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Summer activity patterns of Antarctic and high alpine lichen-dominated biological soil crusts—Similar but different?

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A B S T R A C T

Biological soil crusts (BSCs) are small-scale communities of lichens, mosses, algae, and cyanobacteria that cover much of the surface area in regions where vascular plant growth is restricted due to harsh environmental conditions, such as perpetually ice-free areas in terrestrial Antarctic environments and alpine areas above the tree line. To our knowledge, none of the available studies provides a direct Antarctic-alpine comparison of BSC activity periods and the water use, both key traits to understand their physiological behavior and therefore related growth and fitness. Here, activity patterns and water relations were studied at two sites, one in continental Antarctica (Garwood Valley 78°S) and one in the High Alps of Austria (Hochtor, Großglockner 2350m). BSCs in continental Antarctica were only rarely active, and if so, then during melt after snowfalls and by fog. In the Austrian Alps, BSCs were continuously active and additionally activated by rainfall, fog, and dew. Consequently, high alpine BSCs can be expected to have much higher photosynthetic productivity supporting higher growth rates than the same functional vegetation unit has in continental Antarctica.

INTRODUCTION

Biological soil crusts are important ecosystem engineers in harsh terrestrial habitats where higher plants' growth is limited or even not possible. The major feature, which enables BSCs to colonize open soil in such habitats, is the poikilohydric lifestyle characterizing all of the assembling species, lichens, mosses, algae, and cyanobacteria. These organisms may, besides using liquid water, also use other sources of water, such as water vapor or fog, which is not available for higher plants. In hot deserts, such as the Namib Desert, they require only very low amounts of liquid water to reach optimal photosynthesis (Lange et al., 1994) and, for example, fog can be used as a water source for thallus

rehydration (Lange et al., 2006). In addition dewfall can also be a primary controlling factor for activation as shown for lichen communities in the Negev Desert under natural conditions (Veste et al., 2001).

BSCs not only occur in warm or hot deserts, but are also major components of vegetation in cold regions like the Arctic (Liengen, 1999; Hansen, 2003; Breen and Levesque, 2008; Yoshitake et al., 2010; Williams et al., 2014) or the Antarctic (Green and Broady, 2003; Colesie et al., 2014). BSCs also occur, but are much less studied, in high alpine areas all over the world—for example, equatorial Andes (Pérez, 1997); Olympic Mountains, Washington, U.S.A. (Gold et al., 2001); and Austrian Alps (Türk and Gärtner, 2003; Peer et al., 2010; Zheng et al. 2014). The polar and alpine

habitats have several features in common: they begin where trees disappear from the vegetation, are commonly stated to have a mean temperature of the warmest month below around 10 °C (Körner, 1998), and are characterized by cold temperatures and snowfall in winter. Besides these general environmental similarities (Billings, 1973), there are also biological details underlining analogy. There is an especially interesting subset of lichens, the circumboreal–high mountains–circumpolar lichens, which are found not only in both polar regions, but also in the alpine environments of the temperate regions. This group contains some of the better-known lichens such as *Xanthoria elegans*, *Usnea sphacelata*, or *Pseudophebe miniscula* (Øvstedal and Smith, 2001). In addition to those lichens, there are also representatives of the algal functional group in BSCs that are underlining the link between these environmentally similar, but geographically very distant systems. Phylogenetic and biogeographic analyses have demonstrated that the dominant algae in culture-independent surveys of soil samples from the Dry Valleys, Antarctica, and the high Himalaya were from the same clade (Schmidt et al., 2011).

It is to be expected that organisms growing in these areas share similar ecophysiological features enabling them to survive under the harsh conditions. In the same context, Green (2008) poses the question as to what selection is occurring so that only a small group of lichens can occupy the more extreme areas. As the most likely environmentally controlled parameter, the author suggests changes in the length of the active time of the lichens mainly influenced by local water availability. Such differences in water availability have already been described to have crucial effects on recovery of continental Antarctic lichens (Schlensog et al., 2004) and overall active time (Schlensog et al., 2013). Schroeter et al. (2010) and Raggio et al. (2015) described activity periods of lichens in Antarctica using qualitative chlorophyll fluorescence and found that temperature conditions during activity are not very different between sites in continental and maritime Antarctica, while the total amount of active days differed significantly. Published quantitative in situ measurements of Antarctic lichens and mosses are focused on the photosynthetic response to different light (Schro-

eter et al., 2012) and water availability conditions (Kappen and Breuer, 1991). In a long-term study on the physiological response of the fruticose lichen *Usnea sphacelata* it was shown that both factors can influence daily activity patterns (Kappen et al., 1991). Additional studies cover short time periods (Sancho et al., 1997; Kappen and Redon, 1987; Kappen, 1990, 2000) or refer more to differences in snow resistance between higher plants and lichens (Kappen, 1993) than to possible water sources and activity periods within the lichens. Contributions to the knowledge about photosynthetic activity of alpine lichens have been made by Lange (1965), Heber et al. (2000), Reiter and Türk (2000a, 2000b), and Reiter et al. (2006). However, detailed knowledge about lichen activity under natural conditions is, to our knowledge, rare (e.g., Reiter et al., 2008). The authors focus on rock inhabiting species (*Brodoa atrofusca* and *Xanthoria elegans*) and additionally compared the alpine and maritime Antarctic environments using standard meteorological data, showing much higher precipitation and light in the Alps and much more stable conditions in maritime Antarctica.

