

Photosynthetic performance of *Xanthoria mawsonii* C. W. Dodge in coastal habitats, Ross Sea region, continental Antarctica

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Abstract: *Xanthoria mawsonii* C. W. Dodge was found to perform well physiologically in a variety of habitats at high latitudes in continental Antarctica. The net photosynthetic rate of $7.5 \mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ is exceptionally high for Antarctic lichens. Field and laboratory measurements proved the photosynthetic apparatus to be highly adapted to strong irradiance. The cold resistance of the photosystem II reaction centres is higher than the photosynthetic CO_2 fixation process. Optimum temperature for net photosynthesis was *c.* 10°C . The lichen grows along water channels where it is frequently inundated and hydrated to maximum water content, although net photosynthesis is strongly depressed by super saturation. In these habitats the lichen is photosynthetically active for long periods of time. *Xanthoria mawsonii* also grows at sites where it depends entirely on the early spring snow melt and occasional snow fall for moisture. It has an exceptionally short reactivation phase and is able to utilize snow immediately. Recovery of activity by absorbing water vapour from air, though practically possible, seems to be of ecological importance only under snow at subzero temperatures.

Key words: chlorophyll *a* fluorescence, lichens, photosynthesis, temperature, water content

Introduction

In continental Antarctica environmental conditions are extremely hostile to terrestrial vegetation with intense cold, high summer irradiance, strong winds and drought (Green *et al.* 1999). Away from the Antarctic Peninsula the vegetation is composed entirely of poikilohydric organisms, the occurrence of which depends on the distribution of available water (Rudolph 1966*a, b*) during the brief spring and summer seasons, thought to be the main period of primary

productivity (Howard-Williams & Vincent 1986; Hovenden *et al.* 1994).

The ornithocoprophilic lichen *Xanthoria mawsonii* C. W. Dodge is abundant in coastal continental Antarctic areas (Rudolph 1966*a, b*; Øvstedal 1983; Pickard & Seppelt 1984; Lewis-Smith 1993) but can also be found further inland wherever bird faeces occur. Despite its common occurrence throughout continental Antarctica, *X. mawsonii* has received little attention from ecophysiologicalists. Some of the earliest field studies of the gas-exchange of Antarctic lichens were made on this species at Cape Hallett in the mid-1960s (Gannutz 1971). *Xanthoria mawsonii* was reported to be the most productive of the lichen species studied and to be capable of significant photosynthetic rates at subzero temperatures. It appears to be particularly tolerant of subzero temperatures and it never suffers from low temperature stress even in the fully hydrated state (Kappen & Schroeter 2002). It survives rapid freezing to -196°C , although this

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might be considered ecologically irrelevant (Kappen 1973), but net photosynthesis is still measurable at temperatures as low as -16.5°C (Lange & Kappen 1972).

Xanthoria mawsonii grows in various habitats in continental Antarctica. It frequently occurs in depressions and along drainage lines (Pickard & Seppelt 1984) where it can be submerged by melt-water for long periods. This is unexpected because lichens are not common in aquatic habitats. It has been suggested that green algal lichens fail to grow in melt streams (Kappen & Schroeter 2002) in part because many species suffer from depressed net photosynthesis at high water contents (Lange & Tenhunen 1981; Lange *et al.* 1993; Kappen & Schroeter 2002). In contrast, *X. mawsonii* is also often found in habitats where available water exists only for short periods during spring and early summer (Pannewitz *et al.* 2003). When melt-water is no longer available the lichen desiccates immediately; however, a near-total water loss can be tolerated (Kappen & Valladares 1999; Kappen & Schroeter 2002; Proctor & Tuba 2002). *Xanthoria mawsonii* can successfully utilize light and occasional snow falls (Green *et al.* 1999; Rudolph 1966a; Fritsen *et al.* 2000) because it appears to be one of a group of species able to regain normal metabolic rates within minutes of being rehydrated (Proctor & Tuba 2002; Schlenso *et al.* 2004). In addition, Lange & Kappen (1972) as well as Gannutz (1967) and Ahmadjian (1970) proposed that *X. mawsonii* might maintain substantial photosynthesis during snow free periods because of its ability to recover its photosynthetic activity by absorbing water vapour from air. However, Hovenden *et al.* (1994) were unable to find evidence of such a capacity in their studies and suggested that the dryness of the air prevents its occurrence. Accordingly, whether or not this phenomenon occurs in nature is open to question. Nevertheless, the capacity in *X. mawsonii* for photosynthesis at subzero temperatures and absorption of water from high air humidity (Lange & Kappen 1972), does enable the lichen to reactivate its potential PSII activity under

snow at temperatures around -10°C . In this way the total active period may be extended for a few days (Pannewitz *et al.* 2003).

Physiological information about this widespread species still remains scarce and there have been few field studies since the early pioneering work. The results presented in this paper were compiled from laboratory measurements and field data obtained during three expeditions to coastal continental Antarctic sites in the Ross Sea region. The aim of the study was to investigate the water-dependent physiological activity pattern of the lichen from different habitats by monitoring the chlorophyll *a* fluorescence under ambient light and temperature conditions during spring under an undisturbed snow cover, and summer. In an attempt to improve the interpretation of the field data, we also studied the photosynthetic performance of *X. mawsonii* (CO_2 gas exchange, chlorophyll *a* fluorescence) under controlled laboratory conditions.

Materials and Methods

Site description and plant material

The endemic bright orange foliose to subfruticose lichen *Xanthoria mawsonii* C.W. Dodge is abundant and forms dense colonies in coastal continental Antarctica. The research was carried out in Cape Hallett, northern Victoria Land ($72^{\circ}19'S$, $170^{\circ}13.5'E$) and in Granite Harbour, southern Victoria Land ($77^{\circ}00'S$, $162^{\circ}32'E$).

The snow-free slopes of Cape Hallett (an Antarctic Special Protected Area 106, see Lewis-Smith *et al.* 1994) have a westerly aspect and rise steeply from their base at near sea level to reach *c.* 300 m a.s.l. This scree slope shades the Cape during night hours resulting in a significant reduction of radiation and temperature. Extensive climatic and microclimatic research was carried out by Rudolph in 1966. He concluded that the area is snow free during the late spring and summer season, precipitation is low (approximately 12 cm y^{-1}), rainfall was absent (not recorded) and the summer mean temperature is -2.4°C with a maximum of 8.3°C (for a complete description see Rudolph 1966a, b). The thalli ($1.5 \times 1\text{ cm}$) used for measurements grew along drainage lines where they were protected from wind and where melt-water from a local glacier and/or snow accumulations flowed nearly every day from late afternoon to just after midnight. *Xanthoria mawsonii* was particularly abundant at this site because of the large input of organic matter from south polar

(McCormick) skuas (*Catharacta maccormicki*) and Adélie penguins (*Pygoscelis adeliae*). Physiological and microclimate measurements were carried out for a period of 42 days (4 January–15 February 1999).

