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Activity pattern of the moss *Hennediella heimii* (Hedw.) Zand. in the Dry Valleys, Southern Victoria Land, Antarctica during the mid-austral summer

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Abstract The activity pattern of the moss *Hennediella heimii* (Hedw.) Zand. was monitored over a period of 18 days during the austral summer season 2000/2001 at the Canada Flush in Taylor Valley, continental Antarctica. Provided with melt water from the massive Canada Glacier, the moss showed a constant potential photosynthetic activity during the entire measurement period. Permanently hydrated, the moss faced high light levels at surprisingly low moss temperatures, which is commonly supposed a deleterious situation for plants. The electron transport rate response of the moss to photosynthetic photon flux densities was linear at all temperatures and did not show a sign of saturation or photoinhibition. *H. heimii* seems to be well adapted to its environment and tolerates the ambient conditions without apparent harm. This might be due to the fact that mosses can acclimatise to high light conditions by building up highly effective non-photochemical quenching systems.

Introduction

The Dry Valleys, continental Antarctica (77°36′S; 163°02′E), are often described as being one of the driest and coldest places on earth (Fritsen et al. 2000). Mean annual temperature is −20°C (Fritsen et al. 2000) but daily values can range from −46°C in the dark winter to +7°C in January. Mean temperature of January, the warmest month, is −2.5°C. Precipitation is very low and rarely amounts to more than 10 cm of snow per year and this is combined with low air humidities (rH < 50%; Fritsen et al. 2000). As a result, lichens and mosses are excluded from the valley except where melt water occurs in the summer. The high insolation in the summer months leads to high flows of melt water in a large number of small streams in the valleys. The water source is glacial tongues that are present on both valley sides but reach the valley floor from the north side. Growth of mosses can still only occur where there is a regular supply of melt water, where the flow is not strong and where there is protection from the high winds that can blow along the valley from the polar plateau at any time of the year.

One of the largest areas of mosses in southern Victoria Land, the Canada Glacier flush, occurs adjacent to the eastern side of the Canada Glacier, Taylor Valley (Schwarz et al. 1992). This glacier not only provides melt water during the summer growth period, up to 85 $l\,s^{-1}$ at its peak (1995–1996), but its high, 20–30 m, cliffs act as a most effective shelter from the winds. Two mosses dominate the flush: *Bryum subrotundifolium* Jaeg., Ber. S. Gall. (also described as *B. argenteum* Hedw.; Seppelt and Green 1998) dominates the central wetter areas, and *Hennediella heimii* (Hedw.) Zand. [previously known as *Pottia heimii* (Hedw.) Hampe (Zander 1993)], which forms the outer flanks of the vegetated zone (Schwarz et al. 1992). *H. heimii* is distinguished as being a xeric Antarctic moss species (Kappen and Schroeter 2002) that grows in habitats with changing water availability and is, therefore, exposed to alternating cycles of desiccation and rehydration. Mosses are typically poikilohydric organisms and are able to desiccate to extremely low water contents without any severe damage (Kappen and Valladares 1999; Proctor and Tuba 2002). In the desiccated state, most poikilohydric cryptogams are resistant to extremely low temperatures (Kappen 1988; Kappen and Lange 1970, 1972; Smith 2000) and high light intensities (Demmig-Adams et al. 1990; Kappen and Valladares 1999; Kappen et al. 1998;

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Schlensog et al. 1997; Smirnoff 1993). Desiccation is proposed as a strategy to avoid the harsh environmental conditions in continental Antarctica (Schlensog and Schroeter 2000; Schlensog et al. 2003a). In the case of *H. heimii* during the Antarctic summers, it is wet during the day when it can be exposed to high light intensities at low temperatures. This is a combination of environmental factors known to be damaging to the photosynthetic systems of higher plant leaves (Baker 1994; Öquist 1983).