To our knowledge, none of the available studies compares in situ activity periods and water use from BSCs in polar regions with those from high alpine regions. In this study, we aimed to determine general activity patterns and the in situ sources for thallus hydration activating positive net photosynthesis of BSCs from these regions. As possible water sources we suggest snow, rain, fog, dewfall, and soil water, which have all been described to influence BSC photosynthesis (Lange, 2003a). Understanding these features may be a step toward understanding of the physiological capacity of BSCs in Antarctic and alpine habitats, both regions suggested to be particularly vulnerable (Robinson et al., 2003; Theurillat, 1995) in recent climate change scenarios (<http://www.ipcc.ch>).

MATERIAL AND METHODS

Activity patterns (chlorophyll fluorescence and CO₂ exchange), microclimate, and modes of hydration were studied at two different sites, one in continental Antarctica and one in the European Alps.

Site Descriptions

Site Garwood (Continental Antarctica)

The research site was in Garwood Valley, Dry Valleys region, Southern Victoria Land (78°2'S, 164°7'E) and measurements were made for 29 days from 14 December 2009 until 18 January 2010. The valley is dominated by outcrops of granites and gneisses, together with amphibolites, marble, and dolomites. This location is characterized as a cold desert with mean temperatures of about -4.2 °C in summer and -21 °C in winter. The amount of precipitation is around 50 mm rain equivalent each year and falls as snow. BSCs have a mean coverage of 3.3% and are composed of all functional groups of photoautotrophic cryptogams (lichens, mosses, green algae, and cyanobacteria). The dominating chlorolichens are *Lecanora expectans* Darb. and *Caloplaca darbishirei* (Hoffm.) Th. Fr. (Colesie et al., 2014).

Site Hochtör (Austrian Alps)

The second research site was in the Austrian Alps at Hochtör in the National Park Hohe Tauern, Austria (47°05'N, 12°50'E), and measurements took place for 10 days from 25 July until 3 August 2012 during the snow-free period. The elevation of the study sites ranged from 2500 to 2600 m, mean precipitation is 2000 mm, and mean air temperature ranges from -10 to -8 °C in January to 2 to 4 °C in July. Seventy to eighty percent of the precipitation falls as snow and snow cover lasts 270 to 300 days (Auer et al., 2002). This site has siliceous and calcareous bedrocks with the siliceous situated within the Brennkogel formation (B1 and B2) and the calcareous within the Seidlwinkl Triassic formation (Plattenkar, Schareck). BSCs cover a major proportion of the local vegetation and are composed of a large variety of different species from all functional groups (Peer et al., 2010; Zheng et al., 2014).

MICROCLIMATE MEASUREMENTS

Site Garwood

General climate conditions (relative humidity, solar radiation, temperature) were simultaneously logged during the whole measuring

period at a sampling interval of 5 minutes by an automatic weather station (AWS) located close to the measuring tent. Air temperature and relative humidity were measured 1 m above ground, and solar radiation at 3 m above ground (<http://nztabs.ictar.aq/science-weather.php>). Data are generously given by nzTABS (<http://nztabs.ictar.aq>).

Site Hochtör

General climate conditions (photosynthetic active radiation [PAR], temperature) were logged simultaneously with each gas exchange measurement using the sensor technology of the gas exchange device itself.

Sampling

Site Garwood

Samples of two lichen-dominated soil crusts were collected on 8 December 2009 (one additional sample was taken on 16 December 2009) and placed in 4.7 cm² CO₂ inert small plastic bowls maintaining their natural arrangement. When not being measured, the samples were placed nearby on the ground similar to their natural exposure.

Site Hochtör

Three samples of lichen-dominated soil crusts (*Psora decipiens*) were collected on 24 July 2012 and treated in the same way as in Garwood Valley.

Chlorophyll Fluorescence of PS II

Site Garwood

The activity status of the crusts was monitored twice a day by Chl_a fluorescence using pulse amplitude modulated fluorometer (IMAGING-PAM; H. Walz, Effeltrich, Germany). Maximum quantum yield of photosystem II (PSII) (F_v/F_m) was measured according to Bilger et al. (1995). Additional activity measurements were made whenever the local climate suggested potential activity in the BSC (snowfall, snowmelt, fog) and CO₂ exchange measurements were made whenever the photosynthetic yield values were higher than 0.2.

Site Hochtör

Here, samples always appeared wet and active, and this indication was supported by overall wet weather conditions, so no prior check for activity using Chl_a fluorescence measurements were necessary and CO₂ exchange measurements were made continuously every day.

CO₂-Gas Exchange

Site Garwood

Whenever chlorophyll fluorescence measurements indicated activity, CO₂ gas-exchange was measured and quantified simultaneously with a portable CO₂/H₂O gas exchange system (HCM-1000; Walz, Effeltrich, Germany) under ambient conditions. After each measurement of photosynthesis in the light, the cuvette was covered with a black sheet in order to obtain dark respiration rates. The measuring period was from 14 December 2009 until 18 January 2010, with one week interruption from 1 January to 8 January.