Continuous chlorophyll *a* fluorescence measurements and microclimate were also recorded in Granite Harbour [Antarctic Special Protected Area (ASPAs) 154] covering Cape Geology and Botany Bay. A cliff protects the vegetation from high winds and shades it during the night. During the summer season Granite Harbour is snow free but several small melt-water flows occur in Botany Bay from a small glacier on the summit of the adjacent ridge. The thalli investigated grew on a weathered rocky step in Botany Bay and during summer were frequently flooded by melt water. Nutrient input is derived from a small colony of south polar Skuas. Investigations were carried out during a 19 day period (14 January–2 February 2000).

The potential photosystem II activity of *X. mawsonii* under snow was measured just outside the western boundary adjacent to ASPA 154 in an area where the vegetation is not influenced by melt-water from the local glacier. The research site was situated 70 m south of the shoreline at about 6 m a.s.l. The lichens grew on the flat, horizontal top of a granite boulder (see also Pannewitz *et al.* 2003). Potential PSII activity measurements were made between 5 November and 5 December 2000 and, after a pause, continued between 3 and 24 January 2001. Climatic data were recorded from 5 November 2000–24 January 2001.

Lichen material for laboratory investigations was collected in Granite Harbour in 2000 dried, transported to Kiel (FRG) and frozen at -20°C until measurements were made.

Field measurements

Microclimatic measurements

Microclimatic data were recorded every 5 min using data loggers (SQ1021, Grant, UK). The photosynthetic photon fluence rate (PPFR) over the 400–700 nm waveband was measured with GaAsP photodiodes (Hamasutu, J., Osaka, Japan) equipped with cosine correction according to Pontaillier (1990). The sensors were mounted on the ground with the same exposure as the thalli and had been calibrated before use with an optical radiation calibrator model 1800-02, LiCor (USA). Thallus temperature (TT) was measured with microthermistors ($\varnothing 0.3$ mm, Grant UK) attached to the lower side of the thalli. Air temperature (shielded thermistors $\varnothing 0.3$ mm, Grant, UK) and relative air humidity (RH, capacitive humidity probes, HMP35, Vaisala, SF) were recorded at 1 m above the ground.

Continuous measurement of ΦPSII

Portable pulse amplitude-modulated chlorophyll *a* fluorometers (MiniPAM, Walz, FRG, for detailed information see Schreiber *et al.* 1994) were used as *in situ* activity-monitoring devices (Schroeter *et al.* 1999). The glass fibre optics were fixed in place using special aluminium holders that allowed adjustment so that they pointed at the sample with an angle of approximately 60° with minimal shading (Schlensog & Schroeter

2001). This arrangement guaranteed a fixed position of the fluorescence probe in relation to the sample surface and allowed better measurement of fluorescence parameters. The apparent quantum use efficiency of photosystem II $[(F_M' - F)/F_M' = \Delta F/F_M' = \Phi\text{PSII}]$; Genty *et al.* 1989) was monitored under ambient PPFR at 20 min intervals and the relative electron transport rate (ETR, $\mu\text{mol e}^{-1} \text{m}^{-2} \text{s}^{-1}$) through PSII was calculated using concurrent PPFR ($\text{ETR} = \text{PPFR} \times \Delta F/F_M'$, Bilger *et al.* 1995).

Measurement of the maximal efficiency of PSII (F_v/F_M), often used as a stress indicator for photosynthetic organisms subjected to excessive PPFR (Gauslaa & Solhaug 1999; Lovelock *et al.* 1995), requires pre-darkening of the sample. Under continental Antarctic conditions where surface and sample temperatures depend so much on incident radiation this will automatically lead to a cooling of the sample. It has been suggested that this sudden drop in TT affects F_v/F_M (Hovenden *et al.* 1994); for this reason this parameter was not measured in the field.

Potential PSII activity under snow

Glass fibre optics for the chlorophyll *a* fluorescence measurements were installed, using special holding devices (Schlensog & Schroeter 2001), at Cape Geology, Granite Harbour in January 2000 and measurements then made ten months later in November 2000 whilst the winter snow cover was still intact (see Pannewitz *et al.* 2003). Thallus temperature and climatic conditions above the snow cover were measured as described above. The design of this experiment allowed only the measurement of potential PSII activity and measurements equate to the variable transient fluorescence yield, ΔF_T , as a percentage of the maximal transient fluorescence measured over the entire research period. These results can only be used as an indication of the potential photosynthetic activity (defined as $\Delta F_T > 15\%$) of the lichen.

Laboratory measurements

CO_2 gas exchange

The photosynthetic response of thalli ($n=3$) to temperature, PPFR and water content (WC) was analysed under controlled temperature and PPFR conditions using a compact mini-cuvette system (CMS4P, Walz GmbH, FRG) operated in differential mode (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). The polymethacryl cuvette (720 ml volume) was placed in a freezer (Rubarth, FRG). PPFR was provided by an incandescent halogen lamp (FL 400, 400F, Walz GmbH, FRG). CO_2 exchange [net photosynthesis (NP); dark respiration (DR)] and WC were related to the oven thallus dry weight (DW, 24 h at 105°C).

Before commencing all experimental procedures in the laboratory, the wetted and metabolically active lichen samples were kept in a controlled climate chamber under constant conditions (5°C and 12 h/12 h light, PPFR = $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ /darkness regime).

Response of net photosynthesis to thallus water content

Before starting CO₂ gas exchange measurements the pretreated samples were submerged in mineral water. Adhering excess water was shaken off and the maximally hydrated samples were enclosed in the cuvette at 10.0°C. Thallus temperature and CO₂ gas-exchange were recorded alternating between 250 and 0 μmol m⁻² s⁻¹ PPFR while the samples slowly dried. In order to determine the WC during the drying process, the thalli were temporarily removed after each pair of readings, weighed on a precision balance (accuracy: 1 mg; Bp310S, Sartorius, FRG) and replaced in the cuvette.

A fibre optic, integrated in the lid of the cuvette, arranged so that no shading occurred, allowed concurrent chlorophyll *a* fluorescence measurements (details below).

Response of net photosynthesis to PPFR and temperature

The response of NP to PPFR was measured at TT values between -7.5 and 25°C, and at an external CO₂ concentration of 360 ppm, starting with DR and continuing in steps up to 2000 μmol m⁻² s⁻¹. It was not possible to make measurements at higher PPFR and TT values due to technical restrictions. A small water loss could not be avoided during this procedure so thallus weight was checked regularly and CO₂ gas exchange measurements were confined to a thallus WC close to the optimum value.

