

ACTIVITY OF LICHENS UNDER THE INFLUENCE OF SNOW AND ICE

Ludger KAPPEN^{1,2} and Burkhard SCHROETER²

¹*Institut für Polarökologie der Christian-Albrechts-Universität Kiel, Wischhofstr. 1–3, 24148 Kiel, Germany*

²*Botanisches Institut der Christian-Albrechts-Universität Kiel, Olshausenstr. 40, 24098 Kiel, Germany*

Abstract: A major aim of our investigations is to explain the adaptation of vegetation to the peculiar environmental conditions in polar regions. Our concept describes the main limiting and favorable factors influencing photosynthetic production of cryptogams, mainly lichens. Snow and ice—usually stress factors to the activity of plants—can be effectively used by lichens because of their poikilohydrous nature. Light, the basic driving force for photosynthetic activity, may be deleterious under certain circumstances of the cold environment. In moderate climates the summer season is most favorable to plant activity and production and is therefore called the growing season. In the continental Antarctic as well as in the high Arctic region the favorable light and temperature conditions during the summer period may not be as profitable to the productivity of lichens as expected because water is deficient. As in many arid regions, climatic conditions during transient seasons (early summer, fall) merit greater attention if lichen activity is considered and investigated. Our way of investigating this is to establish measuring systems that automatically record micro-environmental parameters and lichen activity over the whole annual period. Another is to investigate physiological responses of lichens to the environmental conditions with experiments mainly carried out in the field.

1. Introduction

Lichens are a very prominent element in polar and high alpine regions. In the Arctic regions they and also vascular plants reach the northernmost habitats on land. Their existence mainly depends on the climatic moisture regime and on the stability of the substratum. Like most vascular plants lichens cannot grow on cryoturbated ground. On solid rock they are superior to vascular plants because they do not need soil for water and nutrient uptake. Lichens solely depend on the aerial moisture and nutrient supply. In polar habitats lichens and vascular plants have about the same size. In Antarctica lichens together with bryophytes form the dominant element of the vegetation on rock and on scree with many species, whereas the only two existing species of vascular plants are restricted to climatically favorable sites in the maritime Antarctic (part of the Antarctic Peninsula and the adjacent islands). On the Antarctic continent, however, vegetation is very scattered. Lichens are even able to exist in climatically very extreme environments such as the Antarctic Dry Valleys and on top of nunataks (KAPPEN, 1988). The following brief survey of studies on the performance of lichens in polar and frigid regions is based on data gained during a 15-year period of research carried out by the Kiel terrestrial working group during more than 12 expeditions to Antarctica, Greenland and subarctic mountain tundra ecosystems, and earlier experimental studies.

2. Metabolic Activity and Freezing Tolerance

The existence of the lichen symbiosis is based on maintenance and growth. Maintenance may play a greater role than growth for these long-living lichen thalli. Maintenance means coping with extremely low temperatures and periodical drought, wind chill, erosion and cover by ice and snow. Our investigations have revealed that the freezing tolerance of lichens is extremely high (KAPPEN and LANGE, 1970). With respect to the carbon balance of the system this capacity is established on the account of carbon for the production of freeze-protective agents in the fungal and algal cells. Also the changes between freezing and thawing may cost the thallus loss of carbon compounds due to leaching (KAPPEN *et al.*, 1995).

Growth depends on a complex of environmental conditions. The basic process for carbon production is photosynthesis and respiration. These processes proved to be very resistant and still effective at low temperatures. Field experiments in Antarctica with several macrolichens of the genera *Usnea* and *Umbilicaria* revealed that photosynthesis was still active at temperatures as low as -20°C (KAPPEN, 1989; SCHROETER *et al.*, 1994, and unpublished results). Low-temperature scanning electron microscopy (LTSEM) is capable of demonstrating the situation of the cells at below zero conditions (SCHROETER and SCHEIDEGGER, 1995). Below -8°C the mycobiont cells are increasingly cavitated, which means that the protoplast has receded and is closely attached to the cell wall. In contrast, the photobiont shrivels strongly but comprises an obviously highly concentrated unfrozen cellular content which fills the whole interior (SCHROETER and SCHEIDEGGER, 1995). Other experiments with variation of the freezing treatments demonstrate that lichen cells will be killed if intracellular ice is formed (KAPPEN and LANGE, 1972).

