ECOPHYSIOLOGY

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Are lichens active under snow in continental Antarctica?

Received: 4 March 2002 / Accepted: 3 December 2002 / Published online: 8 February 2003 Springer-Verlag 2003

Abstract Photosynthetic activity, detected as chlorophyll a fluorescence, was measured for lichens under undisturbed snow in continental Antarctica using fibre optics. The fibre optics had been buried by winter snowfall after being put in place the previous year under snow-free conditions. The fibre optics were fixed in place using specially designed holding devices so that the fibre ends were in close proximity to selected lichens. Several temperature and PPFD (photosynthetic photon flux density) sensors were also installed in or close to the lichens. By attaching a chlorophyll a fluorometer to the previously placed fibre optics it proved possible to measure in vivo potential photosynthetic activity of continental Antarctic lichens under undisturbed snow. The snow cover proved to be a very good insulator for the mosses and lichens but, in contrast to the situation reported for the maritime Antarctic, it retained the severe cold of the winter and prevented early warming. Therefore, the lichens and mosses under snow were kept inactive at subzero temperatures for a prolonged time, even though the external ambient air temperatures would have allowed metabolic activity. The results suggest that the major activity period of the lichens was at the time of final disappearance of the snow and lasted about 10–14 days. The activation of lichens under snow by high air humidity appeared to be very variable and species specific. Xanthoria mawsonii was activated at temperatures below -10°C through absorption of water from high air humidity. Physcia dubia showed some activation at temperatures around -5° C but only became fully activated at thallus temperatures of 0° C through liquid water. *Cande*-

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L. G. Sancho Dept. Biologia Vegetal II, Fac. de Farmacia, Universidad Complutense, 28040 Madrid, Spain lariella flava stayed inactive until thallus temperatures close to zero indicated that liquid water had become available. Although the snow cover represented the major water supply for the lichens, lichens only became active for a brief time at or close to the time the snow disappeared. The snow did not provide a protected environment, as reported for alpine habitats, but appeared to limit lichen activity. This provides at least one explanation for the observed negative effect of extended snow cover on lichen growth.

Keywords Antarctica · Chlorophyll a fluorescence · Lichen · Microclimate · Snow cover

Introduction

In continental Antarctica almost all fresh water is biologically unavailable because it is in the form of ice. The vegetation, dominated by poikilohydric lichens, mosses, algae and cyanobacteria (Green et al. 1999), is restricted to ice-free areas where melt water occurs during the brief summer season for about 2 months, the probable main period of productivity (Howard-Williams and Vincent 1986). In habitats where meltwater streams are absent vegetation activity is dependent on other sources such as snow patches (Kappen et al. 1990; Kappen 1993) and sporadic snowfall. In these niches biologically available water may exist only for weeks or even days (Kennedy 1993). It is possible that the protected environment below snow could considerably extend the active season of lichens as has already been found in the maritime Antarctic (Schroeter et al. 1997b, 2000; Winkler et al. 2000), in the subarctic (Sommerkorn 2000) and in the alpine zones of mountains (Körner 1999). The snow cover not only influences the availability of water and light but also, because of its insulating qualities, the temperature regime (Kappen et al. 1995; Winkler et al. 2000). Davey et al. (1992) showed that snow cover in the maritime Antarctic can protect the vegetation from cold temperatures so that the thalli remain hydrated and active.