Although the photosynthetic performance of other mosses has been studied in continental Antarctica, e.g. *B. subrotundifolium* (Green et al. 1998, 1999, 2000a, 2000b), *B. pseudotriquetum* community (Ino 1990), *Grimmia antarctici* (Lovelock et al. 1995), the only works on *H. heimii* are the pioneering studies of Rastorfer (1970) carried out in the laboratory, the work of Ino (1983), who investigated the production rate of *H. heimii* as a part of the moss community on East Ongul Island (East Antarctica), and the microclimatic studies by Longton (1974) on Ross Island. The species is, apparently, not common as extensive patches elsewhere in the continent and maritime zones. This study was carried out at the Canada Glacier flush in order to investigate the microclimate and its influence on the photosynthetic potential of *H. heimii*. We wanted to learn if the moss did avoid the combination of high light intensities and low temperatures and, if not, was it deleteriously affected? In order to monitor the activity pattern, we used the non-destructive chlorophyll-a-fluorescence measurement technique.

Materials and methods

The experimental site was located inside SSSI (Site of Special Scientific Interest) no. 12 established in 1985 (77°37′S; 163°03′E at 84 m a.s.l.; approximate area 1.47 km^2), Taylor Valley, Southern Victoria Land, Antarctica. The site contains the entire catchments of melt water draining from the eastern side of the lower Canada Glacier on the north shore of Lake Fryxell. In summer, a network of streams runs through the area and coalesce to form the Canada flush. The vegetated area (14,450 m^2, for a detailed area description, see Schwarz et al. 1992) forms one of the largest areas of plants in the Dry Valleys and southern Victoria Land. The vegetation itself is described as a ''short moss turf'' formation (Longton 1974). The bipolar moss *H. heimii* (Hedw.) Zand. [= *Pottia heimii* (Hedw.) Hampe] forms large, mainly dark-pigmented, cushions adjacent to *B. subrotundifolium* Jaeg., Ber. S. Gall. with small areas of *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb. Two samples of *H. heimii* were chosen growing on soil and gravel near a melt-water stream. Both samples grew next to rather large rocks (about half a metre square) in such a position that the moss turfs were naturally shaded for a period during the day. The samples had a healthy appearance and did not belong to the encrusted growth form, which is covered by an algal/cyanobacterial assemblage (Schwarz et al. 1992). The vegetation is wetted by the streams rather than by snowfall, which is only a few centimetres a year. At times with high flow rates, the two samples were submerged in slow-flowing side arms of the main melt stream.

Two portable pulse amplitude-modulated fluorometers (Mini-PAM, Walz, Germany, for further information see Schreiber et al. 1994) were used as in-situ activity-monitoring devices (see Schroeter et al. 1999). The apparent quantum use efficiency of PSII ($\Delta F/Fm' = \Phi PSII$, Genty et al. 1989) of the two samples was measured every 20 min over a period of 18 days (16.12.2000–3.1.2001). Permanent power was supplied by two hand-carry solar panels (Siemens, Germany). The fibre optics were fixed to the ground using fibre-optic holding devices described by Schlensog and Schroeter (2001). These devices guarantee a fixed position of the fluorescence probe in relation to the sample surface and were installed so that shading of the sample by the device was negligibly low. The measurement of a depression in maximal solar energy conversion efficiency in PSII (Fv/Fm) is a successfully used stress indicator of photosynthetic organisms subjected to excessive PPFD (Gauslaa and Solhaug 1999; Lovelock et al. 1995). The measurement procedure demands a pre-darkening of the samples until all energy has passed the PSII. An artificial darkening would result in a sudden drop of the moss-turf temperature and a temperature-dependent decrease of Fv/Fm (Lovelock et al. 1995). We therefore abandoned the attempt to measure Fv/Fm. However, additional Fv/Fm measurements under controlled conditions could provide valuable information on the phototolerance of this species.

The moss-turf temperature, as well as the photosynthetic photon flux density (PPFD, μmol photon m^{-2} s^{-1}) at the surface of the plant, were measured using the PPFD and temperature sensors provided with the Mini-PAMs (Walz, Germany). The PPFD sensors were calibrated against a cosine-corrected GaAsP photodiode (Hamamatsu, J, see below). In addition, a Squirrel data logger (SQ1021, Grant Instruments, UK) was installed at the site to record microclimate of the mosses every 5 min. PPFD was measured with GaAsP-photodiodes (Hamamatsu, J) equipped with filter and cosine correction according to Pontaillier (1990) that had been calibrated against a quantum sensor (190 SB, Licor, USA) using an Optical Radiation Calibrator (1800–02, Licor, USA). The sensors were mounted to a rock with the same exposure as the moss, and in order to register the ambient light conditions in a horizontal non-shaded position. Air temperature was measured at 1 m above the ground with shielded thermocouples, and turf temperature was measured in the top layer (5 mm) of the moss-turf.

