible due to logistic restrictions. Diel measurements were also made at Granite Harbour with specimens at ambient or elevated (about 2000 ppm) CO₂.

Results

Climatic conditions

The maxima and minima for PPFD incident on the mosses are summarized in Table I and daily PPFD for both moss species at Granite Harbour are given in Fig. 1. Zero PPFD was never measured at Granite Harbour but, because of the lower latitude, did occur towards the end of the research period at Cape Hallett. However, at both locations, the sun vanished behind mountains for part of each night resulting

Table I. Minima and maxima for PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and moss turf temperatures (TT °C) measured at two continental Antarctic sites (Cape Hallett, CH; Granite Harbor, GH) during the summer seasons 1999, 2000 and 2001.

Site	Date	Species	TT (°C)		PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
			T _{max}	T _{min}	max.	min.
CH	4.01.–15.02.1999	<i>B. subrotundifolium</i>	21.2	-5.9	1982	0
		<i>B. pseudotriquetrum</i>	24.5	-2.0		
GH	14.01.–30.01.2000	<i>B. subrotundifolium</i>	23.5	-8.2	1979	19
		<i>C. purpureus</i>	18.6	-1.8		
	23.11.–11.12.2000	<i>B. subrotundifolium</i> pot. active*	17.4	-9.3	1639	69
	12.12.2000–16.01.2001	pot. inactive*	38.2	-12.2	2000	73
	23.11.2000–24.01.2001	<i>C. purpureus</i>	35.7	-10.3	2000	40

*potentially active and inactive time of *B. subrotundifolium* during the summer season 2000/2001 (for further explanation see text).

in a rapid decrease in solar radiation and surface soil and water freezing almost every day (see also Rudolph 1966a). Daily maxima were often very high at both locations and, at Granite Harbour, 9% of the readings were above $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and values over $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ were measured on about two thirds of the days (horizontal sensor, Fig. 1a)

There were no days with air temperature continuously above freezing but the high incident radiation meant that TT exceeded air temperature for most of the time at both locations. At Cape Hallett, the moss turf temperature was above 0°C for 55% of the readings in contrast to air temperature which was below 0°C for 88% of the readings. Absolute thallus temperature maxima were 21.2°C and 24.5°C , and minima were -5.9°C and -2.0°C , for *B. subrotundifolium* and *B. pseudotriquetrum*, respectively. TT of *B. subrotundifolium* between -2°C and 0°C were most frequent with 34% (of 2k bands), but 55% of the readings were $>0^\circ\text{C}$, with 47% between 1°C and 11°C .

Greater extremes in TT were measured at Granite Harbour with *C. purpureus* reaching 35.7°C (20 December) and a minimum of -12.2°C (15 January). TT of *C. purpureus* between -2°C and 2°C were most frequent with 30% of the readings $\leq 0^\circ\text{C}$ and above 0°C and 12°C for

63% and 27% of the time, respectively (Fig. 1e). The most common TT for *B. subrotundifolium* were between -2°C and 2°C (36%) and the moss turf was above 0°C for 66% of the time with a maximum of 38.2°C (Fig. 1c). Daily maxima and minima were much less extreme when the plants were wet and the most frequent TT for moist thalli were still between -2°C and 2°C (58%), with 49% of the readings $\leq 0^\circ\text{C}$ and another 49% between 1°C and 15°C . TT of *C. purpureus* were also affected by hydration status and, when wet, hardly declined below 0°C during the first nights of measurements (23 November–5 December 2000). This probably indicated a buffering effect from the high WC in the moss. Mosses were hydrated for long periods with intermediate dry phases. Chl *a* fluorescence measurements (data not show, for further details on methods see Pannewitz *et al.* 2003a) showed that *B. subrotundifolium* was potentially active, i.e. wet, from 23 November–11 December 2000, and after 15 January 2001.