A snow depth of 15 cm still allows enough light for photosynthesis, although at low rates (Kappen and Breuer 1991; Kappen et al. 1995). Excessive snow, however, can cause problems. Below 30 cm the environment is too dark for photosynthesis (Körner 1999; Pomeroy and Brun 2001) and, under these circumstances, hydrated lichens can have a high loss of carbon dioxide due to respiration (Gannutz 1970; Kappen et al. 1995). For lichens, continental Antarctica is a different environment to both the maritime Antarctic and arctic-alpine zones. Winter temperatures, in particular, are much lower and commonly reach -50° C. Precipitation is also much less and most of continental Antarctica is best described as a cold desert (Green et al. 1999). Snowfall occurs mostly in winter and any falls in summer are usually very light. Photosynthetic activity under accumulated snow in spring or early summer, therefore, could be of major importance for productivity (Kappen et al. 1990). This work investigates whether snow cover provides the same protection from extremes for the vegetation as in the maritime Antarctic and, in particular, whether lichens can be photosynthetically active under the snow. Antarctic lichens are known to be able to regain photosynthetic activity by rehydration from air humidity alone (Lange and Kilian 1985; Kappen and Redon 1987; Kappen et al. 1995), including from snow at temperatures below 0° C (Schroeter et al. 1994; Schroeter and Scheidegger 1995). This is a physical process by which the hydration of the lichen thallus equilibrates with the water vapour pressure of the surrounding ice (Kappen 1993; Schroeter and Scheidegger 1995). However, except for the work of Kappen (1989) and Friedmann et al. (1993), no information exists for lichens under snow in their natural habitat in continental Antarctica.

There are obvious difficulties in working on lichens below snow without causing a disturbance that would alter their environment. We attempted to overcome these problems by using a fibre-optic system that allowed us to monitor potential photosynthetic activity of lichens and mosses under undisturbed snow cover.

Materials and methods

The research site was near Cape Geology, Granite Harbour, southern Victoria Land, continental Antarctica (77°00' S, 162°32' E). The area is known for its exceptional moss and lichen vegetation and the SSSI (Site of Special Scientific Interest) no. 37, covering Cape Geology and Botany Bay, is adjacent to the site. The research site was situated 70 m south of the shoreline at about 6 m above sea level.

Previous studies on exposed lichens from the area have shown that photosynthetic activity occurred early in the summer (November) due to local solar warming of rocks when air temperatures were still around -12°C (Kappen et al. 1998; Schroeter et al. 1997a). It was suspected (in view of the well developed vegetation) that there could also be extensive productivity whilst the lichens were still snow covered (Schroeter et al. 1994). In order to investigate this possibility without disturbance to any snow cover we decided to fix fibre optics in place one summer (January 2000) and use them whilst there was still snow cover early the following summer. The fibre optics (glass fibre \varnothing 3 mm and up to 1 m long)

were held in place using specially designed holding devices (Schlensog and Schroeter 2001). These stands were firmly attached to rocks by gluing them into drilled holes and the fibre optics fixed into them. The stands were then adjusted so that the ends of the fibre optics were close to the upper surface of the lichen or moss to be monitored. This stopped the entry of snow crystals between the thalli and the fibre optic that would have prevented optimal measurements (for details see Schlensog and Schroeter 2001). The other end of the optic, the connector for the chlorophyll fluorescence measuring system, was covered with a black cap in order to prevent ambient light passing down the fibre to the thallus surface. In addition, several PPFD sensors [photosynthetic photon flux density in the 400–700 nm waveband, self-made according to Pontaillier (1990) and calibrated with an optical radiation calibrator; LiCOR 1800-02, USA] were installed in the direct vicinity of the thalli. As Körner (1999) mentioned, radiation under snow creates back-scatter. The PPFD sensors were not specially screened against back-scatter and it is possible that the PPFD might be enhanced due to this effect, because the sensor's diffuser cap was about 5 cm above the ground and surrounded by snow. Thallus temperature measurements were made using microthermistors $(\emptyset$ 0.3 mm, Grant, UK) placed in contact with the lower surface of the thalli.

The measurement set-up was left in place over the following southern winter season 2000 with the free ends of the sensors held in an elevated position by attachment to bamboo stakes. On return in early November 2000, the vegetation was found to be under a snow cover of varying depth due to drifting (Fig. 1). Two data loggers (SQ1021, Grant, UK) were connected to the previously installed sensors and additional air temperature and PPFD sensors were used to measure ambient light and air temperature above the snow. Climatic and microclimatic data were stored at an interval of 5 min.