3. Water Uptake in the Cold

Water is an essential precondition for metabolic activity as was, for instance, demonstrated with a foliose lichen in Greenland (SCHROETER *et al.*, 1991). Because lichens are poikilohydrous systems they strictly depend on moisture from the surrounding atmosphere. Thus, lichens can be activated by rain, fog and dew and even high air humidity ($>80\%$ rh). An interesting observation is, however, that cyanophilous lichens are not able to take up water from the air (LANGE and KILIAN, 1985). In Antarctica cyanolichens are restricted to the moist and mild climate of the maritime region. Cyanolichens are absent in the continental region although free-living *Nostoc* is widely distributed over the continent, living particularly in melt ponds. It is hypothesized that the absence of cyanolichens from the continental Antarctic region is due to their inability to take up water from snow and ice (KAPPEN, 1993; SCHROETER, 1994; SCHROETER *et al.*, 1994).

On the Antarctic continent and in the high Arctic rainfall is a rare event and may occasionally occur in the coastal regions. However, the major source of moisture for lichens is snow and ice. Water in the liquid phase is only provided if melting occurs. Figure 1 depicts the photosynthetic activity of the fruticose lichen *Usnea antarctica* that was hydrated by snowfall. Hydration was maintained in the thalli for about 20

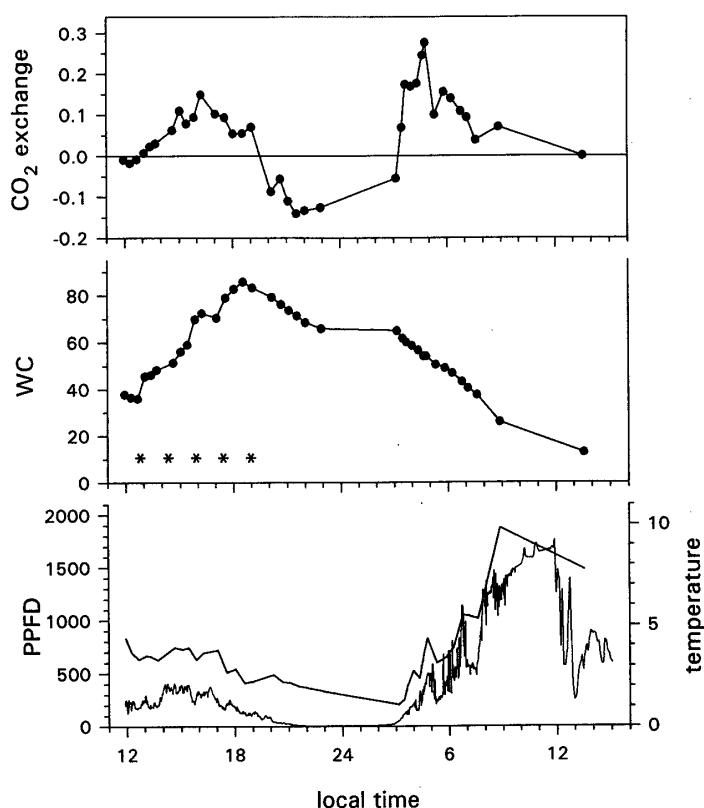


Fig. 1. Net photosynthesis and dark respiration ($\text{mg CO}_2 \text{ mg Chl}^{-1} \text{ h}^{-1}$), water content (WC, % d wt), thallus temperature ($^{\circ}\text{C}$, thick line) and photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{ s}^{-1}$, thin line) of *Usnea antarctica* during December 28 and 29, 1987 on King George Island, South Shetland Islands. Asterisks indicate period of snowfall which resulted in a maximum thallus water content of 87% dry weight. Measurements were taken in situ using a $\text{CO}_2/\text{H}_2\text{O}$ Porometer (Walz, Germany). Thallus water content was determined gravimetrically.