Site Hochtör

Gas exchange measurements at Site Hochtör were made every day starting in the morning before dawn and ending in the evening after sunset. Measurements were made with a portable CO₂/H₂O gas exchange system (GFS 3000; Walz, Effeltrich, Germany) under ambient conditions. At least two measurements were made in complete darkness (before dawn and late evening) in order to obtain dark respiration values. The measuring period lasted for two weeks and all possible water sources (rain, fog, dewfall, water vapor, snow, and soil humidity) occurred at least once. Water content of the samples was calculated by weighing after each measurement and determining the dry weight after the end of the measurements (3 days over silica gel).

Lichen Rhizine Water Uptake

Water uptake by the lichen (*Psora decipiens*) via the rhizines was investigated in the laboratory using randomly collected samples from Site Hochtör. First the lichens were cleaned and all the adhering sand was carefully removed. Samples were then sectioned vertically to produce one clean edge. The

samples were then arranged so that the ends of the rhizines were immersed in water stained with blue ink and the water uptake was documented using a video camera (Canon EOS 50D). The speed of water uptake into the algal layer was then calculated. No equivalent experiments were made for the *Caloplaca* species from Garwood Valley, because they lacked rhizines.

RESULTS

Activity Patterns and Photosynthesis

Site Garwood

Activation of the BSC was easily detectable by chlorophyll fluorescence (Fig. 1), and BSCs were active for 34% of the days during total measuring period (Table 1). BSCs were reactivated on five occasions after snowfall events and on five occasions during foggy conditions (Table 1). Highest CO₂ uptake was measured on days following snowfall events (Fig. 2), and the longer a snowfall event lasted (accumulating snow), the longer was the resulting activity period during the following melting periods. One snowfall event from 21 to 23 December 2009 resulted in two consecutive active days with positive net photosynthesis. On 16 December 2009 fog and very cloudy conditions led to activity (Fig. 1), but at lower values than by snowmelt, as indicated by both measuring methods (Figs. 1 and 2). On days with sunshine or only scattered cloud cover, no activity was measured either with chlorophyll fluorescence or with gas exchange (Fig. 1, first row; Fig. 2). Activity was not obviously correlated with temperature (graph not shown).

Site Hochtör

BSCs were active on every day during the measuring period (Table 1), and hydration was by foggy conditions on 4 days and by dew and rain on 3 days each (Table 1). Highest CO₂ uptake rates took place while the samples dried out after a rainfall event (Fig. 3), indicating that net photosynthesis was depressed at high thallus water contents (Fig. 4). The duration of rain had no influence on the maximum net photosynthesis and rates after one day of rain (26 July 2012) were similar to those after a long rain period (28 to 31 July 2012). During the rain events net photosynthesis was low while respiration rates were at