A portable PAM fluorescence system (MINI-PAM, Walz, Germany) was used to monitor the potential activity pattern of the lichens (see Green et al. 2002; Schroeter et al. 1992, 1997c, 1999; for a description of PAM methodology see Schreiber et al. 1994). The apparent quantum use efficiency of PSII $(\Delta F/Fm')$ was measured every second hour by briefly attaching the fluorometer to each fibre optic. The intention in the present study was to use the fluorometer only as a monitoring system to detect hydrated thalli by measuring the maximal quantum use efficiency. We do not, therefore, provide data like relative electron transport rate through PSII which is generally used as an indicator of photosynthetic rate (Genty et al. 1989). In the presented results, the variable transient fluorescence yield, ΔF_t , is given as a percentage of the maximal transient fluorescence measured over the entire research period. Therefore, our measurements indicate the potential photosynthetic activity of the photobionts of the lichens.

Measurements took place between 9 November and 5 December for a continuous period of 26 days. The species presented here, all growing either on, or close to, large granite boulders, were Candelariella flava (C.W. Dodge et Baker) Castello et Nimis, Physcia dubia (Hoffm.) Lettau, Xanthoria elegans (Link) Th. Fr. and Xanthoria mawsonii C.W. Dodge. All lichens were growing in similar habitats but with site-specific differences, i.e. aspect, shading and snow accumulation (see Discussion).

Results

Snow cover

The research site contained several large granite boulders that affected both direction and magnitude of the wind and led to drifting of snow (Fig. 1). As a result, each of the lichens with attached fibre optics had been buried to a different depth of snow when we returned in November (Fig. 2). Melting of the snow was due to absorbed solar

Fig. 1a–e Pictures of the investigation site with Xanthoria elegans at Granite Harbour, Antarctica (77°00'S, 162°32'E) over a period of 10 days. a Overview of the site with X. elegans under snow cover; b same site 9 November, fibre optic holder still just covered by snow; c 14 November, snow now clear of the measuring probe but still supplying melt water; d 16 November and e 19 November 2000, progressive disappearance of the snow, lichen no longer active. The arrow indicates the location of the fibre optic

radiation but was enhanced by the granite rocks that heated up if exposed to full sunlight and contributed significantly to the melting process. X. elegans was covered to a depth of only 3 cm at the beginning of the measurements (9 November). The snow on top of the

lichen vanished quickly during the following days but surrounding snow remained for a few more days and provided melt water at times of high insolation. A similar, but delayed pattern, was observed for X. mawsonii where snow depth was 10 cm at the start.

Fig. 2 Snow depth above the selected lichen species during the investigation period between 9 November and 8 December 2000 in Granite Harbour, Antarctica (Xe Xanthoria elegans, Xm X. mawsonii, Cf Candelariella flava, Pd Physcia dubia)

A quite different situation was found for P. dubia and C. flava. In these cases, snow depth above the lichen was not a good indicator of the actual situation. The angle of the sun during the day, together with heating of the surrounding granite rocks during the sunny days, meant that the snow cover melted more rapidly at its edge than it thinned. As a result, for C. flava, the lichen became exposed by retreat over it of the snow edge rather than by thinning of the cover. The sample was covered under a deep snow layer for most of the time until suddenly the sample was exposed fully at the beginning of December. The sample of P. *dubia* was initially buried under a snow cover of about 30 cm that had steadily thinned to around 18 cm by early December. However, towards the end of measurements, the much higher PPFD suggests that the actual snow depth was much less and that a cavity might have formed around the lichen.