The relative electron transport rate through PSII (ETR in μmol e^{-1} m^{-2} s^{-1}) was obtained by multiplying the measured PPFD with the simultaneously calculated $\Delta F/Fm'$ (Bilger et al. 1995).

Results

Climatic conditions

Ambient

A wide range of climatic conditions occurred during the measurements, from sunny days to overcast days with light snow fall (Fig. 1A). Incident PPFD was never below 59 μmol m^{-2} s^{-1} whilst PPFD between 500 and 1,000 μmol m^{-2} s^{-1} was most frequent at 30% of readings and only 5% of readings were above 1,500 μmol m^{-2} s^{-1} (Fig. 1B). Ambient air temperatures tended to track incident PPFD (Fig. 1B) and were ≤ 0°C for 71% of the measurement period. Minima, around −7.5°C, occurred at times with overcast skies and snowfall during the nights of 24, 30 and 31 December and, on 24 December 2000, PPFD levels did not exceed 969 μmol $m^{-2}s^{-1}$ and air temperature reached only −3.4°C.

Moss

Moss temperatures also tracked insolation (Fig. 2) and the highest moss temperature, 10.5°C, occurred on 1 January 2001, but temperatures higher than 10°C were rare and PPFD above 1,500 μmol $m^{-2}s^{-1}$ was