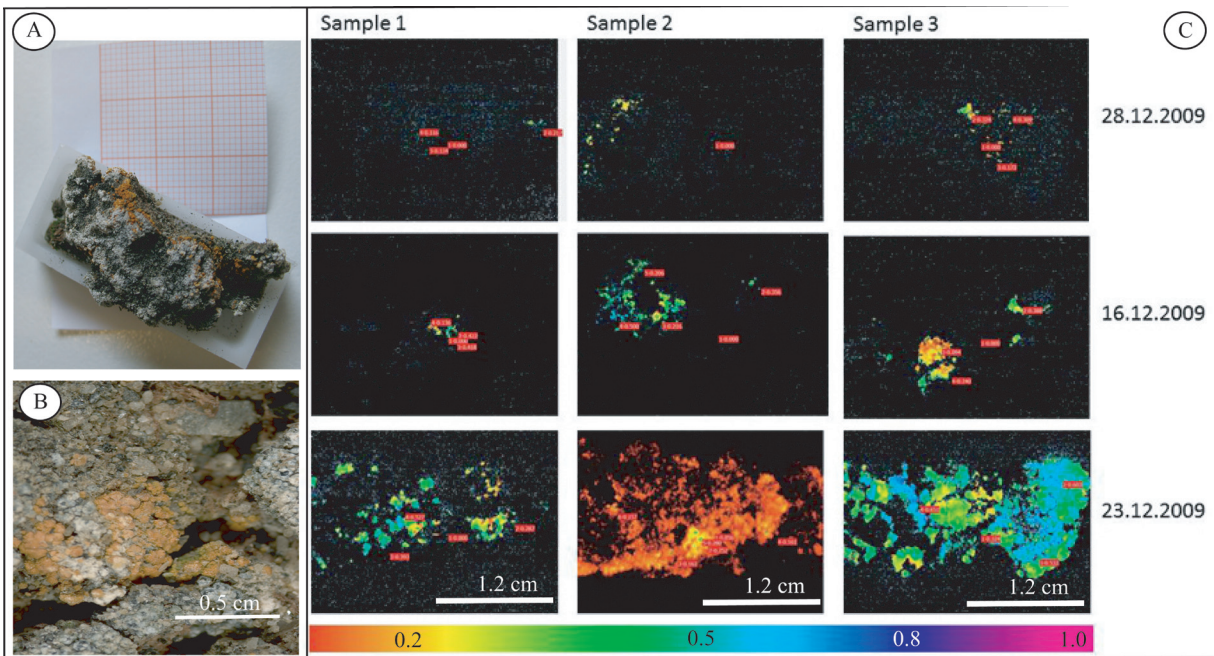


FIGURE 1. (A) Photograph of one original sample placed in 4.7 cm² CO₂ inert small plastic bowls while maintaining their natural arrangement. (B) Close-up of the same sample. The measured biological soil crust (BSC) is a conglomerate of several lichen thalli [*Lecanora expectans* Darb. and *Caloplaca darbishirei* (Hoffm.) Th. Fr.]. (C) False color chlorophyll fluorescence images of the effective quantum yield (Y) of photosystem II distribution over three 4.7 cm² samples from continental Antarctica (Site Garwood), obtained using an Imaging Pulse Amplitude Modulated Fluorometer (PAM) (Walz GmbH, Effeltrich, Germany). Yield intensity is color coded covering a range from 0.0–1, with red indicating very low values and violet high values. Each column represents one individual sample. First row: a typical day without activity; second row: a typical activity pattern after short snowfall event; third row: activity pattern during the melting event after three days of continuous snow fall. Red flags indicate Yield values at a chosen area of interest in the picture. Dates are given as dd.mm.yyyy.

their highest. The samples were also activated during misty and foggy conditions (25 July 2012), by hail during a thunderstorm (28 July 2012) and by dewfall (28 July and 1 August 2012, Fig. 3). The samples were inactive for only two short periods of clear sky and strong radiation (morning of 27 July and afternoon of 1 August 2012, Fig. 3).

Water Uptake via Lichen Rhizines

During the first minutes after immersion, only the rhizines were hydrated (Fig. 5), but the water (blue staining) reached the algal layer of the lichen after 17 minutes and could also be seen in the medulla after about 3 hours.

DISCUSSION

The present study shows the summer activity patterns of Antarctic and alpine lichen communi-

ties in BSCs under near-natural conditions. In the Austrian Alps, activity was almost continuous over the entire two weeks of measurements, whereas Antarctic BSCs were only active on 10 days over the 29 day measurement period. BSCs in continental Antarctica were activated by melt after snowfalls and by fog, whereas BSCs in the Austrian Alps were additionally activated by rainfall, fog, and dew.

Snow and Rain as Reactivating Water Sources

Snowfall is the most obvious water supply for the monitored organisms in continental Antarctic cold deserts even in summer. Under the low humidity and cold conditions in these habitats, especially in winter, snow mainly sublimates instead of melts, which limits water availability. However, in summer there were rare events when temperature was high enough and so-

TABLE 1

Comparison of the water sources used for thallus reactivation in situ. Given are the numbers of reactivation events, the total measuring period, and the total days with activity (plus the percentage of the days with activity per total measuring period).

Water source	Hochtor	Hoher Sonnblick*	Garwood Valley	Garwood Valley**	Casey Station***	Botany Bay****
Snow	—	—	5			
Rain	3	1	—			
Fog	4	9	5			
Dew	3	1	—			
Measuring period (d)	10	14	29	4 months	2 months	2 Years
Days with activity (d)	10 (100%)	11 (78%)	10 (34%)	1.7%†	27%	4.6%†

*Data from Reiter et al. (2008).

**Data from Raggio et al. (2015).

***Data from Kappen et al. (1991).

****Data from Schroeter et al. (2010).

†Percentage of total active hours.