Lichen microclimate

The effect of the snow cover on the microclimate of the covered lichens is clearly seen in Fig. 3 and, summarised, in Table 1. The deeper the snow cover the lower the PPFD

Table 1 A summary of the ambient and microclimatic conditions at the research site. Mean, maximal and minimal photosynthetic photon flux density (PPFD) for the research period of an external horizontal sensor and sensors adjacent to the lichens, and mean,

Thallus temperatures showed little relationship with external ambient air temperatures. When the lichens were under snow, they were strongly insulated from ambient conditions. However, in contrast to what might be expected, the snow cover did not keep the lichens warmer than ambient but actually prevented them from warming up from the very cold temperatures reached in winter. The most deeply buried lichen, C. flava, was at -18.3 °C at the start of measurements when ambient air temperatures were positive every day. The sample warmed, at an average daily rate of about 1° C, from -18.3° C to -13.3° C over the first week demonstrating that heat transfer through the snow from ambient was reaching the thallus at a depth of 60 cm of snow. P. dubia, with a snow cover of about 30 cm, warmed more slowly at about 0.7° C per day (Fig. 3). The difference between C. flava and P. dubia indicated that the rate of warming was not solely dependent on snow depth but was influenced by other factors, possibly snow composition, aspect or shading. In a similar pattern to that found for PPFD, the temperatures of lichen thalli showed much increased diel variation and more rapid warming just before the snow cover disappeared. Once the snow cover had completely gone, high thallus temperatures occurred because of the high insolation. The two lichens which were the first to be exposed, X. elegans and X. mawsonii, reached temperatures around 20° C because they had dried out; the remaining two lichens were still moist at the end of measurements and were cooler at $12-14$ °C. Similar magnitudes of aboveambient temperatures were found by Schroeter et al. (1997a) and Kappen et al. (1998) for the crustose lichen species *Buellia frigida* in early summer in the same area.

Each temperature record for the individual lichens was allocated to a two degree class from -20 to $+20^{\circ}$ C and represented as a proportion of the total number of records (Fig. 4). The coldness of the lichens with respect to ambient air temperature is again very clear. Only X.

maximal and minimal temperatures in the ambient air and of the thallus of the four measured lichens. Lichen activity is calculated as the percentage of the total measurement period that the particular lichen had a variable fluorescence yield $(\Delta F_t) > 15\%$

PPFD	Horizontal	Xanthoria elegans	X. mawsonii	Candelariella flava	Physcia dubia
Mean	605.5	460.9	380.0	119.6	63.7
Min	54.0	59.0	6.0	0.0	0.0
Max	1.980.0	1,388.0	1.711.0	1,889.0	1,643.5
Temp. °C	ambient				
Mean	-2.0	1.7	-1.8	-6.7	-7.5
Min	-16.0	-8.4	-12.6	-18.3	-16.7
Max	10.6	19.3	21.3	12.1	14.7
Activity in % of $\Delta F_t > 15\%$		22	35	24	27

Fig. 3 Ambient and microclimate conditions at the research site at Granite Harbour in the early austral summer from 5 November to 10 December, 2000. Upper two panels, ambient conditions: top panel incident photosynthetic photon flux density (PPFD) from horizontal sensor in μ mol m⁻²s⁻¹, lower panel air temperature (AT) , °C. Lower eight panels, microclimatic conditions of Xanthoria elegans, X. mawsonii, Candelariella flava and Physcia dubia. For each lichen the top panel is PPFD adjacent to the thallus (μ mol m⁻²s⁻¹) and *lower* panel is thallus temperature, TT, from a sensor attached to the thallus, in $^{\circ}C$

November/December 2000

mawsonii had a substantial number of records above ambient reflecting the very early date that it became clear of snow.