Chlorophyll a fluorescence

Chlorophyll *a* fluorescence was measured using a MiniPAM (Walz GmbH, FRG). The measuring- and saturation-light passed through a fibre optic pointing at an angle of 60° to the lichen surface. $\Delta F/F_M'$ was measured at a chosen PPFR value generated by an infinitely variable incandescent halogen lamp (FL 400, Walz GmbH, FRG). Potential maximum photosystem II (PSII) quantum yield (F_V/F_M = variable fluorescence / maximal fluorescence; for nomenclature see van Kooten & Snel 1990) was measured after the samples had been sufficiently pre-darkened so that all reaction centres were open, Q_A fully reduced (Schreiber *et al.* 1994) and zero nonradiative dissipation (NRD). Non-photochemical quenching (NPQ) was calculated according to Bilger and Björkmann (1990) using the Stern-Volmer equation $NPQ = (F_M - F_M')/F_M' = F_M/(F_M' - 1)$. The expression of NPQ is based on the assumption that non-photochemical quenching traps are available (Schreiber *et al.* 1994).

Recovery from desiccation

The dry thalli were removed from a freezer (-20°C) and immediately placed in a controlled temperature chamber at 5°C. They were then hydrated by spraying with pre-cooled water (5°C) and chlorophyll *a* fluorescence parameters measured every 5 min as the thalli dried. The procedure was repeated on the same thalli after a further 3 days desiccation at 5°C.

Cooling experiment

The thalli were hydrated by submerging in mineral water, placed in a aluminium dish and enclosed in a controlled climate chamber. The samples ($n=2$) were

allowed to equilibrate to the chosen temperature and chlorophyll *a* fluorescence parameters then recorded. Measurements were made at 0 and 160 μmol m⁻² s⁻¹ PPFR starting at a TT value of 20°C lowered in 5°C steps to -20°C. When the measurement at the lowest temperature had been completed, the procedure was continued but in reverse order up to 5°C TT and in darkness so that only the F_V/F_M values could be measured.

Results

Microclimate and chlorophyll *a* fluorescence field data

The climatic conditions in Cape Hallett were diverse and daily conditions ranged from overcast to very sunny (Fig. 1). Maximal incident PPFR at the lichen thallus level was 2000 μmol m⁻² s⁻¹ and, whilst at the beginning of the investigation period the PPFR overnight was around 90 μmol m⁻² s⁻¹, towards the end it was zero (Fig. 1). PPFR values between 0 and <100 μmol m⁻² s⁻¹ were most common and occurred for 29% of the recorded time and 7% of the readings were above 1500 μmol m⁻² s⁻¹. The air temperature tracked the incident PPFR and the average air temperature was -0.6°C during the time of the investigations whilst the minimum was -9.1°C. The mean RH value (data not shown) was about 59% with a maximum of 93% and a minimum of 14%.

Mean thallus temperature was 1.9°C and although the thalli heated up to maximum values of 15.5°C at times of high PPFR, they also experienced minima of -8°C (measurements on another thallus, which was dry most of the time, produced a maximum TT value of 38.8°C, data not shown). Thallus temperatures between -2 and 0°C were most frequent (23% of time) and the thallus was above 0°C for 58% of the time. When TT values were below 0°C, PPFR was >100 μmol m⁻² s⁻¹ for 14% of the measurements but >250 μmol m⁻² s⁻¹ for only 1.4% of the time. Light snowfall occurred on several days.

The climatic conditions at Granite Harbour (Fig. 2) were less diverse during the measurement period than at Cape Hallett,