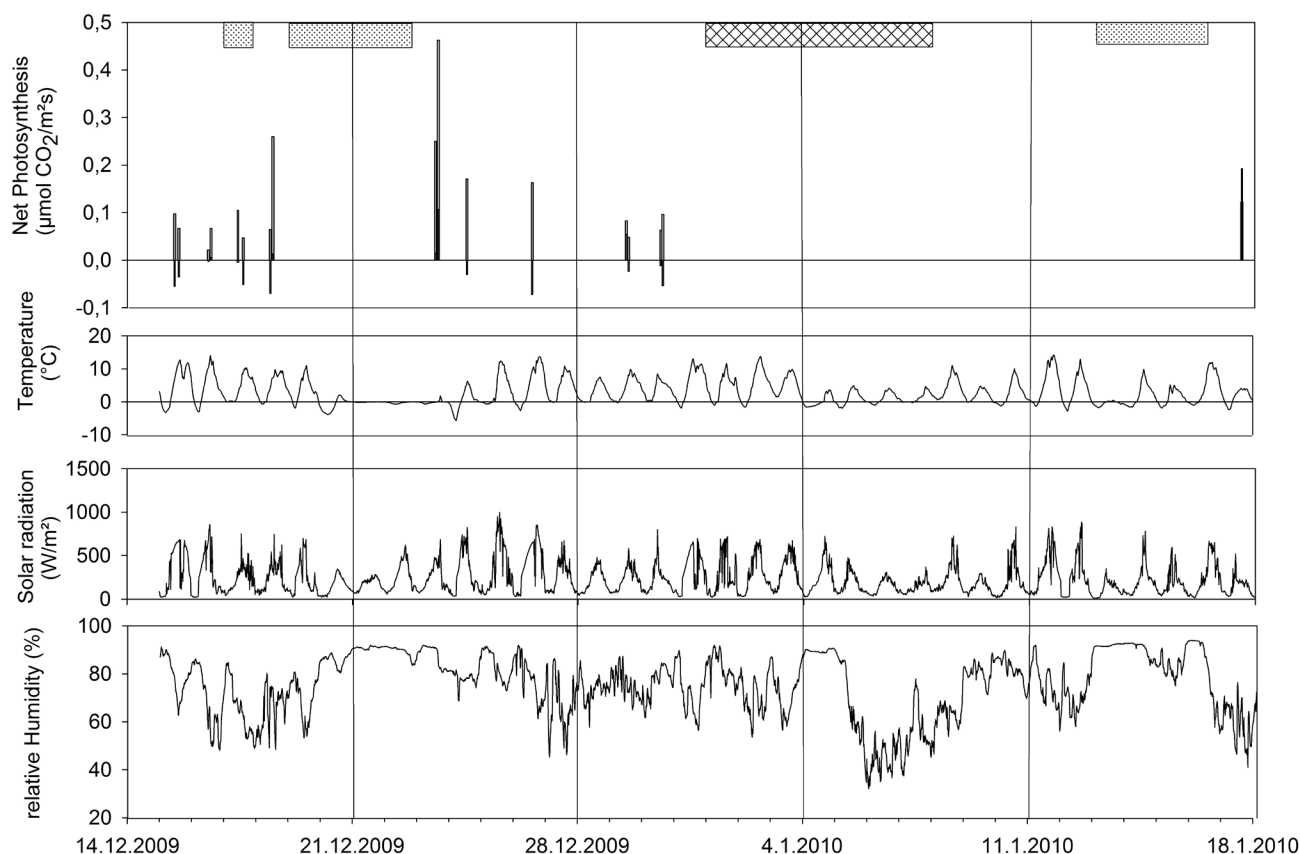


FIGURE 2. Net CO₂-exchange (positive values), dark respiration (negative values, upper panel) and corresponding microclimatic conditions (temperature, solar radiation and relative Humidity, second, third, and lower panels, respectively) from Antarctic BSCs (Site Garwood). Measured from 14.12.2009 until 18.01.2010 with 8 days without gas-exchange measurements between 02.01.2010 and 08.01.2010 (measuring break is indicated with a dark bar). CO₂ exchange (net and dark respiration) is expressed on a surface area basis. Gray bar highlight snow events. Vertical lines delineate the weeks.