Potential photosynthetic activity

All samples reactivated their potential PSII activity during the measurement period of 26 days but at different times depending primarily on snow depth (Figs. 2, 5). X.

elegans was already active at the start of measurements on 9 November. Continued melting of snow both above the lichen and then in its immediate surroundings maintained activity for 6 days after which it stopped due to thallus desiccation. X. mawsonii showed a slow but steady increase in activity. Thallus hydration reached levels that supported potential PSII activity when the snow cover depth was still 5 cm and thallus temperature was between -10 and -5° C (Fig. 4). Maximal potential PSII activity occurred when the snow cover had com-

Fig. 4 Relative frequency (%) of temperature classes between \geq -20 $^{\circ}$ C and +20 $^{\circ}$ C for ambient air temperature (*upper panel*), and the three lichens Xanthoria mawsonii, Candelariella flava and Physcia dubia (three lower panels). In each panel the height of the bar represents the proportion $(\%)$ of the total research period spent in that temperature class. In the lower three panels for the lichens the filled part of the bars represents the proportion of the total research time that the lichens showed potential PSII activity defined as $\Delta F_t > 15\%$

pletely disappeared and thallus temperatures became mainly positive with maximal values of 5° C. The lichen remained hydrated because of continued water supply from the melting of snow close to the lichen. After 12 days of steady potential photosynthetic activity, it finally dried out and stopped on the 26 November. Both X. elegans and X. mawsonii were reactivated on one day (29 November) later in the measurement period by a light snowfall (Fig. 5).

C. flava suddenly showed potential PSII activity on the 27 November when the thallus was still not fully exposed. Potential PSII activity started when the thallus reached

temperatures close to 0° C strongly suggesting that liquid water had hydrated the lichen. Activity continued during the following days but with a steady decline in absolute values and, although the thallus did not cease activity within the measurement period, it was obvious that this would happen soon after the end of the measurements with the total active period estimated to be 14 days. P. dubia first showed measurable potential PSII activity at temperatures around -7° C and a steep increase occurred when the thallus warmed up to 0° C on 29 November. At that time, the snow surface was still 20 cm above the lichen. The lack of strong diel cycles in temperature and PPFD suggest that the snow cover was intact and that activation had probably occurred by melt water flowing from a nearby rock surface. This could not be confirmed because it would have meant disturbing the snow conditions around the thallus and no interference was a key guideline for this investigation. Potential PSII activity still continued at the end of the measurement period on 5 December.

When measurements with $\Delta F_t > 15\%$ (deemed to be active) are distributed according to temperature two features are clear (Fig. 4). First, all lichens were active only at the warmer times with peak activity around 0° C. Second, X. mawsonii was active over a much broader range of temperatures than the other two lichens. It was active between -8 and -10° C and this must mean activation through high humidity because it was unlikely that any melt had occurred at those temperatures. P. dubia became active above -8°C and *C. flava* above -6°C . However, all species showed a very similar total activity period of 22–35% of the measurement period regardless of when they became activated (Table 1).

Discussion

The technique of placing fibre optics at the research site in the preceding season proved to be successful and the measurements obtained are the first to use chlorophyll a fluorescence to monitor potential PSII activity of lichens under an undisturbed snow cover in continental Antarctica. In addition, by placing temperature and PPFD sensors alongside the fibre optics it was possible to gain considerable insight into the microclimate of the lichens. The results of the study are clear. The accumulated winter snow cover was a very effective insulator but acted to prolong winter conditions rather than behaving as a "glasshouse" as described previously (Lange 1969; Llano 1965). Lichens under deeper snow received very low irradiation and were much colder than external ambient temperatures because insulation by the snow cover prevented heat transfer from the warmer air. This is a marked contrast to the situation in the maritime Antarctic and arctic-alpine areas where winter snow cover maintains more equitable conditions for the lichens (Davey et al. 1992; Körner 1999; Winkler et al. 2000). Kappen et al. (1995) found such a positive effect when an early spring Fig. 5 Thallus temperature and percentage of maximal transient fluorescence under snow during the snow melt process for the four measured lichens Xanthoria elegans, X. mawsonii, Candelariella flava and Physcia dubia. In each panel the solid line is thallus temperature (right) hand axis in $^{\circ}$ C), whilst the chlorophyll a fluorescence activity, ΔF_t as percentage of maximal transient fluorescence reached (left hand axis), is shown as a solid black line with filled circle symbols and light grey filling beneath

snow layer on lichens in northern Sweden protected them against temperature extremes.