*CO*₂ gas exchange

Diel *CO*₂ gas exchange

A comparison of the photosynthetic responses of

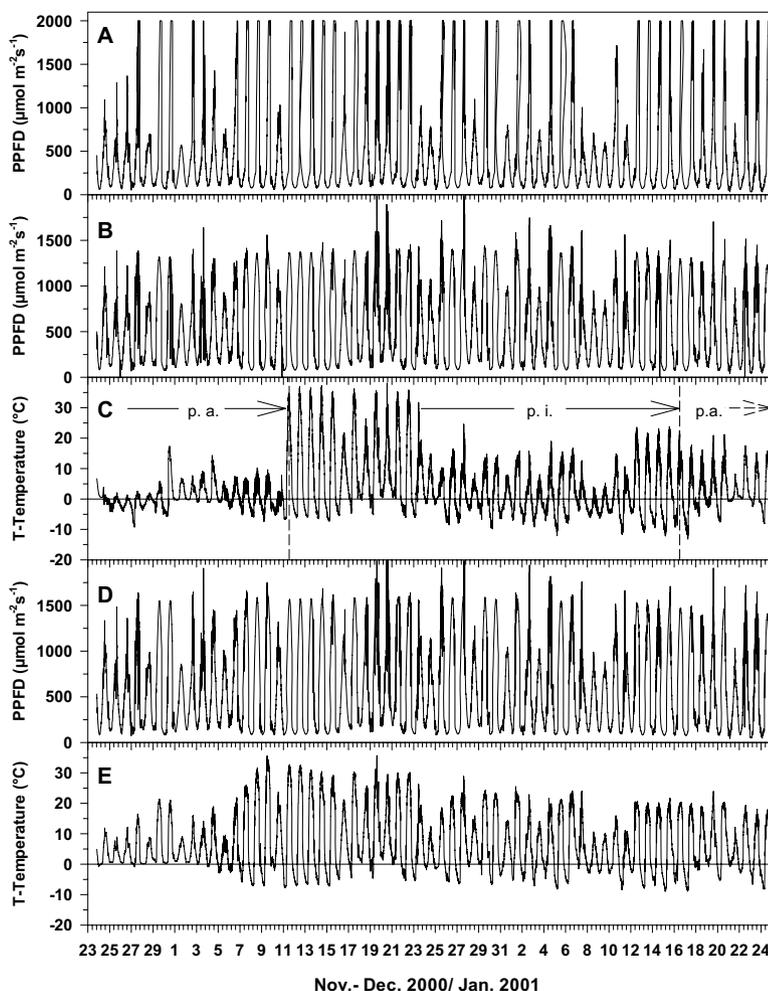


Fig. 1. a. Daily course of ambient PPFD (horizontal) and at moss turf level of **b.** *B. subrotundifolium* and **d.** *C. purpureus*), as well as the corresponding turf temperatures (C+E) measured between 23 November 2000 and 24 January 2001 at Granite Harbour. **c.** indicates the potentially active (p.a.) and inactive (p.i.) time of *B. subrotundifolium*.

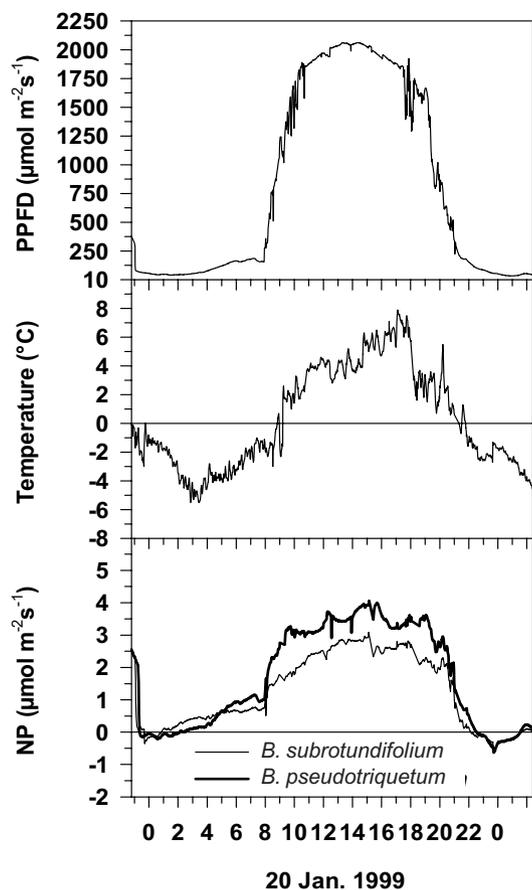


Fig. 2. Diurnal course of net photosynthesis (NP) of *Bryum subrotundifolium* and *B. pseudotriquetrum* under similar ambient climatic conditions measured on 20 January 1999 at Cape Hallett ($72^{\circ}19'S$). Thallus temperature ($^{\circ}\text{C}$) is shown for *B. subrotundifolium*.

B. subrotundifolium and *B. pseudotriquetrum* to ambient conditions on 20 January 1999 at Cape Hallett is presented in Fig. 2. The typical diel pattern for PPFD was a sharp rise at about 08h00 and a sudden decline around 20h00, both due to the shadowing effect from the cliffs to the east of the research site. TT tracked PPFD and showed a sharp increase and decrease at the same times. Respiration occurred when PPFD reached its nightly minimum of around $30 \mu\text{mol m}^{-2}\text{s}^{-1}$ and TT fell below 0°C . However, the respiration rates at TT of -3°C were very low ($\leq 0.2 \mu\text{mol m}^{-2}\text{s}^{-1}$) and a slight increase in PPFD to $>50 \mu\text{mol m}^{-2}\text{s}^{-1}$ resulted in positive NP in both species although TT were still below zero. At about 15:00 h the samples were exposed to maximal measured PPFD of around $2000 \mu\text{mol m}^{-2}\text{s}^{-1}$, TT was 6°C and maximal NP rates were $4 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ for *B. pseudotriquetrum* and $3 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ for *B. subrotundifolium*. *Bryum subrotundifolium* had 27% lower daily CO_2 gain per day than *B. pseudotriquetrum* ($24.7 \mu\text{mol CO}_2 \text{ m}^{-2}\text{d}^{-1}$) under very similar microclimatic conditions.

Diel CO_2 gas exchange measurements were also

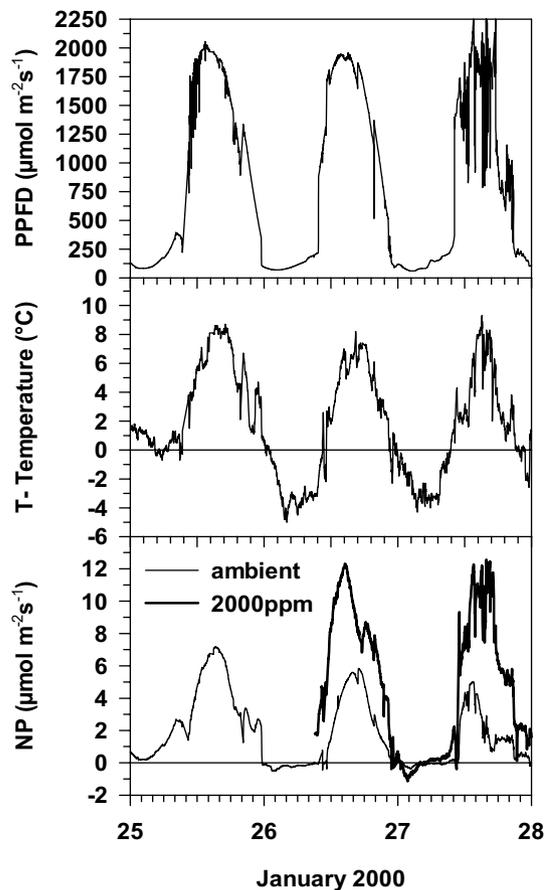


Fig. 3. Diurnal course of net photosynthesis (NP) of *Bryum subrotundifolium*, at the ambient CO_2 concentration, and at elevated CO_2 concentration (2000 ppm) under similar ambient climatic conditions in Granite Harbour ($77^{\circ}00'S$). Thallus temperature is shown for *B. subrotundifolium* under ambient CO_2 concentration.