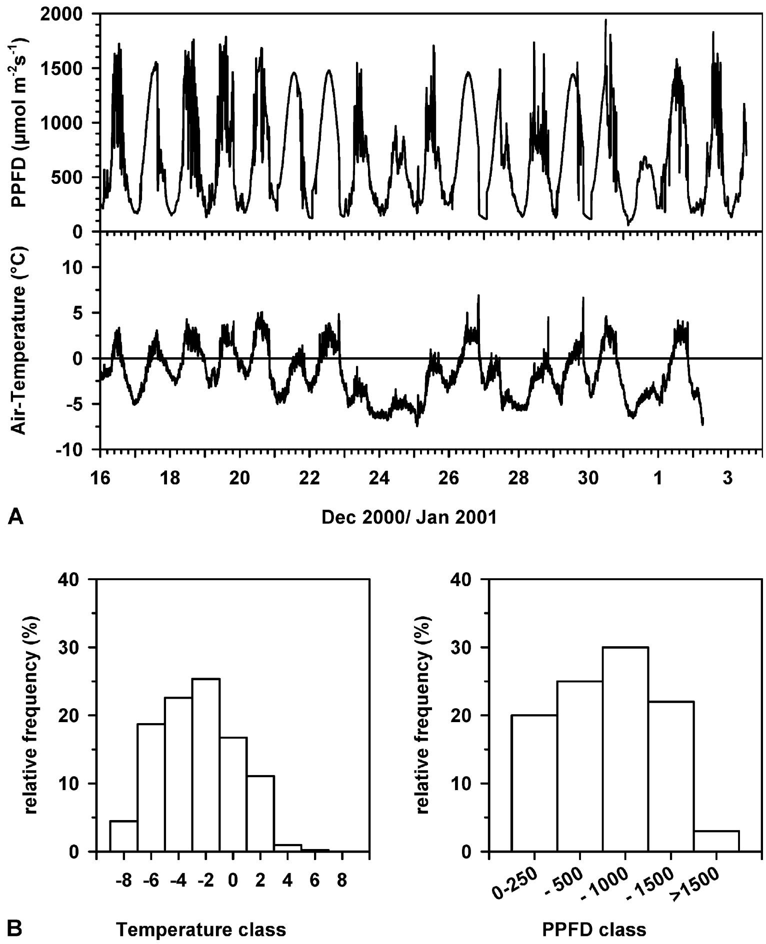


Fig. 1A Diurnal course of air temperature (1 m above the ground) and Photosynthetic Photon Flux Density (*PPFD* µmol $m^{-2}s^{-1}$, *horizontal*) measured at the research site near Canada Glacier, Taylor Valley, Southern Victoria Land, Antarctica (77°37′S; 163°03′E at 84 m a.s.l.) in the austral summer between 16 December 2000 and 3 January 2001. **B** Relative frequency distribution of the air temperature and incident PPFD (µmol $m^{-2}s^{-1}$) measured at the research site near Canada Glacier (Taylor Valley, Southern Victoria Land, Antarctica)

uncommon (1.4% of measurements). Moss temperatures between −2°C and <2°C were most common (67% of measurements) and the moss temperatures were above 0°C for 60% of the time (Fig. 3). The mosses were always much warmer than the air at night and moss temperatures never fell below −2°C. This might reflect the buffering action of the water in and around the moss, and the steady turf temperature at 0°C on some nights showed that freezing occurred.

The highest measured PPFD was 1,991 µmol m^{-2} s^{-1}, which is actually comparatively low for continental Antarctic conditions probably because of the low albedo of the valley-floor soils. One of the two moss turfs grew very close to a rock, explaining why PPFD at the moss surface was low during the first half of every sunny day (data not shown) but would then rise rapidly as the shadow cleared the moss. One example is 22 December when, on a sunny day from 12.00 p.m. to 12.40 p.m., PPFD rose from 182 µmol m^{-2} s^{-1} up to 941 µmol m^{-2} s^{-1} within 20 min.

Physiological activity

Both samples of *H. heimii* showed continuous photosynthetic activity throughout the entire measuring period, as indicated by an effective quantum yield of photosystem II (ΔF/Fm′) around 0.4 and ETR (ΔF/Fm′*PPFD) that tracked incident PPFD (Fig. 2). Substantial flows of water from the glacier kept the mosses continuously wet. There was a steady trend of declining ΔF/Fm′ over the entire measuring period, from around 0.4 to 0.3 at the end, which resulted in lower ETR at identical PPFD. A maximal ΔF/Fm′ value of 0.48 at 125 µmol $m^{-2}s^{-1}$ PPFD was much lower than the expected values of around 0.7 for unstressed plants at comparable PPFD, and it is probable that low temperatures are actually depressing the efficiency of PSII at all times. ΔF/Fm′ reached its lowest value during the overcast and colder days of 23 and 24 December.

There was a very clear and linear relationship between ETR and PPFD ($r^2=0.96$) with no indication of saturation at the highest PPFD (Fig. 4). However, if ETR was plotted against moss-turf temperature, the relationship was very poor with a clear boundary at freezing point (Fig. 4). If the data were separated into temperature classes for the most frequent temperatures (Fig. 5), ETR showed a linear relationship with nearly identical slope for all temperature classes (linear regression with $a=0.37$–0.42). There were no obvious photoinhibitory effects in the lowest temperature class, −2°C to 0°C, not even at PPFD above 1,000 µmol m^{-2} s^{-1}.