Activation by high air humidity alone has been shown for Antarctic lichens under controlled laboratory conditions (Schroeter 1994; Schroeter and Scheidegger 1995) but there was mixed evidence for this phenomenon in this study. X. mawsonii showed the clearest signs of activation by humidity alone. It had a substantial fluorescence signal, about 20% of maximum, at around -10° C and about 5 days before the first wetting by water occurred (estimated to have been on 18 November). Similarly, P. dubia had initial potential PSII activity at about -8 to -7° C for about 5 days before the major increase occurred that followed wetting at thallus temperatures of around 0° C. In contrast, *C. flava* showed no signs of potential PSII activity until it became almost fully activated on 28 November.

Activation by air humidity, however, may not be of major importance to overall productivity because, even though it occurred for up to about 33% of the active period (X. mawsonii), photosynthesis would have been less efficient at the low temperatures. The short period of hydration by water vapour may result from slower equilibration rates at low temperatures possibly in combination with high relative humidities only occurring transiently. High quality measurements of relative humidity under snow are required to clarify the situation. It must also be remembered that the lichens are warming steadily as the snow thins and there is not a long time between the lichens becoming warm enough to be active

through water vapour uptake and eventual wetting by liquid water.

The four lichens studied showed different activation patterns that reflected their ecology. X. elegans, a lichen that grows on more or less horizontal surfaces of granite boulders with high nutrient input (Øvstedal and Lewis Smith 2001), was already active at the beginning of November. After the loss of the snow from above the thallus, the activity period was extended by meltwater from nearby residual snow patches when hydration in combination with maximal thallus temperatures of around 10° C produced substantial potential PSII activity. This lichen is probably one of the first in the season to become active each summer at Granite Harbour because the snow cannot accumulate to any depth on top of the boulders. After the snow patches vanish because of melting or sublimation the lichen is then fully dependent on snowfall events.

X. mawsonii occurs on horizontal substrates that can be a rock surface, small gravel or sediment. Snow accumulated more deeply and kept the lichen at low temperatures that did not allow activity until later in November. Once active the lichen remained so until 26 November when the snow disappeared and activity ceased due to desiccation. C. flava grows on flat sediment, often on moribund mosses, in a habitat where water flow would always be expected to occur. The high insulation factor of the deep snow cover kept the lichen at temperatures well below freezing until 27 November when the rapid rise in activity suggests the first melt had occurred and that water was flowing under the snow.

However, for all four lichens the active (defined as ΔF_t) above 15%) periods were very similar (22–35% of total time, see Table 1). It appears that, regardless of when the lichen first became hydrated, they had an activity period of very similar length. Only one extra day occurred during the measurements when there was activation through snowfall and productivity gains from summer snowfalls are likely to be low (Schroeter et al. 1997a).

It seems, in continental Antarctica, that snowdrifts regularly form each winter at identical locations (confirmed by photographs from other sites over 35 years) with lichens buried beneath them (Schroeter et al. 1994; Kappen et al. 1998; Green et al. 1999). The retreat of the snow margin over the lichens represents both their major water supply and their major period of productivity. Lichens under the snow remain inactive from the cold temperatures maintained through insulation by the snow whilst those exposed become rapidly inactive through desiccation. Lichens exposed for the first time late in the season will have almost the same productivity as those exposed earlier and there is little disadvantage to extended burial in snow as long as melting does eventually, and consistently, occur each season. This contrasts with the temperate alpine zones where Benedict (1990) reported that prolonged snow cover could have a negative effect on lichen survival both by shortening the productive season and by increasing respiration losses when thalli are hydrated at low PPFD beneath the snow. Under the latter conditions there would be a significant advantage in early loss of the snow cover.