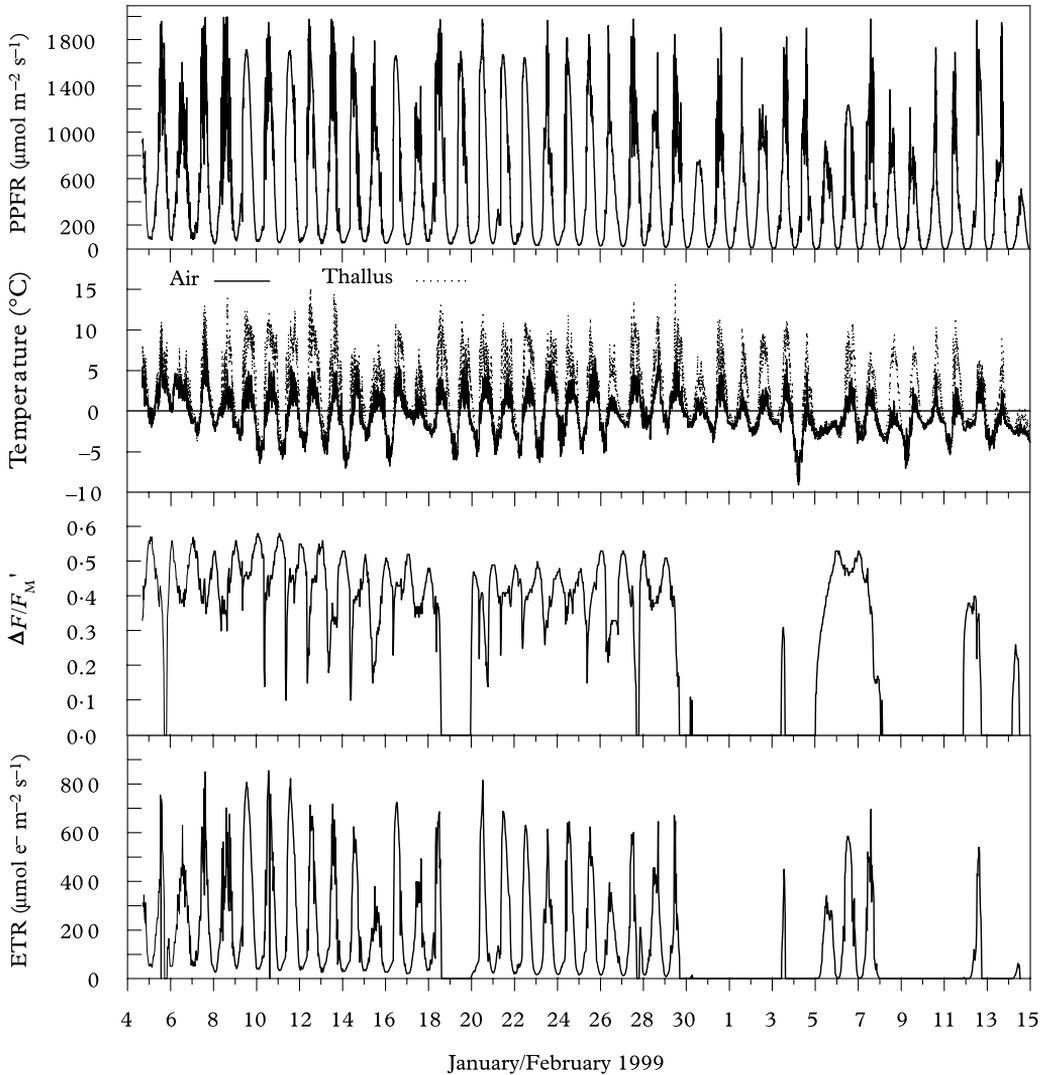


FIG. 1. Daily course of microclimate variables [photosynthetic photon fluence rate (PPFR), thallus temperature, air temperature], the effective quantum yield ($\Delta F/F_M'$) and the electron transport rate through PSII (ETR) of the lichen *Xanthoria mawsonii* between 4 January to 15 February 1999 measured at the research site at Cape Hallett, northern Victoria Land, continental Antarctica ($72^{\circ}19'S$, $170^{\circ}13.5'E$).

for example, there was no snow fall. Maximum incident PPFR was $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and values below $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ never occurred during the experimental period. The most frequently recorded PPFR values were between 25 and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ and occurred for 36% of the measurement period. Whilst 61% of the PPFR were between 25 and $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ only 9%

were in the highest PPFR class with values $>1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Mean air temperature was -1.8°C with a minimum of -8.5°C and the mean relative air humidity was 50% with a maximum of 85%, both lower than at Cape Hallett, whilst the minimum was similar. The thallus temperature rose to a maximum of 24.9°C on 22 January 2000 when the thallus was in a desiccated

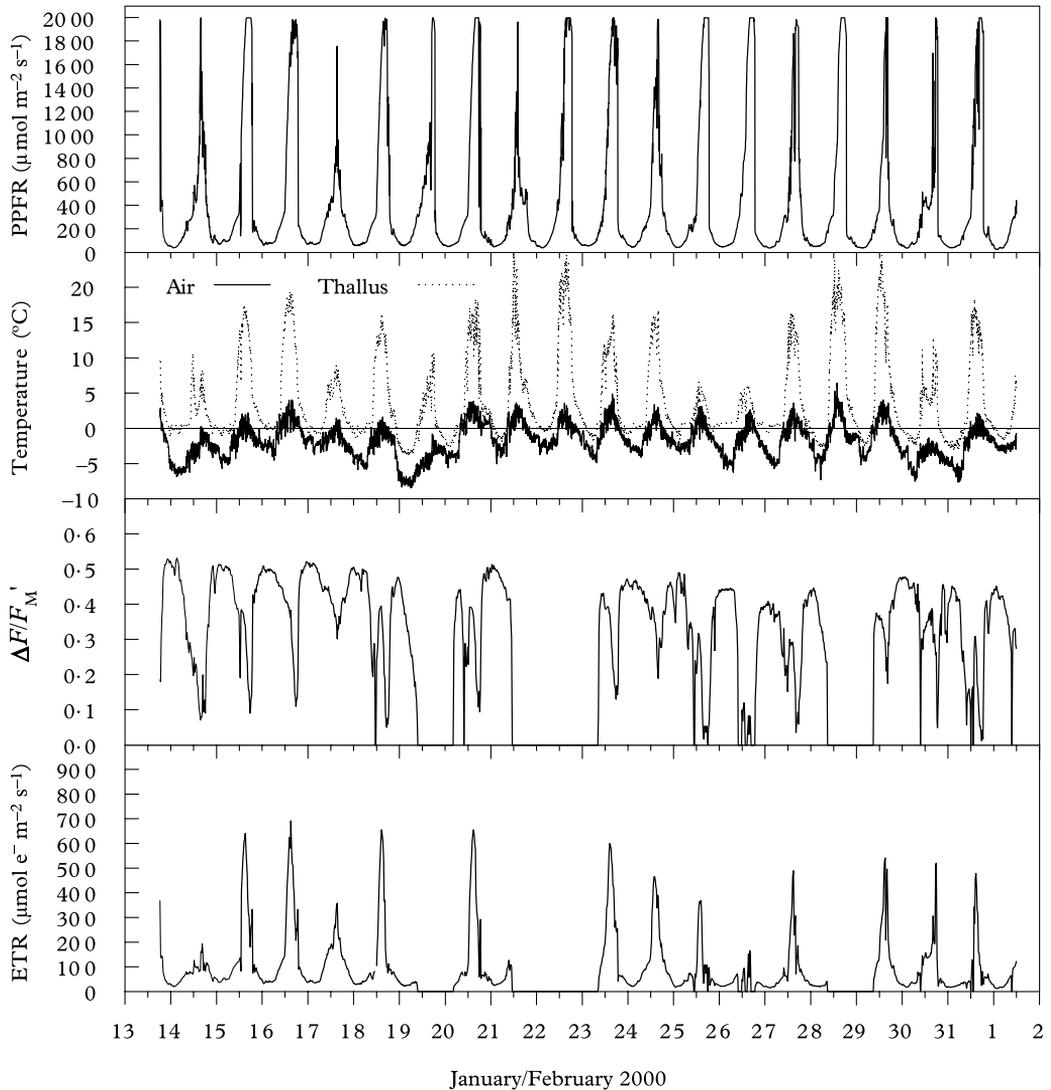


Fig. 2. Daily course of microclimate variables [photosynthetic photon fluence rate (PPFR), thallus temperature, air temperature], the effective quantum yield ($\Delta F/F_M'$) and the electron transport rate through PSII (ETR) of the lichen *Xanthoria mawsonii* between 13 January to 2 February 2000 measured at the research site at Botany Bay, Granite Harbour, southern Victoria Land, continental Antarctica ($77^{\circ}00'S$ $162^{\circ}32'E$).

state. Even though the mean air temperature was quite low, TT never fell below -3.9°C and the mean TT of 3.7°C was remarkably high. When TT values were below zero, PPFR values were above $100\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ for 6% of the measurements but above $250\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ for only 0.4%.