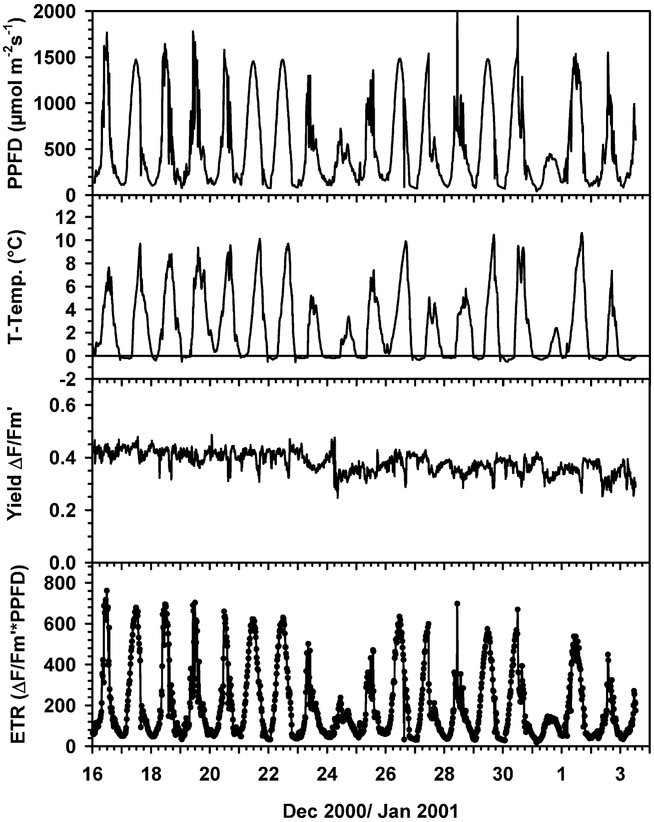


Fig. 2 Daily course of the microclimatic conditions (*PPFD* in μmol $m^{-2}s^{-1}$, and moss-turf temperatures in °C) and the Chl-a-fluorescence parameters ΔF/Fm′ and ETR of the moss *Hennediella heimii* (Hedw.) Zand. between 16 December and 3 January, measured at the research site near Canada Glacier [Taylor Valley, Southern Victoria Land, Antarctica (77°37′S; 163°03′E at 85 m a.s.l.)]

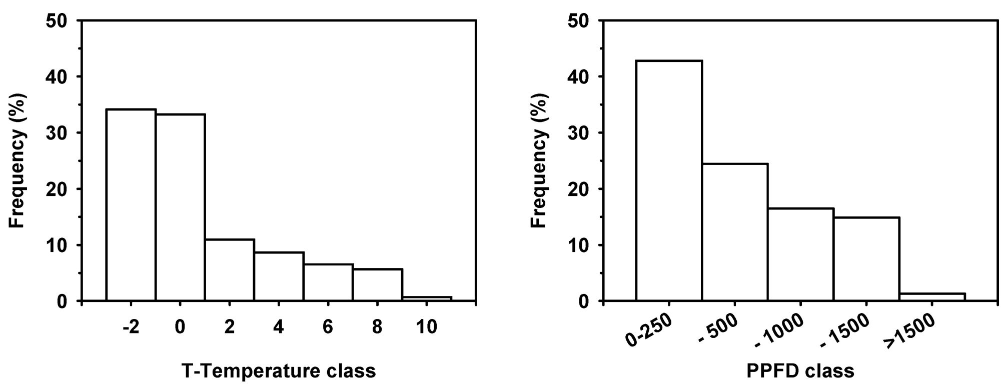
Discussion

The chlorophyll-a-fluorescence data confirmed that *H. heimii* was potentially photosynthetically active over the entire 18-day measurement period. This agrees with the results of Schlensog and Schroeter (2000) for *B. pseudotriquetrum* at Leonie Island in the maritime Antarctic, which also remained hydrated whilst the neighbouring lichens went through desiccation/rehydration cycles. Apparently, these plants are almost continuously hydrated during the summer months.

Continental Antarctic melt streams may flow up to 8 weeks during the brief austral summer, with pronounced diel variation (Howard-Williams and Vincent 1986). The discharge pattern of the Canada Glacier flush corresponds to the average ambient temperature and total incident radiation. During the austral summers 1993–1994 and 1994–1995, maximal flows were during the period between 15 December and 25 January (Moorhead 1996). When the face air temperature of the Canada Glacier drops below 0°C, the stream flow declines or even shuts down (Lewis et al. 1996). Such shut downs took place several times during our measuring period. The smaller side streams vanished or froze solid at times with low insolation and, because of overcast weather, even the main streams stopped flowing between 23 and 24 December, and again for 24 h on 31 December. Nevertheless, this did not result in inactivation of the moss thalli through desiccation because of water stored in the ground or the turf. Noakes and Longton (1988) found that water uptake from the wet ground kept mosses at nearly full turgor or even oversaturated at 10°C and 40% rH. If *H. heimii* behaves as a typical xeric species, as suggested by Kappen and Schroeter (2002), this should be reassessed for the thalli at the site presented here, especially if the summer "growing" season is considered.