The lichens studied here were not active to any great extent under snow and the effect of snow cover appears to be very different for lichens in Antarctica and in alpine regions of mountains. In the alpine zones of mountains the snow cover is known to be a very effective protectant against the climatic extremes in the cold seasons and survival of many plants depends on the consistent presence of the snow (Körner 1999). In the Antarctic the lichens also depend on the consistent presence of snow banks for their water supply. However, the snow preserves the cold conditions of winter and there is no or little additional productivity while it is still present. In fact, because almost all the wetted period for the lichens appears to be when the snow edge melts over the thalli, there is actually little difference in the total length each year of the active period, and therefore productivity, for the lichens whether exposed early or late in the season. The results demonstrate that, for lichens, the continental Antarctic regions cannot be considered as high latitude, alpine zones.

Acknowledgements SP, MS and BS thank the Deutsche Forschungsgemeinschaft for financial support (SCHR 473/4-3). LGS thanks the Spanish Ministry of Science and Technology (ANT99-0680) for financial support. Antarctica New Zealand is thanked for providing logistics both for the research in Antarctica and movements to Antarctica. The Vice-Chancellor of Waikato University is thanked for a special grant to support the work.

References

- Benedict JB (1990) Lichen mortality due to late-lying snow: results of a transplant study. Arct Alp Res 22:81–89
- Davey MC, Pickup J, Block W (1992) Temperature variation and its biological significance in fellfield habitats on a maritime Antarctic island. Antarct Sci 4:383–388
- Friedmann EI, Kappen L, Meyer MA, Nienow JA (1993) Longterm productivity in the cryptoendolithic microbial community of the Ross desert, Antarctica. Microb Ecol 25:51–69
- Gannutz T (1970) Photosynthesis and respiration of plants in the Antarctic Peninsula Area. Antarct J US 5:49–52
- Genty B, Briantais J-M, Baker N (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 990:87–92
- Green TGA, Schroeter B, Sancho LG (1999) Plant life in Antarctica. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. Dekker, New York, pp 495–543
- Green TGA, Schlensog M, Sancho LG, Winkler JB, Broom FD, Schroeter B (2002) The photobiont determines the pattern of photosynthetic activity within a single lichen thallus containing cyanobacterial and green algal sectors (photosymbiodeme). Oecologia 130:191–198
- Howard-Williams C, Vincent WF (1986) Ecosystem properties of Antarctic streams. NZ Antarct Rec 6:21–27
- Kappen L (1989) Field measurements of carbon dioxide exchange of the Antarctic lichen Usnea sphacelata in the frozen state. Antarct Sci 1(1):31–34
- Kappen L (1993) Plant activity under snow and ice, with particular reference to lichens. Arctic 46:297–302
- Kappen L, Breuer M (1991) Ecological and physiological investigations in continental Antarctic cryptogams. II. Moisture relations and photosynthesis of lichens near Casey Station, Wilkes Land. Antarct Sci 3:273–278
- Kappen L, Redon J (1987) Photosynthesis and water relations of three maritime Antarctic lichen species. Flora 179:215–229
- Kappen L, Meyer M, Bölter M (1990) Ecological and physiological investigations in continental Antarctic cryptogams. I. Vegetation pattern and its relation to snow cover on a hill near Casey Station, Wilkes Land. Flora 184:209–220
- Kappen L, Sommerkorn M, Schroeter B (1995) Carbon acquisition and water relation of lichens in polar regions – potentials and limitations. Lichenologist 27:531–545
- Kappen L, Schroeter B, Green TGA, Seppelt RD (1998) Microclimatic conditions, meltwater moistening, and the distributional pattern of Buellia frigida on rock in a southern continental Antarctic habitat. Polar Biol 19:101–106
- Kennedy AD (1993) Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. Arct Alp Res 25:308–315
- Körner C (1999) Alpine plant life. Springer, Berlin Heidelberg New York
- Lange OL (1969) Die funktionellen Anpassungen der Flechten an die kologischen Bedingungen arider Gebiete. Ber D Bot Ges 82:3–22
- Lange OL, Kilian E (1985) Reactivation of photosynthesis of dry lichen thalli through water vapor uptake from air: species specific response patterns. Flora 176:7–23
- Llano GA (1965) The flora of Antarctica. In: Hatherton T (ed) Antarctica: a New Zealand Antarctic Society survey. Methuen, London, pp 331–350
- Øvstedal DO, Lewis Smith RI (2001) Lichens of Antarctica and South Georgia. Cambridge University Press, Cambridge
- Pomeroy J, Brun E (2001) Physical properties of snow. In: Jones HG, Pomeroy J, Walker DA, Hoham R (eds) Snow ecology: an interdisciplinary examination of snow-covered ecosystems. Cambridge University Press, Cambridge, pp 45–127
- Pontaillier JY (1990) A cheap quantum sensor using gallium arsenid photodiode. Funct Ecol 4:591–596
- Schlensog M, Schroeter B (2001) A new method for the accurate in situ monitoring of chlorophyll a fluorescence in lichens and bryophytes. Lichenologist 33:443–452
- Schreiber U, Bilger W, Neubauer C (1994) Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of photosynthesis. Ecological studies vol 100. Springer, Berlin Heidelberg New York, pp 49–70
- Schroeter B (1994) In situ photosynthetic differentiation of the green algal and the cyanobacterial photobiont in the crustose lichen Placopsis contortuplicata. Oecologia 98:212–220
- Schroeter B, Scheidegger C (1995) Water relations in lichens at subzero temperatures: structural changes and carbon dioxide exchange in the lichen Umbilicaria aprina from continental Antarctica. New Phytol 131:273–285
- Schroeter B, Green TGA, Seppelt RD, Kappen L (1992) Monitoring photosynthetic activity of crustose lichens using a PAM-2000 fluorescence system. Oecologia 92:457–462
- Schroeter B, Green TGA, Kappen L, Seppelt RD (1994) Carbon dioxide exchange at subzero temperatures. Field measurements on Umbilicaria aprina in Antarctica. Cryptogam Bot 4:233–241
- Schroeter B, Kappen L, Green TGA, Seppelt RD (1997a) Lichens and the Antarctic environment: effects of temperature and water availability on photosynthesis. In: Lyons WB, Howard-Williams C, Hawes I (eds) Ecosystem processes in Antarctic ice-free landscapes. Balkema, Rotterdam, pp 103–117
- Schroeter B, Kappen L, Schulz F (1997b) Long-term measurements of microclimatic conditions in the fruticose lichen Usnea