Physiological activity

At Cape Hallett melt-water from long lasting snow patches and/or a local glacier kept the thallus hydrated and, therefore, photosynthetically active for 70% of the entire period of the investigation

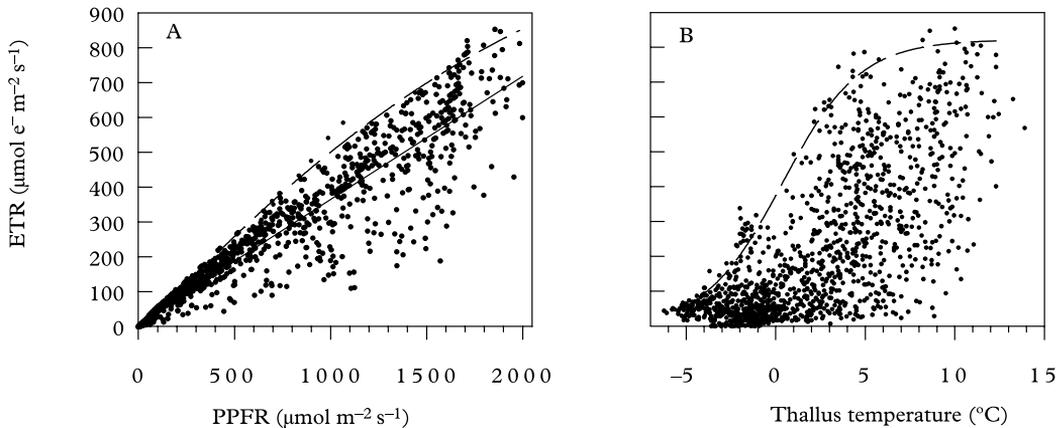


FIG. 3. Measured electron transport rate through PSII (ETR) in *Xanthoria mawsonii*. A, versus thallus temperature; B, versus photosynthetic photon fluence rate (PPFR). (— linear regression; - - regression line on maximum measured data).

(4 January–14 February 1999). Photosynthetic activity, as indicated by $\Delta F/F_M'$, was continuous between the 4 and 30 January 1999 with only one break for 24 h on the 19 January (Fig. 1). This phase was followed by longer periods of inactivity as the water flow became smaller and less reliable. The maximum measured effective quantum yield of PSII was around 0.58 and ETR tracked incident PPFR. There was a slight trend of declining maximum $\Delta F/F_M'$ over the period between 11 and 25 January resulting in lower ETR at similar PPFR values. However, during 5–7 February $\Delta F/F_M'$ returned to near maximum values (0.53).

There was a linear relationship between ETR and PPFR ($r^2=0.9$) with no clear sign of saturation at the highest light levels (Fig. 3A). When only the highest ETR values at a given PPFR level were extracted from the data then the relationship was quadratic ($r^2=0.99$) but PPFR saturation is still scarcely perceptible. It is suggested that all data below the regression line were obtained under sub-optimal conditions, such as desiccation due to insufficient water supply, or low TT. Although these data do not allow a definite statement concerning photoinhibition, it seems likely that it does not play a major role. Days with high PPFR, such as 6 or 10 January, were not followed by a decline in $\Delta F/F_M'$ at low light.

Electron transport rate and temperature show a similar effect and, if the highest values measured at a given TT are extracted, an exponential regression ($r^2=0.97$) is obtained with an obvious maximum at $TT>12^{\circ}\text{C}$ (Fig. 3B).

The *X. mawsonii* thallus in Granite Harbour received melt-water from a local glacier and was active for 78% of the measuring period (13 January–1 February 2000). Maximum $\Delta F/F_M'$ was, at 0.53, slightly lower than the values measured for the Cape Hallett sample, a difference that is not likely to be significant. Overall the results were generally similar, except for the occurrence of activity ($\Delta F/F_M'$) at temperatures $>15^{\circ}\text{C}$. Photosynthetic activity was continuous with interruptions first on 19 January 2000 and second on 21 to 23 January 2000 (Fig. 2), both probably a result of lower air temperatures stopping the melt-water flow. High PPFR led to a TT value $>20^{\circ}\text{C}$ of the desiccated thallus at those times.

Activity outside the melt water influenced habitats

The potential PSII activity of *X. mawsonii* thalli growing on a rock surface not influenced by melt-water flows is presented in Figure 4, together with thallus and air

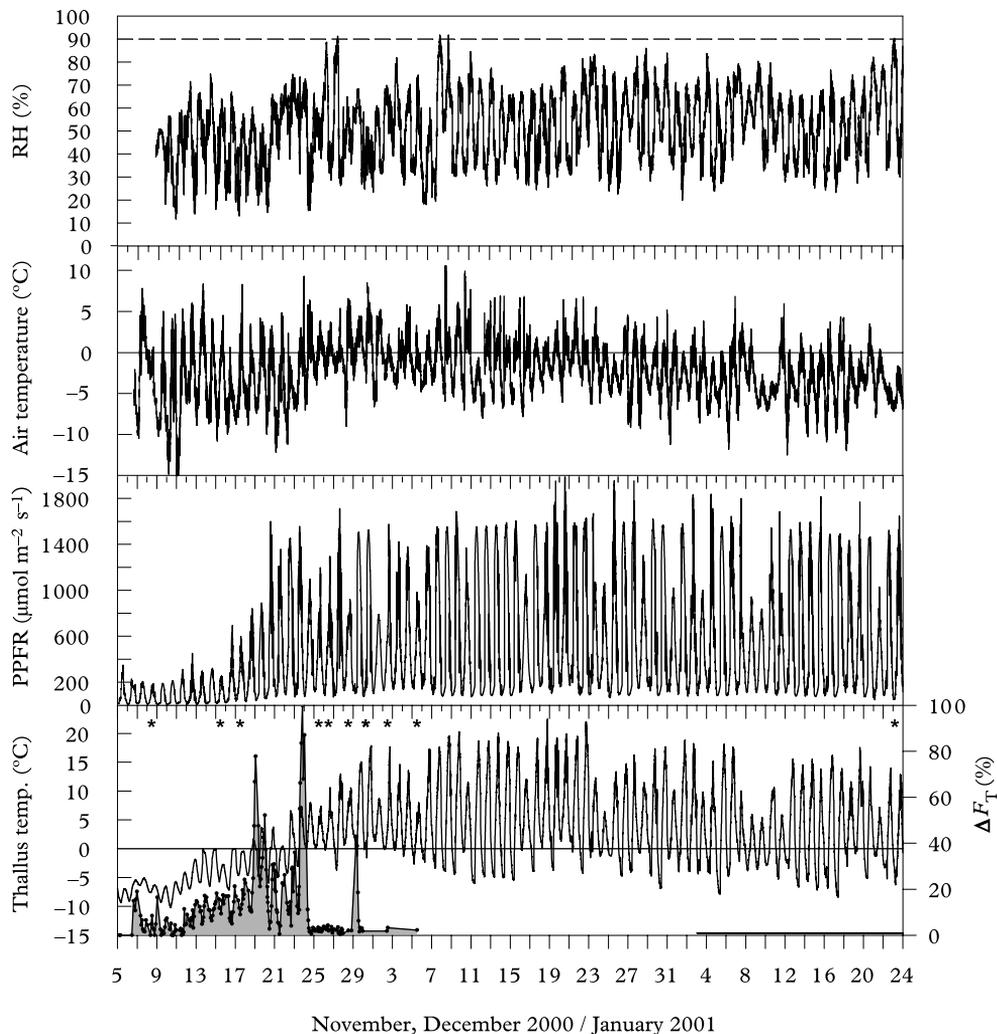


FIG. 4. Ambient microclimatic conditions [Relative humidity (RH), air temperature, photosynthetic photon fluence rate (PPFR), thallus temperature] and the percentage of the maximum transient fluorescence (ΔF_T) of *Xanthoria mawsonii* under snow at the research site at Granite Harbour, continental Antarctica. (no ΔF_T measurements between 6 Dec. 2000 and 3 Jan. 2001). * snow fall; ■ ΔF_T .