performed for *B. subrotundifolium* at Granite Harbour (25–27 January 2000; Fig. 3). Ambient c_a was raised to 2000 ppm for two days for one sample whilst a second remained at ambient. Carbon gain per day at the higher CO_2 level was increased by 63% on 26 January and by 82% on 27 January, compared to that at ambient c_a . In general TT followed the diel course of PPFD, with minima of -5°C at the lowest PPFD of $48 \mu\text{mol m}^{-2}\text{s}^{-1}$ and maxima around 10°C with PPFD above $2000 \mu\text{mol m}^{-2}\text{s}^{-1}$. Respiration occurred at low TT and PPFD but was not high with maxima of $0.7 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$.

Dependence of NP and DR on WC

The dependency of CO_2 assimilation rate on moss turf moisture content at Cape Hallett showed the expected pattern for mosses (Fig. 4). At low WC photosynthesis and DR were biochemically limited due to high water deficit in the moss turfs. Increase in hydration was accompanied by a steep rise in both NP and DR. Optimal NP was reached at 390–470% d.wt. for *B. subrotundifolium* and 245–330%

Table II. Temperature optima for net photosynthesis of *Bryum subrotundifolium*, *B. pseudotriquetrum* and *Ceratodon purpureus* at PPFD ranging between 100 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and PPFD_{max}* measured at two continental Antarctic sites (CH = Cape Hallett, GH = Granite Harbor) during the summer seasons 1999, 2000 and 2001.

PPFD ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Temperature optimum ($^{\circ}\text{C}$)					
	<i>B. subrotundifolium</i>		<i>B. pseudotriquetrum</i>		<i>C. purpureus</i>	
	CH 1999 (n = 4)	GH 2000 (n = 3)	GH 2001 (n = 4)	CH 1999 (n = 3)	GH 2000 (n = 5)	GH 2001 (n = 3)
100	0.9	2.7	1.1	-0.2	0.8	0.3
200	3.4	4.9	5.0	2.9	3.4	2.0
500	8.2	6.8	8.8	6.7	5.2	3.3
Max*	14.9	9.1	15.9	12.0	6.8	6.3

*PPFD_{max} = ranging between 1300 and 1350 $\mu\text{mol m}^{-2}\text{s}^{-1}$

d.wt. for *B. pseudotriquetrum*. Further increase in hydration resulted in a decline in NP, which was less pronounced in *B. pseudotriquetrum* than in *B. subrotundifolium*. At full saturation, NP of *B. subrotundifolium* was about 60% and of *B. pseudotriquetrum* about 10% below the rates at optimal WC. DR showed a similar pattern in *B. pseudotriquetrum*, with maximal rates occurring at WC between 400–450% d.wt., but, for *B. subrotundifolium*, were more or less stable above 250% d.wt. Maximal NP were similar in both species but DR of *B. subrotundifolium* were about half those of *B. pseudotriquetrum*.

Response of NP to PPFD and TT

Net photosynthesis of the three species showed the typical response to increase in PPFD with an initial steep rise and an approach to saturation at the maximal PPFD measured (Fig. 5). NP for all three species were not saturated at optimal or near-optimal TT and maximal PPFD, and none showed any examples of depression in NP due to excessive PPFD. NP response curves for different samples of each species were often very different as indicated by the error bars (Fig. 5). This was especially obvious for *C. purpureus* (2001) at PPFD ≥ 250 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ($P = 0.009$) with a standard deviation of 2.95 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ at maximal PPFD.

The quantum efficiency (Φ , initial slope of the PPFD response curves) of photosynthesis was temperature

Table III. Light compensation points ($\mu\text{mol m}^{-2}\text{s}^{-1}$) of *B. subrotundifolium*, *B. pseudotriquetrum* and *Ceratodon purpureus* at moss turf temperature (TT) ranging between 0 and 30 $^{\circ}\text{C}$, measured at two continental Antarctic sites (CH = Cape Hallett, GH = Granite Harbor) during the summer seasons 1999, 2000 and 2001. Results are given as the means (\pm SD) of n independent measurements.

TT ($^{\circ}\text{C}$)	Light compensation ($\mu\text{mol m}^{-2}\text{s}^{-1}$)					
	<i>B. subrotundifolium</i>		<i>B. pseudotriquetrum</i>		<i>C. purpureus</i>	
	CH 1999 (n = 4)	GH 2000 (n = 3)	GH 2001 (n = 4)	CH 1999 (n = 3)	GH 2000 (n = 5)	GH 2001 (n = 3)
0	46 (28)	12	49 (17)	42 (6)	32 (10)	41 (5)
5	76 (58)	44 (2)	66 (26)	37 (2)	69 (13)	93 (18)
10	225 (74)	92 (16)	129 (53)	134 (34)	129 (68)	228 (79)
15	213 (81)	135 (12)	235 (71)	260 (5)	374 (162)	379 (131)
20	312 (93)	204 (5)	329 (99)	429 (36)		637**
25	392 (102)	337 (47)	480 (172)	840*		
30	483 **					

* $n = 2$, ** $n = 1$.

independent (ANOVA $P > 0.1$) and varied between 0.05 and 0.03 in the three species. This contrasts with Smith (1999) who found Φ to be different for the three species with *C. purpureus* apparently having the highest efficiency.