As anticipated, the hydrated mosses faced very high levels of incident PPFD; 1,000 μmol m^{-2} s^{-1} was reached at moss-turf temperatures between −2.0 and 0.0°C, and up to 2,000 μmol m^{-2} s^{-1} at temperatures above 6°C. The ETR response to PPFD was linear at all temperatures and showed no sign of saturation. Therefore the moss never operated at light saturation, and this might be an indication that photoinhibition is not to be expected. The plants seemed well able to tolerate the ambient conditions without apparent harm. However, the linear relationships indicate a near-constant ΔF/Fm′ of around 0.4 (the slope of the fitted lines in Figs. 4 and 5) and this is puzzling on two grounds. First, the value for ΔF/Fm′, 0.4, was rather low in comparison to vascular-plant leaves, being normally around 0.7 at similar

Fig. 3 Relative frequency distribution of the moss-turf temperature and PPFD (μmol $m^{-2}s^{-1}$) measured at the research site near Canada Glacier (Taylor Valley, Southern Victoria Land, Antarctica)



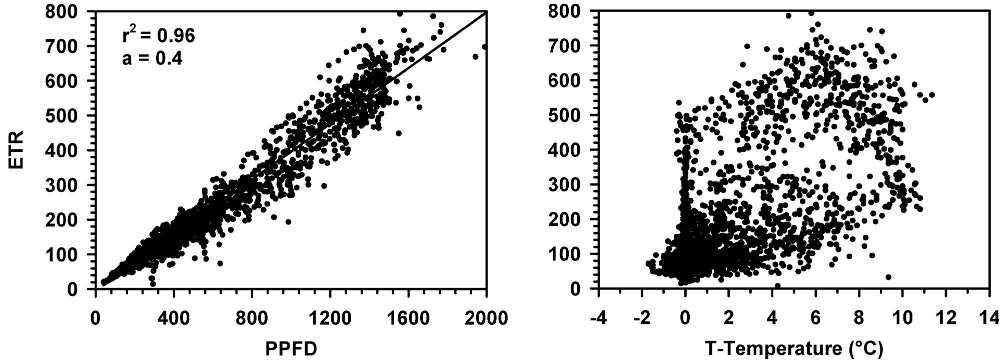


Fig. 4 Measured electron transport rate through PSII (*ETR*) versus PPFD (μmol $m^{-2}s^{-1}$) and versus temperature in *Hennediella heimii* (Hedw.) Zand. (two samples)