temperature, PPFR and RH for a total of 31 days in two periods between 5 November 2000 and 24 January 2001. The thallus was covered by a layer of snow 13 cm deep at the beginning of the measurements. Thallus temperature was not related to the ambient temperature, with a cold temperature being preserved by the highly insulating snow cover. In time, the snow cover thinned by melting and/or sublimation and the thallus warmed up at about 1°C per day. Once the

snow cover disappeared and the thallus became completely exposed, TT tracked the incident PPFR. Potential PSII activity (defined as $\Delta F_T > 15\%$) was first recorded at a TT value of *c.* -7°C on the 6 November 2000. Potential PSII Activity then increased steadily as TT rose. Maximum potential PSII activity was measured when the snow cover on top of the lichen disappeared and TT became positive due to full exposure to PPFR. Once the snow cover and the

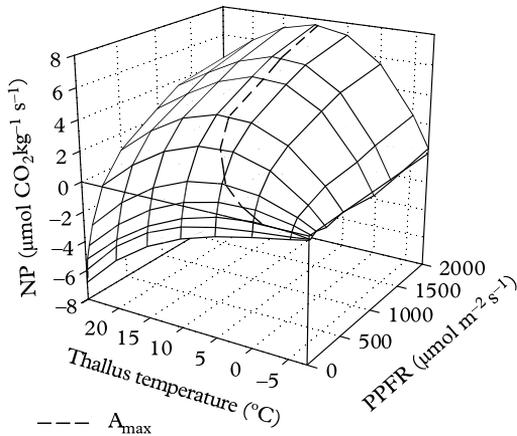


FIG. 5. Three dimensional mesh plot of light and temperature dependent net photosynthesis in *Xanthoria mawsonii*. Data were obtained from gas exchange measurements ($n=3$) in the laboratory.

remaining snow in the near vicinity of the lichen thallus had disappeared (24 November 2000) then further desiccation caused a loss of activity. On the 29 November the thallus was reactivated through snow fall. In total the thallus was active for 28% of the measurements between 5 November and 5 December 2000. No chlorophyll *a* fluorescence measurements were made between 6 December 2000 and 3 January 2001, but during this time there were only a few occasions when snow fall could possibly have reactivated the lichen. One such occasion was on 10 and 11 December when RH exceeded 90% (Fig. 4). Between 3 January and 24 January, when the measurements were resumed, no potential activity of the lichen was recorded.

Laboratory data

Response of net photosynthesis to PPFR and temperature

The rate of net photosynthesis responded sharply to low PPFR values and, at all the temperatures tested except the lowest (-7.5°C), was not light saturated at $2000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (Fig. 5). The optimal temperature for NP was about 10°C at $2000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ but fell rapidly at lower PPFR values. When the incident light levels

declined below $20\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, the optimum TT for NP was *c.* 0°C . The PPFR required for compensation at TT values between -5 and $+5^{\circ}\text{C}$ was constant and low, *c.* $30\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, but at higher temperatures it increased exponentially ($r^2=0.99$) to reach $380\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ at 25°C .

Response of net photosynthesis to thallus water content

At low thallus WC net photosynthesis was limited biochemically through low water potentials (Green & Lange 1994) but increased with increasing hydration until a maximum (A_{max}) was reached at the optimum WC (%DW); A_{max} then remained constant at WC from 120–170% DW (Fig. 6A). A further increase in hydration resulted in a substantial decline in NP, which, at 534% DW, was only about 64% of A_{max} . Dark respiration, as well as $\Delta F/F_M'$ and F_V/F_M , were also strongly dependent on WC and rose with increased hydration until optima were reached at about 120% DW (Fig. 6A & B). Further increases in hydration to levels that were supra optimal for NP, had no additional effect on DR and the fluorescence parameters ($\Delta F/F_M'$ and F_V/F_M).

Recovery of net photosynthesis

ΦPSII ($\Delta F/F_M'$ as % of the maximal measured value) measured at 5°C TT and $250\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFR recovered rapidly after wetting of a desiccated thallus that had been stored at -20°C (Fig. 7). An initial phase was characterized by an increase in ΦPSII to a plateau after which it remained near the maximum. The rehydrated thallus reached 90% of final maximum after a short recovery phase of 45 minutes. When the experimental procedure was repeated on the same thallus after 3 days of desiccation at 5°C , ΦPSII reached 90% of the final maximum within approximately 5 minutes.

Subzero cooling of fully saturated thalli

Gradual cooling of thalli of *X. mawsonii* from 10 to -20°C , both in darkness and at $160\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, resulted in marked

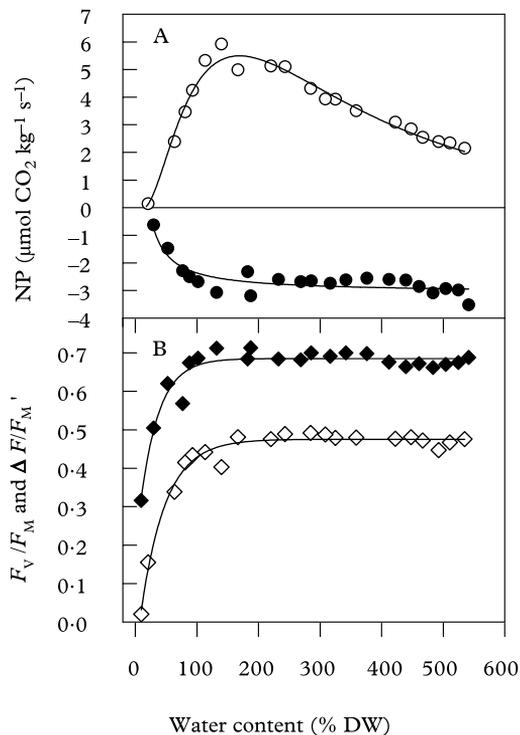


Fig. 6. Net photosynthesis (NP), dark respiration and the chlorophyll *a* fluorescence parameters related to thallus water content (WC; %DW) of *Xanthoria mawsonii* from Granite Harbour, continental Antarctica, measured at 10°C thallus temperature either in light [$250 \mu\text{mol m}^{-2} \text{s}^{-1}$ (\circ)] or in the dark (\bullet). A, net photosynthesis and dark respiration; B, chlorophyll *a* fluorescence parameters, $\Delta F/F_M'$ (\diamond) and F_V/F_M (\blacklozenge).