Thallus temperature for maximal NP (TT_{opt}) also changed with incident PPFD, so that the lower the light level the lower the TT_{opt}. Optimal temperatures could even be at subzero temperatures under low PPFD conditions. TT_{opt} at maximal PPFD differed between years and location for *B. subrotundifolium* with a mean TT_{opt} of 13.7 $^{\circ}\text{C}$ ($n = 11$). TT_{opt} was 12.0 $^{\circ}\text{C}$ for *B. pseudotriquetrum* ($n = 3$) and 6.6 $^{\circ}\text{C}$ for *C. purpureus* ($n = 8$). The latter species showed little difference in TT_{opt} between years (Table II) despite large changes in NP_{max}.

Assimilation rates at -5 $^{\circ}\text{C}$ TT were low in all three mosses (maximal 0.1–0.8 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$) but were always substantial at 0 $^{\circ}\text{C}$ TT. At PPFD_{max} and 0 $^{\circ}\text{C}$ TT, *B. subrotundifolium* (1999) had a mean NP of 4.3 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ (SE mean = 1.1), *B. pseudotriquetrum* of 2.6 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ (SE mean = 0.8) and *C. purpureus* (2001) of 1.95 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ (SE mean = 0.4).

DR rose exponentially with increasing TT in all samples ($r^2 = 0.93$ –0.96). The mean DR for *B. pseudotriquetrum*

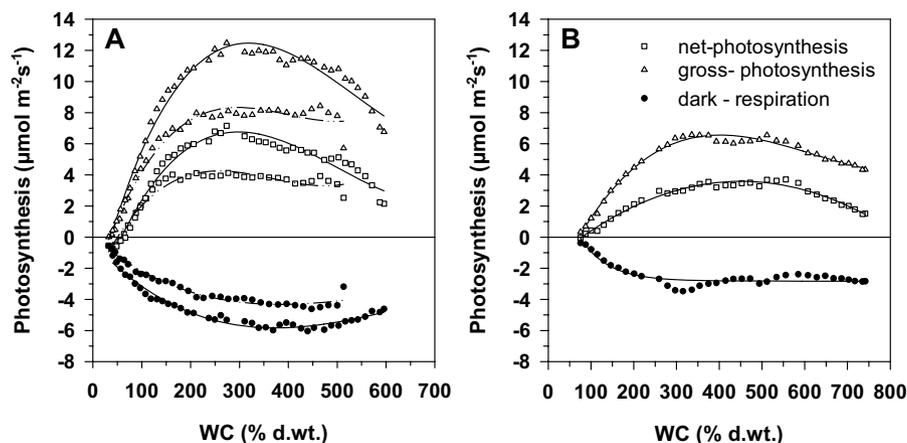


Fig. 4. Gross-photosynthesis (calculated as GP = NP+DR), net photosynthesis (NP) and dark respiration (DR) for **a.** *Bryum pseudotriquetrum* and **b.** *B. subrotundifolium* related to the moss turf water content (WC, % d.wt.) measured at 10 $^{\circ}\text{C}$ turf temperature (TT) and 500/0 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD in the field laboratory in Cape Hallett (72 $^{\circ}$ 19'S).