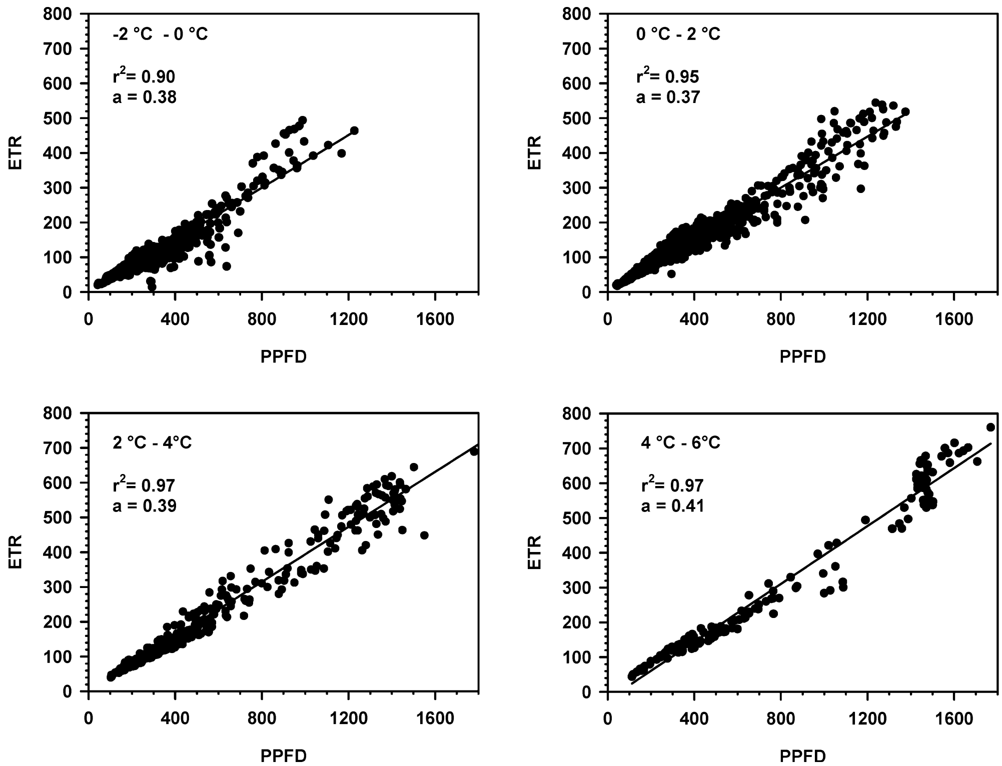


Fig. 5 Dependence of the measured electron transport rate through PSII (*ETR*) versus PPFD (μmol $m^{-2}s^{-1}$) at different temperature classes of *Hennediella heimii* (Hedw.) Zand. (two samples)

light intensities (Bilger et al. 1995; Björkman and Demmig 1987; Schreiber et al. 1994), and 0.6 for other Antarctic mosses (Schlensog et al. 2003a, 2003b); second, the lack of variation of ΔF/Fm′. Normally, there is an inverse relationship between ΔF/Fm′ and PPFD. One possible explanation is that the photosystems of the mosses were chronically depressed by the cold temperatures and this is suggested by the steady decline in ΔF/Fm′ over the whole measurement period as ambient temperatures also declined [ΔF/Fm′: 0.42 ± 0.02 (16.12.–20.12.2000); 0.35 ± 0.03 (30.12.2000–2.01.2001)]. A more likely explanation is that very strong non-photochemical fluorescence quenching (NPQ) systems, i.e. the harmless dissipation of absorbed radiation in the form of heat, were activated and dominated electron quenching. This could explain the linear response of ETR to PPFD at all temperatures and is also suggested by the results of Heber et al. (2000). They found a combination of cyclic electron transport, P700 oxidation and, possibly, a excitation transfer between the photosystems to produce effective phototolerance in *Grimmia alpestris*. The tested moss showed a much stronger capability to induce NPQ than the investigated higher plants.

The temperatures of the moss samples were unexpectedly low; the majority of the time the plants were between −2 and +2°C. It is very likely that they were controlled by the temperature of the flowing water in the day and by the low insolation when the water flow stopped. The physiological optimal temperatures for net photosynthesis for continental Antarctic mosses are estimated to be between 4 and 15°C (Longton 1974: *B. argenteum*; Kappen and Schroeter 2002). These temperatures occurred for only 24% of the entire measuring period, which suggests that the moss is under sub-optimal conditions for most of the time. It is unfortunate that we have no gas-exchange data to see if the depressed

ΔF/Fm′ is also reflected in the net photosynthetic rate. Results from *B. subrotundifolium* would suggest that low ΔF/Fm′ were related to low NPQ rates (Green et al. 2000a, 2000b). ETR in *H. heimii*, albeit low, does occur at subzero temperatures and it would be interesting to see if this is also a consequence of non-photochemical quenching or does represent actual positive net photosynthesis. Kappen and Schroeter (2002) reported that freezing of mosses leads to zero net photosynthesis.

This study has answered some questions; in particular, it is clear that *H. heimii*, like *B. pseudotriquetrum* in the maritime Antarctic, is hydrated and potentially photosynthetically active for extended periods over the austral summer. Photoinhibition does not seem to occur and high rates of non-photochemical quenching might fully protect the photosystems at all PPFD and temperatures measured. However, only Fv/Fm measurements of pre-darkened samples under controlled temperature conditions will provide reliable information on the effectiveness of non-photochemical chlorophyll fluorescence quenching. It does seem that the moss is much colder than might be expected, probably because it was continuously hydrated and the temperature was, on many occasions, controlled by the water flowing through the mosses. We will not obtain substantial answers about daily and seasonal productivity until suitable gas-exchange measurements have been made.

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