effects on $\Delta F/F_M'$ and F_V/F_M (Fig. 8A). Both fluorescence parameters remained steady at about 0.5 between 10 and 0°C then declined sharply at temperatures below 0°C. The decline in $\Delta F/F_M'$ was particularly marked and reached a minimum at about -13°C, whereas F_V/F_M declined less steeply until activity ceased at -20°C. NPQ showed an exponential rise at temperatures below 0°C (data not given). When thalli that had been cooled in darkness were gradually re-warmed from -20°C, F_V/F_M always had lower values compared to when being cooled. F_V/F_M was reduced by an average of 45% at any chosen temperature between -15 and -2.5°C. The maximum

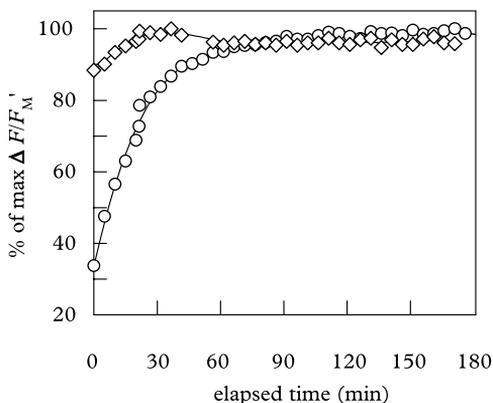


Fig. 7. Time course of recovery of the apparent quantum use efficiency of PSII ($\Delta F/F_M'$) as a percent of the maximum after re-hydration of *Xanthoria mawsonii* at 5°C [after direct recovery from -20°C (\circ) and after 3 days of desiccation at 5°C (\diamond)].

was reached when temperatures returned to above 0°C (Fig. 8B).

Discussion

Xanthoria mawsonii is one of the thirteen species of circumpolar continental lichens defined by Kappen (1988). Our results add to the small number of previous studies and indicate that this lichen performs exceptionally well physiologically in a variety of habitats under Antarctic conditions. The species possesses a net photosynthetic rate which, at $7.5 \mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$, is one of the highest found for Antarctic lichens. *Umbilicaria aprina* reaches an average rate of about $5.5 \mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ at Granite Harbour (Sancho *et al.* 2003), but more typical rates for continental Antarctic species are in the 1 to $2 \mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ range for a variety of lichens (Longton 1988; Kappen 1988). The properties of the photosynthetic apparatus suggest that *X. mawsonii* is adapted to strong irradiance (Schlensog & Schroeter 2000). At all temperatures above -5°C, NP was not saturated at the maximum PPFR tested and the rates recorded in the field are similar to those recorded in the laboratory. There is almost a linear relationship between PPFR and maximum ETR indicating that there was no light saturation

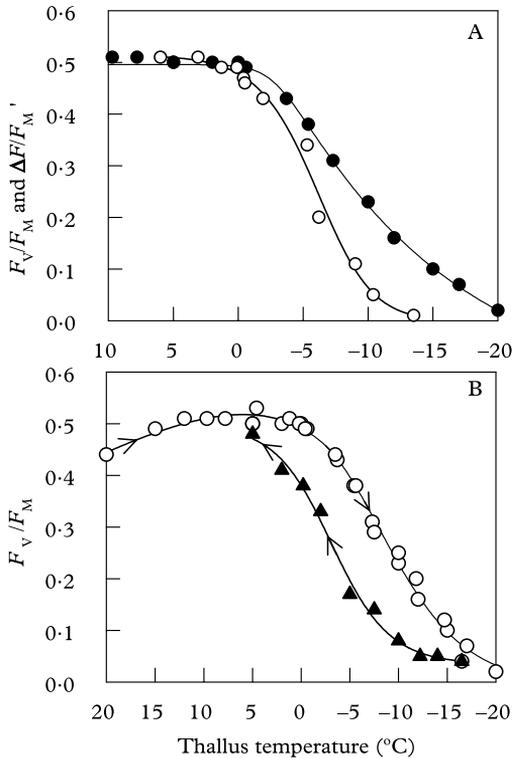


FIG. 8. Temperature dependence of fluorescence characteristics in hydrated *Xanthoria mawsonii* from Granite Harbour, continental Antarctica. A, response of apparent quantum use efficiency of PSII ($\Delta F/F_M'$) at $160 \mu\text{mol m}^{-2}\text{s}^{-1}$ PPFR (○) and the optimal quantum yield (F_V/F_M , ●) to temperatures between 5 and -20°C ; B, response of optimum quantum yield (F_V/F_M) to temperatures between 20 and -20°C (○, cooling down) and during the process of re-warming to 5°C (▲). $n=2$ in both cases.

of ETR (Fig. 3A). The optimum temperature for NP was about 10°C which, although higher than the average air temperature, makes the species well suited to an environment where high light occurs in conjunction with wetting by melt-water at cool temperatures. This is a common combination in continental Antarctica (Pannewitz *et al.* 2003) because spring snow melt is thought to be the major source of hydration for the activity of lichens in continental Antarctica. Whilst active, *X. mawsonii* experienced a wide range of combinations of incident PPFR and temperature; hydrated

thallus temperatures reached 14°C in Cape Hallett and up to 15°C in Botany Bay.

In the cooling experiments the fluorescence parameters were constant and well above 0°C but both $\Delta F/F_M'$ and F_V/F_M declined as temperature fell below 0°C . Although both chlorophyll *a* fluorescence and NP can continue at low temperatures (to -10°C at least) it appears that the lichen shows little cold adaptation of its photosystems with photochemical limitations starting at below -0°C . It is not so surprising then to find that the temperatures of the active thalli were usually above ambient air temperature (incident radiation heating) with the mean temperature at Granite Harbour being 3.7°C compared to an air mean of -1.8°C . At Cape Hallett the lichen was above freezing for 58% of the active time.