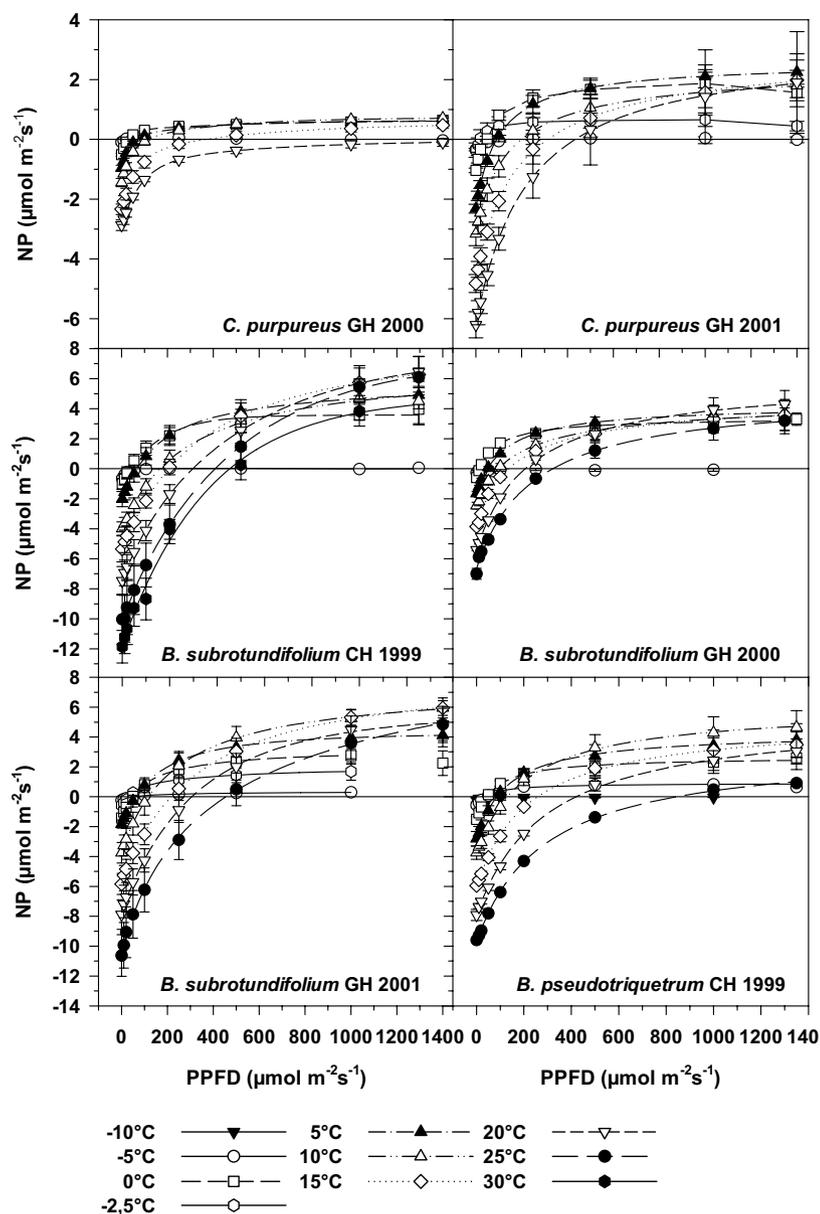


Fig. 5. Dependence of net photosynthesis of *C. purpureus*, *B. subrotundifolium* and *B. pseudotriquetrum* on PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measured at various temperatures. Data points were obtained from gas exchange measurements in the field laboratory at Cape Hallett (CH) and Granite Harbour (GH).

($n = 3$) was $0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at -5°C TT and $7.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 20°C TT. The corresponding rates for *B. subrotundifolium* ($n = 4$) were 0.7 and $7.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 30°C TT. DR rates were variable between years with *B. subrotundifolium* significantly lower at $\text{TT} \geq 15^\circ\text{C}$ in samples from the year 2000 ($P < 0.05$). *Ceratodon purpureus* had average DR rates of $0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at -5°C TT and $2.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 20°C TT in 2000 ($n = 5$) compared to $0.34 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $6.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ($n = 3$), respectively in 2001.

Light compensation (L_c) values were affected by changes in DR (Fig. 5). For *B. subrotundifolium* this meant that NP became positive at $12\text{--}46 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD at 0°C but required $337\text{--}480 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 25°C TT (Table III) whilst PPFD had to be almost twice as high for

B. pseudotriquetrum ($840 \mu\text{mol m}^{-2} \text{ s}^{-1}$; $n = 2$). Interspecific differences in L_c were remarkably at $\text{TT} > 15^\circ\text{C}$, and *C. purpureus* needed higher PPFD to compensate for respiration than the other two species (Table II).

Response of CO_2 exchange to CO_2 concentration

The responses of gross photosynthesis (GP) of *B. subrotundifolium* and *B. pseudotriquetrum* to c_a (100–2000 ppm), TT (0, 10, 20°C) and incident PPFD are shown in Fig. 6a–f. The dominating effect of TT was obvious for both species with GP depressed at $< 10^\circ\text{C}$ and at 0°C were only around 15% of those at 20°C .

NP for both species saturated at around $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD at 0°C TT but showed no saturation at 10°C TT and, even more clearly, at 20°C TT. The response of NP to c_a differed for the two species. Comparisons are made for the