aurantiaco-atra in the maritime Antarctic. Actas del V. Simposio de Estudios Antárticos, Barcelona, pp 63–69

- Schroeter B, Schulz F, Kappen L (1997c) Hydration-related spatial and temporal variation of photosynthetic activity in Antarctic lichens. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities. Species, structure and survival. Cambridge University Press, Cambridge, pp 221–225
- Schroeter B, Sancho LG, Valladares F (1999) In situ comparison of daily photosynthetic activity patterns of saxicolous lichens and mosses in Sierra de Guadarrama, Central Spain. The Bryologist 102:623–633
- Schroeter B, Kappen L, Schulz F, Sancho LG (2000) Seasonal variation in the carbon balance of lichens in the maritime Antarctic: long-term measurements of photosynthetic activity in Usnea aurantiaco-atra. In: Davison B, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. Caxton Press, Christchurch, NZ, pp 258–262
- Sommerkorn M (2000) The ability of lichens to benefit from natural CO2 enrichment under a spring snow-cover: a study with two arctic-alpine species from contrasting habitats. Bibl Lichenol 75:365–380
- Winkler JB, Kappen L, Schulz F (2000) Snow as an important ecological factor for the cryptogams in the maritime Antarctic. In: Davison W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. Caxton Press, Christchurch, NZ, pp 220–224