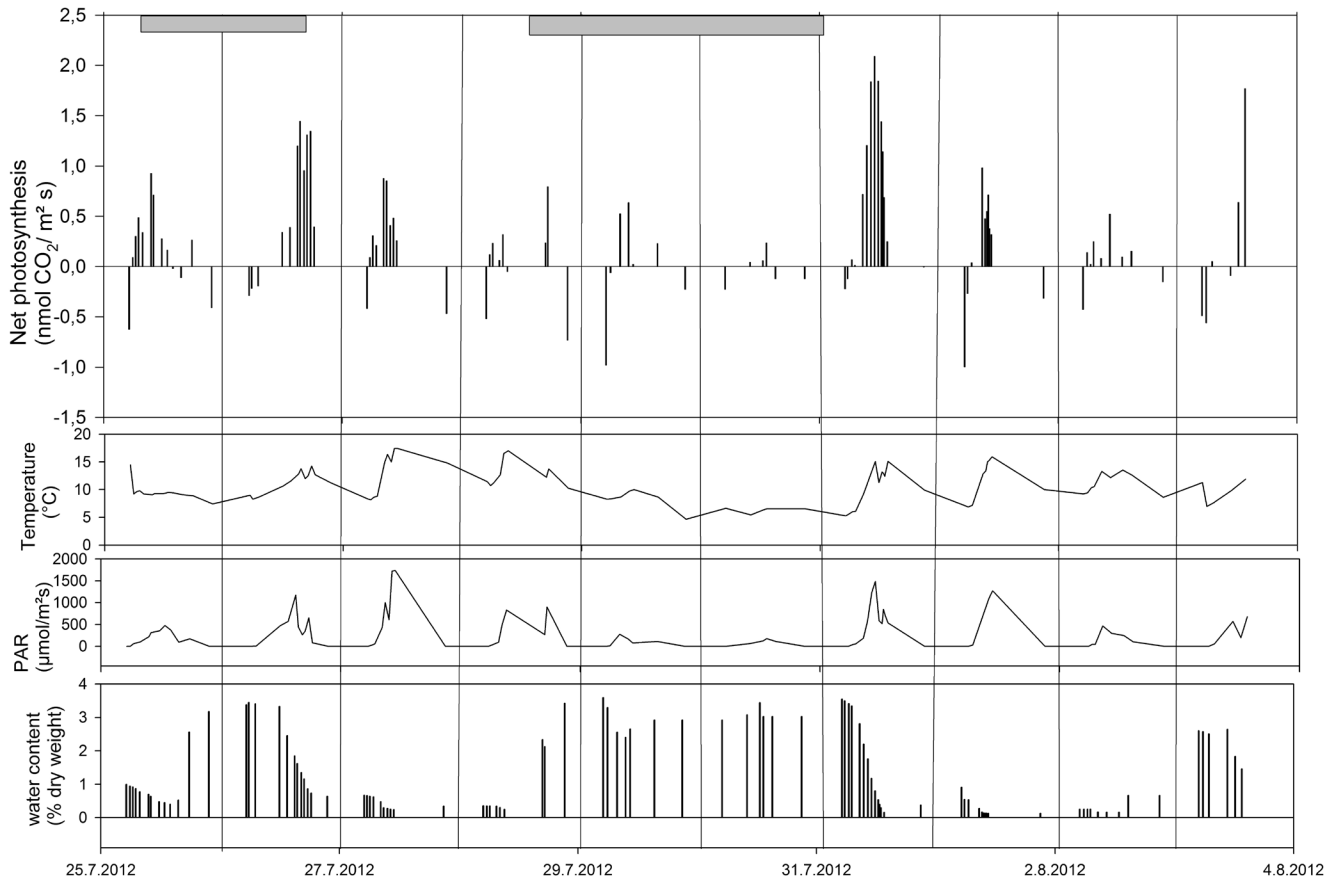


FIGURE 3. Net photosynthesis and respiration (upper row) with corresponding microclimatic conditions (temperature, photosynthetic active radiation (PAR), and water content of the sample, second, third, and bottom rows, respectively) of alpine BSCs (Site Hochtor). Measured from 25.07.2012 until 03.08.2012. CO₂-exchange is expressed on a surface area basis. Gray bars delineate rain events, and vertical lines separate individual days.

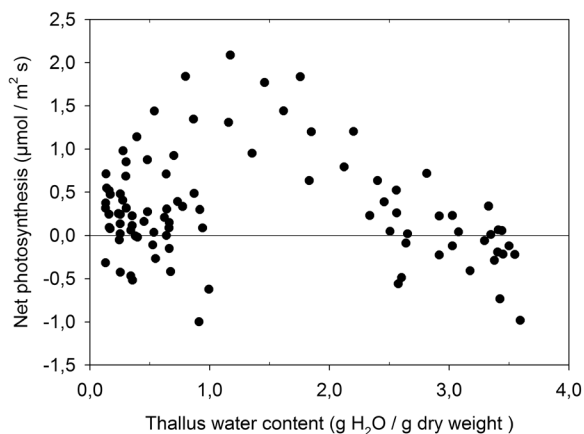


FIGURE 4. The response of net photosynthesis (vertical axis) to thallus water content (horizontal axis) for BSC from Site Hochtor; all data points from in situ CO₂ exchange measurements are plotted.

lar radiation strong enough to generate some snowmelt and we found that snowmelt initiated BSC activity on 50% of the total active

days and resulted in a positive net photosynthesis for a brief time at, or close to the time, the snow disappeared. This agrees with a study by Kappen et al. (1998) who showed the crustose lichen *Buellia frigida* to be activated briefly by melt from the retreating margin of a snowbank. Pannowitz et al. (2003) showed that the majority of activity by lichens did not occur under the snow due to cold temperatures, but over the period when the snow finally melted, although the reactivation process itself may be a species (growth location) specific pattern. Schroeter et al. (2010) found that the overall activity of *Umbilicaria aprina* was strongly related to snowfall at Botany Bay. In contrast to the Antarctic BSCs, snow was not an important source of water for BSCs in the high alpine region, at least during the summer measuring period. Snowmelt may, however, be an important water source during the major melting periods following the win-

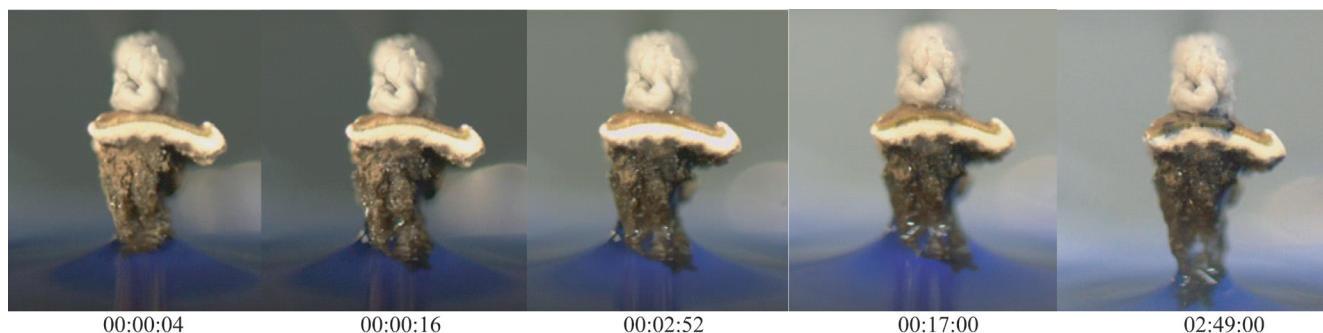


FIGURE 5. Water uptake over the rhizines of *Psora decipiens*. Time after first immersion into ink water is indicated underneath each picture (hh:mm:ss).

ter and can also occasionally occur in summer. From personal observations at our Soil Crust International Project (SCIN) investigation site (2012–2015; see Büdel et al., 2014) at Hochtor in 2600 m altitude, we know that the BSCs there remain under a thick (>40 cm) snow cover extending from the first snow falls, commencing in late September to mid-October until snowmelt at the end of June (Roman Türk and Thomas Peer, University of Salzburg, personal communication).