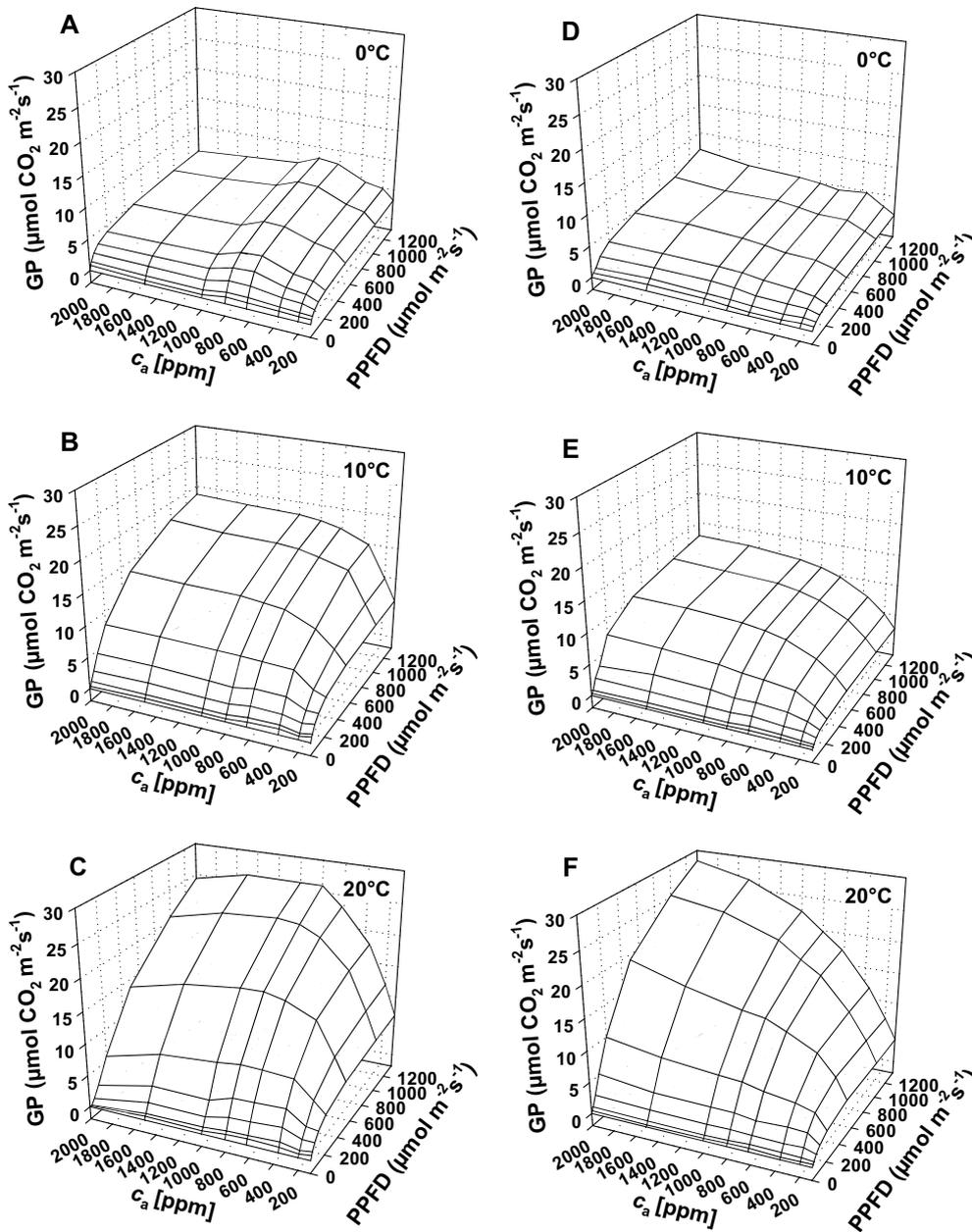


Fig. 6a–c. 3D-mesh plots of gross photosynthesis of *B. subrotundifolium* measured at turf temperatures between a. 0°C, b. 10°C and c. 20°C, PPFD between 0 and 1350 $\mu\text{mol m}^{-2}\text{s}^{-1}$, and c_a between 100–2000 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ in the field laboratory in Cape Hallett. d–f. 3D-mesh plots of gross-photosynthesis of *B. pseudotriquetrum* measured at turf temperature between d. 0°C, e. 10°C and f. 20°C, PPFD between 0 and 1350 $\mu\text{mol m}^{-2}\text{s}^{-1}$, and c_a between 100–2000 $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$ in the field laboratory in Cape Hallett.

higher PPFD because, as expected, saturation was at lower c_a when response curves were generated at lower PPFD. At 0°C and high PPFD both species became CO_2 saturated at c_a of 400–600 ppm. *Bryum subrotundifolium* continued to show CO_2 saturation of NP at about 800 ppm CO_2 at 10°C and 20°C. In contrast, c_a required for saturation of NP in *B. pseudotriquetrum* increased to about 1200 ppm at 10°C and was not reached at all at 20°C.

The responses of NP to c_a are summarized in Table IV where the increase or decrease relative to the nominal ambient CO_2 level (360 ppm) have also been calculated. The maximal capacity of photosynthesis at 10°C TT and the highest PPFD used (1350 $\mu\text{mol m}^{-2}\text{s}^{-1}$) was reduced by 79%, for *B. subrotundifolium* at an ambient c_a of 100 ppm but increased by 48% at a c_a of 2000 ppm. The c_a dependency

was even more pronounced in *B. pseudo-triquetrum* and NP increased by 123% at 10°C TT, PPFD_{max} and a c_a of 2000 ppm.

The carboxylation efficiency (α slope of CO_2 response at low CO_2 concentration) was PPFD and, to a lesser extent, TT dependent (Table V) and, although not statistically significant appeared to be higher for *B. subrotundifolium*. In both species the CO_2 compensation point (Γ) decreased with an increasing PPFD but increased at higher thallus temperatures because of the higher rates of respiration (Table V). At any combination of temperature and PPFD *B. pseudotriquetrum* always had a higher Γ . In general, Γ was well below the natural ambient c_a (360 ppm) at all TT in both tested species except for *B. pseudotriquetrum* at 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD when Γ was 465 ppm.

Table IV. Calculated rates of net photosynthesis (NP $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of *B. subrotundifolium* and *B. pseudotriquetrum* in response to CO_2 concentration (c_a) as a function of moss turf temperature (TT °C) and incident PPFD ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). Percentage increase of NP to CO_2 increase using 360 ppm as a reference level are given in parentheses.

TT °C	PPFD ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)			
	100	200	500	1350
<i>Bryum subrotundifolium</i> Cape Hallett 1999				
100	1.0 (-50)	1.4 (-50)	1.7 (-55)	2.1 (-50)
200	1.8 (-12)	2.4 (-12)	3.4 (-11)	3.8 (-11)
360	2.0	2.8	3.9	4.3
800	3.0 (50)	4.1 (48)	5.4 (40)	6.8 (57)
1000	2.2 (10)	3.2 (14)	4.2 (8)	5.5 (28)
2000	2.0 (0)	2.8 (0)	3.8 (-1)	4.3 (0)
TT 10°C				
100	-0.8 (-200)	0.4 (-90)	1.5 (-77)	2.3 (-79)
200	0.1 (-92)	1.9 (-48)	4.5 (-30)	6.6 (-40)
360	0.8	3.7	6.4	11.1
800	0.3 (-61)	4.0 (8)	8.8 (38)	13.8 (23)
1000	0.9 (8)	4.4 (20)	9.6 (50)	14.6 (31)
2000	1.4 (72)	4.9 (35)	10.3 (63)	15.6 (40)
<i>Bryum pseudotriquetrum</i> Cape Hallett 1999				
TT 0°C				
100	0.6 (-34)	0.8 (-52)	1.0 (-59)	1.1 (-66)
200	1.3 (42)	1.7 (1)	1.8 (-22)	2.3 (-32)
360	0.9	1.7	2.4	3.3
800	2.2 (130)	2.9 (65)	3.4 (43)	4.9 (46)
1000	2.4 (157)	3.4 (94)	3.9 (67)	5.0 (50)
2000	2.3 (143)	3.6 (111)	4.4 (88)	4.8 (43)
TT 10°C				
100	-1.2 (-371)	-0.9 (-137)	-0.4 (-111)	-0.2 (-105)
200	0.4 (-3)	1.5 (-41)	2.3 (-37)	2.8 (-38)
360	0.5	2.5	3.7	4.5
800	1.3 (181)	3.9 (58)	7.0 (90)	8.6 (92)
1000	0.8 (71)	3.5 (41)	6.6 (78)	8.3 (87)
2000	0.9 (98)	4.8 (95)	7.8 (109)	10.0 (123)