hours in this maritime Antarctic habitat. —In continental Antarctica rehydration of epilithic lichens can be observed on inclined or vertical rock walls where meltwater trickles down from time to time. Recently, the authors in cooperation with Dr. T.G.A. GREEN (New Zealand) and Dr. R.D. SEPPELT (Australia) were able to trace the influence of the edge of a few centimeters deep snow layer on crustose lichens such as *Buellia frigida* in southern Victoria Land (Fig. 2). With measurements extended over several diurnal courses the potential photosynthetic activity of the thalli was detected by the chlorophyll-*a*-fluorescence. We used a PAM-2000 fluorometer (Walz, Germany) that records several parameters of chlorophyll-*a* fluorescence (see SCHROETER *et al.*, 1992). A preliminary evaluation of the data indicates that photosynthetic activity is restricted to brief periods of melt along the fringe of the snow layer around noon. This shows that on a rock face within extended patches of lichen thalli only a small fraction of the lichens became activated in one event (SCHROETER, GREEN, KAPPEN and SEPPELT; unpublished).

Like other lichens that have green-algal photobionts, Antarctic lichens are able to take up water vapor from air if its moisture content is near saturation ($>90\%$ rh) (KAPPEN and REDON, 1987). Air-dry, inactive thalli of *Usnea sphacelata* (KAPPEN,



Fig. 2. Members of the field party in Granite Harbour, southern Victoria Land, measure chlorophyll-a fluorescence in thalli of *Buellia frigida*, bordering a snow patch (in front) on a southeast-exposed siliceous rock (December 1994).

1989) or *Umbilicaria aprina* (SCHROETER *et al.*, 1994) can regain metabolic activity at temperatures below 0°C if they were freshly covered by snow crystals. Field and laboratory experiments which carefully prevented any melting have revealed that the lichens must be able to take up water vapor from the snow crystals that touch the thallus or surround the thallus at a small distance. Transport of water vapor into the thallus can be explained if the water vapor pressure gradient between ice and the dry thallus is considered. Since we know from other studies that lichens start photosynthesizing at water potentials around -30 MPa (NASH *et al.*, 1990), a potential gradient of -15 to -20 MPa corresponding to freezing temperatures between -17 and -20°C should be no problem (KAPPEN, 1993). Experiments in the laboratory showed that *Umbilicaria aprina* was able to take up 21% water per dry weight at -14°C, which allowed a photosynthetic rate that was 4% of that what was

gained at -5°C when the lichen was able to absorb more than 50% water per dry weight of the thallus (SCHROETER and SCHEIDEGGER, 1995).

4. Seasonal Distribution of Lichen Productivity

A deep snow layer may be protective against temperature oscillations in winter but may be too thick for light penetration to the lichen thalli under the snow. However, a snow layer of less than 40 cm can provide photosynthetic activity in early spring as has been demonstrated with measurements in May in the mountain tundra of northern Sweden (SOMMERKORN, 1993). Water content of *Cetraria nivalis* reached values between 150 and 250% d wt under a snow layer of 35 cm which is optimal for photosynthesis at temperatures around 0°C . In a time series, photosynthetic photon flux densities and temperatures were measured under a receding snow bank that initially was 35 cm deep and reached 0 cm after 5 days. The calculated photosynthetic yield was considerable (KAPPEN *et al.*, 1995).

The summer season in the continental Antarctic and the high Arctic region is preponderantly poor in precipitation. Consequently lichens are dry for longer periods of time although they may receive plenty of light and heat (KAPPEN and BREUER, 1991). We assume therefore that the most productive periods of the year for lichens are spring to early summer and fall, and to some degree also those parts of the winter which have enough light to provide photosynthetic activity.