Rain never occurs at Site Garwood but, during the summer period it is the major source of water for thallus hydration in the high alpine region. The major activity period and the highest maximum net photosynthesis values in the Alps were reached after rainfall events in a manner equivalent to meltwater hydration after snowfall in continental Antarctica. The brief period of high net photosynthetic rates during drying after a rainfall event indicates that net photosynthesis was depressed at the high thallus water contents that occurred during and immediately after rain events (Fig. 4). Oversaturation with water is a well-described phenomenon severely limiting photosynthetic CO_2 exchange in lichens by increasing CO_2 diffusion resistance (Lange et al., 1993). This phenomenon can be more easily detected with quantitative gas exchange measurements than with chlorophyll fluorescence measurements (Lange et al., 1996), a fact confirming the method applied here. Optimal thallus water content and maximum photosynthesis rates can only be found during the following drying (Lange, 2003b). When rain fell at night, there were high rates of respiration and the same pattern of net photosynthesis occurred after dawn during the early morning.

Fog as a Reactivating Water Source

In addition to thallus hydration by snow and rain, reactivation by fog can also be an important ecological feature under arid conditions with restricted moisture supply (Lange et al., 1986). A characteristic brief peak of photosynthetic activity after sunrise following nocturnal moistening by fog is well described and documented for the multi-branched, fruticose lichen *Teloschistes capensis* in the Namib fog desert by Lange et al. (2006) and for other soil crust lichens as described by Lange et al. (1994). This typical response pattern is also reported from arid and semiarid desert habitats (Kappen, 1988), from mediterranean habitats (Lange et al., 1985), and under temperate conditions (e.g., Lange, 2003b). In this study, the BSCs from Antarctica were reactivated (50% of the total reactivation events) in very foggy conditions, corresponding with results found for *Usnea sphacelata* having most efficient photosynthesis when the sky is overcast (Kappen et al., 1991). In the High Alps, fog was the main water source reactivating BSCs on 4 out of 10 days with activity (Table 1). Here, fog not only reactivated the lichens, but also led to ongoing activity during continuing foggy conditions over several days. Due to the lower light availability during such events, the net photosynthesis was generally lower than during drying events after rainfall or snowmelt, respectively.

Dew as a Reactivating Water Source

Also dewfall is known as an important water source for reactivation of BSC (Lange et al., 1994). The importance of dewfall for Antarctic endolithic cryptogams was shown by Büdel et al. (2008),

who found that rock surface temperature fell below the dew point of the air, and water (rime) was deposited inside the rock pores, which then reactivated endolithic cyanobacteria as temperatures rose in the morning. Dew never reactivated the BSCs at the Antarctic site, and this contrasts with BSCs from the High Alps where dewfall reactivated BSCs on 30% of the total reactivation events. Typically, nocturnal hydration by dew caused dark respiration, which was followed after sunrise by a short period of positive net photosynthesis that continued until metabolic inactivation from desiccation.

Influences of Soil Water Content on Lichen Activity

Soil water content measurements were initially not a part of this study because, in continental Antarctica the cold climatic conditions mean the soil water is mostly frozen and therefore considered not to be available. Additionally, studies from the Brown Hills suggest a very low amount of soil water, around 2% rising to about 4.5% when the snow was present and declining again as soon as the snow had disappeared. This increase in soil water content probably reflected a transfer of water vapor, rather than the formation of liquid water, as soil temperatures were always below 0 °C (Colesie et al., 2014). Taking this into consideration, a reactivation of BSC lichens by soil moisture itself seems very unlikely for Antarctic BSCs. A comparative experiment, such as water uptake via lichen rhizines, is not possible because of the lack of rhizines in *Caloplaca darbishirei*. We suggest there is a very different situation in the high alpine site where soil water content is significantly higher. It is known that a substantial lichen crust cover establishes with moderate snow cover along a snow-cover-soil-moisture gradient along mountain ridges in Colorado (Flock, 1978). We suggest that soil water also influences the activity of high alpine BSC through a transfer of liquid water from the soil to the lichen. For *Psora decipiens*, we were able to show that water can be transferred via rhizines into the algal layer (Fig. 5). This feature opens an additional source of water for thallus hydration to the lichens and may offer new insights into the ecology of *Psora decipiens*-dominated BSC from other habitats as well.

The Alpine-Nival Environment in Comparison with Continental Antarctica

Reiter et al. (2008) compared the alpine and maritime Antarctic environments using standard meteorological data and suggested the main differences to be the much higher precipitation and light in the Alps and much more stable conditions in the maritime Antarctic. The comparison made in the present study benefits from measurements of in situ activity and microclimate data from BSCs at the alpine and Antarctic sites and allows a more informed comparison.

The most obvious difference during summer between the two sites is the overall active time itself. Lichens in the Austrian Alps seem to be active on most days, while those from continental Antarctica rarely show any activity (Table 1). The difference is probably much greater if we include the winter period. Lichens in continental Antarctica are inactive over about 8 months of the winter (Schroeter et al., 2010).