Discussion

These studies were on three species of moss at two locations 5 degrees of latitude apart in the Ross Sea region and, although logistic limitations meant that only a small number of samples could be measured, it is an unusually large dataset for Antarctica. Opportunities, therefore, exist to try and separate variability in net photosynthesis inherent to species from that caused by location and external factors. High variability occurred within each species at each sampling as shown by large error bars in Fig. 5. When we can compare sites, then between year differences exceeded between site differences. The responses of NP to PPFD for *B. subrotundifolium* are more similar for Cape Hallett 1999, and Granite Harbour 2001, than between succeeding years at Granite Harbour (Fig. 5; Table III). *Ceratodon purpureus* at Granite Harbour showed large differences in consecutive years (Fig. 5) with NP_{max} being almost double in the second season. As yet, we do not have sufficient information to identify the reasons for this variability. Length of period of snow cover and the occurrence of regular water flows are

Table V. CO_2 compensation (Γ , ppm) and carboxylation efficiency of Rubisco (α) of *B. subrotundifolium* and *B. pseudotriquetrum* (Cape Hallett 1999).

PPFD ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	<i>B. subrotundifolium</i>		<i>B. pseudotriquetrum</i>	
	CO_2 compensation (Γ , ppm)	Carboxylation efficiency (α)	CO_2 compensation (Γ , ppm)	Carboxylation efficiency (α)
	10°C	20°C	10°C	20°C
? 50	-	-	-	-
100	181	-	0.010	0.028
200	<100	284	0.022	0.029
500	<100	147	0.028	0.039
1000	<100	128	103	185
max	<100	120	0.047	0.047
	10°C	20°C	10°C	20°C
174	-	-	0.017	0.017
125	465	0.019	0.018	
111	176	0.022	0.032	
<100	181	0.024	0.035	

likely to be important but this variability adds complexity to attempts to detect the effects of long-term climate change.

Water availability is probably the most decisive ecological variable for the nature and distribution of moss communities in continental Antarctica (Kennedy 1993). Bryophytes depend on liquid water uptake for metabolic activity (Kappen & Valladares 1999), and water availability is linked to temperature, incident radiation and a local supply of meltwater. The major water sources are melting recent snow fall, and meltwater from semi-permanent snow patches and permanent ice. Precipitation occurs mainly in autumn and winter and is light and infrequent in summer (Kappen & Schroeter 1997). Meltwater streams may occur for about two months in the summer season effectively prolonging the active phase of the plants (Howard-Williams & Vincent 1986, Smith 1999). It has been suggested that their physiological performance would then be mainly dependent on their microclimate (Schlensog & Schroeter 2000, Kappen & Schroeter 2002, Pannowitz *et al.* 2003a, 2003b).

The mosses themselves appeared to be well adapted to high water availability and have relatively broad ranges of WC over which NP was near maximal (390–470% d.wt for *B. subrotundifolium* and 245–330% d.wt. for *B. pseudotriquetrum*). Smith (1999) measured sustained high NP for these species at very high WC that were found to cause depression in NP here (*B. argenteum*: 790%, *B. pseudotriquetrum*: 670% and *C. purpureus*: 470% d.wt.). However, the measurements (Smith 1999) were made at very high CO_2 levels (about 5%) and these would have minimized any depression in NP due to higher CO_2 diffusion resistances at high WC. Differences in the optimal WC for NP may be related to the water availability at the sample sites, as summarized by Kappen & Schroeter (2002): xeric species had optimal NP at 200–300% d.wt. compared to over 500% d.wt in hydric species.

The November/December 2000 and January 2001 season at Granite Harbour appeared to be aberrant because meltwater streams from the local glacier did not occur before 16 January (personal observation) and *B. subrotundifolium* was inactive for a long period after the

snowmelt. We suspect that this was because of cooler than normal air temperatures and emphasises, once again, the importance of macroclimate and year-to-year climate variability. Cryptogamic communities are suggested to be highly sensitive to long term global change where the balance between freezing and melting is precarious (Vincent 1997).

Climate change in Antarctica is under debate due to the differences between observed local changes and model-predicted global temperature trends. There has been a warming over the Antarctic Peninsula but a cooling between 0.08 and 0.7°C per decade during the last 30 years over East Antarctica (Comiso 2000, Doran *et al.* 2002, Thompson & Salomon 2002, Shindell & Schmidt 2004). Bertler *et al.* (2004) recognized that the Antarctic cooling appears to be restricted to the last two decades and that averaged over the past 40 years there has been a slight warming. Recent simulations, which include recovery of the ozone layer suggest that changes in the Southern Hemisphere climate may reverse the cooling trend (Shindell & Schmidt 2004) and that warming will dominate in future in continental Antarctica. However, an expected temperature increase of 0.9–1.2°C per century (IPCC 2001) might well have little direct effect on the melting process, because temperatures, in general, are well below zero, even during summer. Other, at present unpredictable changes, such as in the occurrence of cloud and precipitation, are likely to have important, both positive and negative, effects on vegetation in continental Antarctica.

The second, important factor that influenced NP was thallus temperature. Comparison of the two *Bryum* species at Cape Hallett, showed very depressed NP at all combinations of PPFD and CO₂ concentration at 0°C (75% depressed) and 10°C (33–50% depressed) compared to rates at 20°C. Although thallus temperatures could be warm at times of high insolation, up to around 20°C for hydrated mosses, temperatures around 0°C were more common so that, for *B. subrotundifolium* at Granite Harbour, plants were between -2 and +2°C for 58% of readings. Optimal temperatures for NP certainly fell within the range of temperatures met by the plants but were well above the more common TT. *Ceratodon purpureus* had a much lower optimal temperature for NP (6.6°C) than *B. pseudotriquetrum* (12.0°C) and *B. subrotundifolium* (13.7°C). At present we have no explanations for between-species differences in optimal temperatures for NP and the ecological relevance is far from obvious when one considers that *B. subrotundifolium*, for example, operated at maximal NP under optimal conditions for only 0.1% of the potentially active time period (23 November 2000 and 24 January 2001). The optimal values fall within the temperature range reported for maximal growth rate for *B. argenteum* (15–22°C; Longton & MacIver 1977, Smith 1999) but substantially lower than the 25–30°C reported by Rastorfer (1970).