At Botany Bay (Granite Harbour) and Cape Hallett, spring snow-melt is not necessarily the major active phase. Melt-water streams originating from local glaciers and long-lasting snow patches are significant for the activity pattern of *X. mawsonii* during summer. It was a surprise to find that, at both sites, thalli of *X. mawsonii* were active, indicated by $\Delta F/F_M'$, for long periods. At Granite Harbour chlorophyll *a* fluorescence showed the lichen to be active for 78% of the time (20 day study period in January) in a situation where the predominant source of water was melt-water that ran over rock benches. At Cape Hallett the lichen was active for 70% of the 40 day study period and grew along water channels where it was inundated for several hours almost every afternoon. Similar long periods of activity have been demonstrated for mosses both from the maritime (Schlensog & Schroeter 2000) and the continental Antarctic (Pannewitz *et al.* 2003). It was unexpected that *X. mawsonii* grows at the very edges of runoff and inside drainage lines along with other foliose lichens such as *Physcia caesia*, *P. dubia* and *Umbilicaria aprina*, where thalli are regularly inundated and hydrated to maximum WC values, because it is accepted that green algal lichens are intolerant of wet areas like melt streams (Kappen & Schroeter

2002) and normally occupy drier habitats than mosses (Green *et al.* 1999). At the maximum WC produced by immersion, the excess water can impede CO₂ exchange (Lange & Tenhunen 1981; Lange *et al.* 1996; Lange *et al.* 2001; Kappen 1985; Kappen & Breuer 1991) due to increased diffusion resistance at suprasaturation; fully saturated thalli of *X. mawsonii* show a depression of 64% of the maximum measured at a WC between 100 and 175% DW. Although the species is wetted almost daily, it grows in a line at a certain level along the melt channel and this ensures that it is not continually submerged when CO₂ diffusion would be massively hindered by immersion. The lichen must be at a high WC for long periods so that maximum NP would be rarely achieved (*cf.* *Lecanora muralis*, Lange *et al.* 2001). One suggestion is that the gain in length of the active period from the regular immersion more than offsets the losses due to suprasaturation. It is worth remembering that if lichen thalli were above the maximum flow level of the melt stream they would be hydrated only by infrequent snowfalls. More detailed moisture-related investigations, similar to those performed by Kappen & Breuer (1991), are now needed.

The activity of *X. mawsonii* growing in two distinct habitats, a water channel and an open rock surface was measured. In the latter habitat, once any winter snow had melted the lichen would be totally dependant on occasional snowfall for moisture. When water resources are unavailable *X. mawsonii* desiccates quickly and probably to a point where practically no liquid phase remains in the cells (Proctor & Tuba 2002). Although precipitation in continental Antarctica is low (Rudolph 1966a; Kappen & Schroeter 1997; King & Turner 1997; Green *et al.* 1999) *X. mawsonii* has an exceptionally short reactivation phase (5 min.) and is able to utilize snow immediately, an ability also reported for several other Antarctic lichen and bryophyte species (Proctor & Tuba 2002, Schlensoeg *et al.* 2004). The rapid photosynthetic recovery is a necessary physiological response to the ephemeral wet periods that *X. mawsonii*

encounters but productivity is not so great as along melt channels because activity only occurred for 28% of the time between 5 November and 5 December. Optimal conditions for NP were present for less than 1% of the total measuring period.

Xanthoria mawsonii is able to recover its photosynthesis by absorbing water vapour from almost saturated air (>90% RH, Kappen & Redon 1987) within 24 h and the obvious ecological potential for such capability has been recognized (e.g. Ganutz 1967; Lange & Kappen 1972; Lange *et al.* 2001; Ahmadjian 1970). The capacity for some metabolic activity during snow free, relatively dry periods, may explain the species' abundance in coastal Antarctic regions where periods of high air humidity occur. During our recordings at Cape Hallett and Granite Harbour periods with a RH >90% were rarely observed, and never for time periods longer than one hour. At the site at which the vegetation was entirely dependent on snow for moisture, RH >90% was measured on only 4 occasions during almost 3 months of recordings (Fig. 4). On two occasions there was no detectable potential PSII activity. This result agrees with those of Rudolph (1966b), Hovenden *et al.* (1994) and Longton (1997) and suggests that RH is not high enough for a sufficient length of time to be ecologically important for continental Antarctic lichens.

Several laboratory studies have suggested that it is possible that the ability to absorb water from nearly saturated air might be of major ecophysiological importance at sub-zero temperatures under snow (Green *et al.* 1999; Schroeter *et al.* 1994; Schroeter & Scheidegger 1995; Kappen 1993; Kappen & Breuer 1991) as has also been shown for *X. mawsonii* (Pannewitz *et al.* 2003). Under laboratory conditions *Umbilicaria aprina* gained 25% DW at -14°C after 16 h but with no NP activity (Schroeter & Scheidegger 1995). Lange and Kappen (1972) demonstrated that *X. mawsonii* still performs NP at a TT of -16.5°C by measuring CO₂ gas exchange in a closed system. In our laboratory studies, although F_V/F_M is still significant at a TT of -15°C

(79% of maximum in fully hydrated *X. mawsonii*), $\Delta F/F_M'$ at $160 \mu\text{mol m}^{-2} \text{s}^{-1}$ was zero (Fig. 8A) which indicates a stronger cold resistance for the PSII reaction centres than the photosynthetic CO_2 fixation process.

Water uptake from snow via air humidity is a strongly temperature dependent physical process and, under field conditions, the first signs of potential PSII activity measured under snow were found at the higher TT of between -10 and -7°C . Rates of net photosynthesis at these TT values were low and the significance of this activity for dry matter production is difficult to assess. It may be more important for the maintenance of the photosynthetic apparatus and metabolism of cryoprotective carbohydrates (Kappen 2000). At TT values between -5 and 0°C , CO_2 gas exchange can be significant if the transmitted PPFR through the snow is sufficient. PPFR under a snow pack of 15 cm can reach the equivalent of 10–30% of incident PPFR (Kappen & Breuer 1991) and this would be enough for positive net photosynthesis by *X. mawsonii* with a light compensation of around $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ at ambient temperatures near 0°C . PPFR was $>30 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 69% of the measurements and above $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 38% under a snow layer of between 13 and 10 cm (5–8 November 2000) when TT did not exceed -5.1°C .

The measurement of chlorophyll *a* fluorescence has proved to be an excellent tool to monitor the activity pattern of lichens and has allowed periods of hydration to be detected (Jensen 1994; Schlenz & Schroeter 2000; Leisner *et al.* 1997; Green *et al.* 2002). The parameters $\Delta F/F_M'$ and ETR ($\Delta F/F_M' \times \text{PPFR}$; Schreiber *et al.* 1994) indicate that thalli are active and give a possible indication of photosynthetic activity but little or nothing about the hydration level. In *X. mawsonii* NP was not linearly related to ETR and did not show the NP depression due to suprasaturation. Similar weak or non-linear relationships between ETR and gas-exchange were reported by Leisner *et al.* (1997) and Green *et al.* (1998). It appears that ETR is not a

suitable substitute for continuous CO_2 gas exchange measurements if the total carbon gain of *X. mawsonii* is the main objective of the investigation.

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