In order to prove this hypothesis we have established a station that automatically and continuously records thallus temperature, photosynthetic photon flux density, relative air humidity and chlorophyll-*a* fluorescence as a measure of metabolic activity. By means of a photosynthesis model we are able to calculate the amount of photosynthetic carbon gain and respiratory carbon loss. The values will be an estimate as long as we cannot define the degree of thallus moisture. At the moment a positive fluorescence signal is always counted as the optimally water saturated photosynthetic rate (or respiratory rate). After finishing a third year of recordings in a maritime Antarctic lichen habitat on Livingston Island, South Shetland Islands, we will be able to estimate the seasonal variations as well as the differences between annual carbon balances.

References

- KAPPEN, L. (1988): Ecophysiological relationships in different climatic regions. CRC Handbook of Lichenology 2, ed. by M. GALUN. Boca Raton, CRC Press, 37–100.
- KAPPEN, L. (1989): Field measurements of carbon dioxide exchange of the Antarctic lichen *Usnea sphacelata* in the frozen state. *Antarct. Sci.*, 1, 31–34.
- KAPPEN, L. (1993): Plant activity under snow and ice, with particular reference to lichens. *Arctic*, 46, 297–302.
- KAPPEN, L. AND 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. AND LANGE, O. L. (1970): The cold resistance of phycobionts from macrolichens of various habitats. *Lichenologist*, 4, 289–293.
- KAPPEN, L. AND LANGE, O. L. (1972): Die Kälteresistenz einiger Makrolichenen. *Flora*, 161, 1–29.

- KAPPEN, L. and REDON, J. (1987): Photosynthesis and water relations of three maritime Antarctic lichen species. *Flora*, **179**, 215–229.
- KAPPEN, L., SOMMERKORN, M. and SCHROETER, B. (1995): Carbon acquisition and water relations of lichens in polar regions—potentials and limitations. *Lichenologist*, **27**, 531–545.
- LANGE, O. L. and KILIAN, E. (1985): Reaktivierung der Photosynthese trockener Flechten durch Wasserdampfaufnahme aus dem Luftraum: Artsspezifisch unterschiedliches Verhalten. *Flora*, **176**, 7–23.
- NASH III, T. H., REIMER, A., DEMMING-ADAMS, B., KILIAN, E., KAISER, W. M. and LANGE, O. L. (1990): The effect of atmospheric desiccation and osmotic water stress on photosynthesis and dark respiration of lichens. *New Phytol.*, **116**, 269–276.
- 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. and SCHEIDEGGER, C. (1995): Water relation 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., JACOBSEN, P. and KAPPEN, L. (1991): Thallus moisture and microclimatic control of CO₂ exchange of *Peltigera aphthosa* (L.) Willd. on Disko Island, West Greenland. *Symbiosis*, **II**, 131–146.
- SCHROETER, B., GREEN, T. G. A., SEPELT, R. D. and KAPPEN, L. (1992): Monitoring photosynthetic activity of crustose lichens using a PAM-2000 fluorescence system. *Oecologia*, **92**, 457–462.
- SCHROETER, B., GREEN, T. G. A., KAPPEN, L. and SEPELT, R. D. (1994): Carbon dioxide exchange at subzero temperatures. Field measurements on *Umbilicaria aprina* in Antarctica. *Cryptogam. Bot.*, **4**, 233–241.
- SOMMERKORN, M. (1993): Die Rolle der frühjährlichen Schneebedeckung für den Kohlenstoffhaushalt von *Cetraria nivalis* (L.) Ach und *Cetraria delisii* (Bory) Th. Fr. an einem subarktisch-alpinen Standort. Diploma thesis, University of Bonn.

(Received January 23, 1996; Accepted February 19, 1996)