Photosynthetic activity of all three species was low but, still detectable at -5°C TT and TT below -5°C were found to be tolerated, even in the hydrated state. This contrasts with the suggestion that CO₂ gas exchange ceases as soon as the water freezes in mosses (Kappen & Schroeter 2002) but agrees with Ino (1990) who detected photosynthetic activity to -10°C TT. This tolerance is certainly necessary because the mosses can undergo freeze/thaw cycles almost every day during the summer season (Rudolph 1966a), with the lowest thallus temperatures being around -10°C. However, the mosses do not reach these low temperatures when highly hydrated because of the buffering effect due to latent heat released during the freezing of water (Fig. 1; Pannewitz *et al.* 2003a).

All three species had photosynthetic features that might be expected from high-light or sun adapted specimens. Photosynthetic compensation (L_c) at near optimal TT was between 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 95 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *C. purpureus* and 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *B. pseudotriquetrum*. However, L_c was temperature dependent and, at 15°C TT, were high, between 135 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 235 $\mu\text{mol m}^{-2} \text{s}^{-1}$, for *B. subrotundifolium*, around 260 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *B. pseudotriquetrum* and 370 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *C. purpureus*. These are expected values for mosses growing in the full Antarctic sun light (Green *et al.* 2000b).

NP was not saturated at the highest tested PPFD and did not decline at optimal TT due to high PPFD although this has been found in other Antarctic species (Kappen *et al.* 1989, Lovelock *et al.* 1995a, 1995b). Recent research on Antarctic mosses from sun exposed sites with sufficient water supply suggest that NP is not saturated at high insolation (Green *et al.* 2000b) and photoinhibition must not necessarily be expected (Schlensog & Schroeter 2000, Green *et al.* 2000b, Schlensog 2001, Lud *et al.* 2002, Pannewitz *et al.* 2003a). This is probably not surprising, because the mosses often encounter high light levels at times of greatest water availability and one would expect substantial protection. *Bryum pseudotriquetrum* contains considerable quantities of UV-B absorbing compounds (Dunn 2000) and *Bryum* species generally show the ability to accumulate flavonoids, highly effective preventors of damage from UV radiation (Robinson *et al.* 2003, Cockell & Knowland 1999). Post (1990) found photoprotective substances in *C. purpureus* that, perhaps, reduce the light intensities at the chloroplast level. This is supported by the results of Smith (1999) who found that samples of *C. purpureus* lost their pigmentation when kept beneath UV-B filters. Smith (1999) reported a significant growth increase in *B. argenteum* in the absence of UV-B suggesting a metabolic cost for the protection. The photosynthetic apparatus of bryophytes has been described as shade-adapted; a property normally associated with low light compensation points and low light saturation levels (Valanne 1984, Green *et al.* 1999, Kappen & Schroeter 2002). The results presented here with the high light

compensation and lack of light saturation of NP would tend to suggest that the plants were sun plants. This is in agreement with Marschall & Proctor (2004) who recently concluded that bryophytes include but are not inherently shade plants. However, it must be remembered that if there is substantial protection against high PPFD in the form of pigments or refractive structures then little light might reach the photosynthetic centres. The species could, perhaps, be better considered as being protected shade plants.

The two *Bryum* species differed substantially in their response to CO₂. *Bryum pseudotriquetrum* showed no saturation up to 2000 ppm CO₂, particularly at 20°C, whilst *B. subrotundifolium* was saturated at CO₂ concentrations above about 1000 ppm. The NP of both species, therefore, were substantially limited at normal ambient CO₂ levels of 360 ppm. When measured at an increased CO₂ level of 2000 ppm, net photosynthetic rates for *B. subrotundifolium* were 60–80% higher than at the accepted ambient level of 360 ppm and NP of *B. pseudotriquetrum* was more than doubled. These were only short-term experiments and such an enhancement might be short-lived under natural conditions, as demonstrated for the moss *Hylocomium splendens* (Sonesson *et al.* 1996) and Arctic higher plants (Oechel *et al.* 1997). Sustained, increased photosynthesis over extended time periods requires sufficient nutrient availability or improved nutrient use efficiency (Oechel & Billings 1992). Nutrient deficiency seems to be unlikely at sites like Cape Hallett which are rich in bird life (Green *et al.* 2000a, 2000b) and has been very rarely shown in Antarctic bryophytes (Kappen & Schroeter 2002). A 0.2–0.8% increase of the amount of CO₂ in the atmosphere per year, as being used in global change models (IPCC 2001), would have few consequences on the carbon metabolism of *B. subrotundifolium* and *B. pseudotriquetrum* in the short term. The photosynthetic rates of both *Bryum* species were certainly increased by experimentally generated elevated CO₂ but, because ambient levels might already be high (Tarnawski *et al.* 1992, Green *et al.* 2000a) the effect of increasing background atmospheric CO₂ concentrations could be minimal.

Summary

The high variability in NP response to major factors like PPFD and the present lack of any understanding of the causes means that it will be difficult to use the results of carbon dioxide exchange studies to detect or predict the effects of climate change, especially warming. We also need to learn more about the carbon balance of these mosses to discover if they are in a carbon shortage or whether utilisation of photosynthetic products is the real limitation as suggested for alpine plants (Körner 2003). It is, perhaps, too early to predict what the effects of global climate change will be in these polar environments.

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