Reactivation during foggy and very cloudy conditions seems to be a common feature for BSCs in both ecosystems, where it caused 50% of the reactivation events in Garwood Valley, 40% at the Hochtort, and 64% at the Hoher Sonnblick (Reiter et al., 2008; Table 1). These conditions always coincided with low light availability and therefore resulted in low, but positive net photosynthesis. Reiter et al. (2008) categorized these days as Type 1 days, and those were days when the lichens were wet all day and had some of their least productive periods, as photosynthesis was severely depressed by high water content in addition to low light availability.

The two sites differed in activation by snow, which only occurred at Site Garwood and where it caused 50% of the reactivation events. On the other hand, dewfall as water source for thallus hydration occurred in the Alps but not in continental Antarctica, where the lack of contact with cold subsurface does not promote dewfall events in BSCs.

Some shortcomings in the sampling and measuring design have to be considered when evaluating the data. Due to external factors such as equipment availability in the field, the climatic data of this study were taken with different devices. The data available from the Antarctic site were origi-

nally taken for overall climatic description of the valley conditions with energy sensors, so that light is reported in $W\ m^{-2}$. Recalculations from $W\ m^{-2}$ to PAR in $\mu E\ m^{-2}\ s$ cannot be easily done, due to the wavelength specific information given in PAR. Additionally, rH was not available for site Hochtor. In order to avoid rapid drying of the sample during the measurement, rH inside the cuvette was regulated at 85%.

General Conclusions

For the BSCs examined in this study, there are two obvious features that are shared. First, carbon gain is highest at both locations on those days when the thalli are drying out and are able to photosynthesize for at least a short time at near-optimal or optimal water content. Second, under foggy conditions the lichens are active but the maximal net photosynthesis values are low. Other than snow/rain or fog, no other sources for thallus hydration could be shown for BSCs in continental Antarctica. However, in the High Alps, BSC apparently benefited from dewfall and soil water.

Taking these results into account we suggest that high alpine BSC can be expected to have much higher photosynthetic productivity than the same functional unit in continental Antarctica. This suggestion is also supported by the much higher maximal photosynthetic rates under optimal conditions for BSC in the Alps. Both of these effects, the lower maximum net photosynthesis rates and restricted active time, would contribute to the lower growth rate for Antarctic BSC.

Knowledge about BSC performance in the cold may be suitable for modeling of lichen carbon budgets in continental Antarctica. Studies like Schroeter et al. (2011) provide excellent information about lichen activity over several years measured with chlorophyll fluorescence. Such information could now be combined with quantitative carbon fixation and thus be a baseline for measuring growth in one of the harshest and least accessible regions of the world. Our comparison between alpine and continental Antarctic sites fits well to the results from Sancho et al. (2007) and Raggio et al. (2015) showing significant differences in growth rates and active time exist between the warm and moist maritime Antarctic sites and the dry and cold Dry Valleys.

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REFERENCES CITED

- Auer, I. R., Böhm, M., Leymüller, S., and Schöner, W., 2002: Das Klima des Sonnblicks—Klimaatlas und Klimatographie der GAW Station Sonnblick einschließlich der umgebenden Gebirgsregion. *Österreichische Beiträge zur Meteorologie und Geophysik*, 28: 1–408.
- Bilger, W., Schreiber, U., and Bock, M., 1995: Determination of the quantum efficiency of photosystem II and of nonphotochemical quenching of chlorophyll fluorescence in the field. *Oecologia*, 102: 425–432.
- Billings, W. D., 1973: Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience*, 23: 697–704.
- Breen, K., and Levesque, E., 2008: The influence of biological soil crusts on soil characteristics along a High Arctic glacier foreland, Nunavut, Canada. *Arctic, Antarctic, and Alpine Research*, 40: 287–297.
- Büdel, B., Bendix, J., Bicker, F. R., and Green, T. G. A., 2008: Dewfall as a water source frequently activates the endolithic cyanobacterial communities in the granites of Taylor Valley, Antarctica. *Journal of Phycology*, 44: 1415–1424.
- Büdel, B., Colesie, C., Green, T. G. A., Grube, M., Suau, R. L., Loewen-Schneider, K., Maier, S., Peer, T., Pintado, A., Raggio, J., Ruprecht, U., Sancho, L. G., Schroeter, B., Türk, R., Weber, B., Wedin, M., Westberg, M., Williams, L., and Zheng, L., 2014: Improved appreciation of the functioning and importance of biological soil crusts in Europe: the Soil Crust International Project (SCIN). *Biodiversity and Conservation*, 23: 1639–1658.

- Colesie, C., Gommeaux, M., Green, T. G. A. and Büdel, B., 2014: Biological soil crusts in continental Antarctica: Garwood Valley, southern Victoria Land, and Diamond Hill, Darwin Mountains region. *Antarctic Science*, 22: 115–123, doi <http://dx.doi.org/10.1017/S0954102013000291>.
- Flock, J. W., 1978: Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot Ridge, Colorado. *Arctic and Alpine Research*, 10: 31–47.
- Hansen, E. S., 2003: Lichen-rich soil crusts or Arctic Greenland. In Belnap, J., and Lange, O. L. (eds.), *Biological Soil Crusts: Structure, Function, and Management*. Ecological Studies, Volume 150, Second edition. Heidelberg, Berlin: Springer, 57–66.
- Heber, U., Bilger, W., Bligny, R. and Lange, O. L., 2000: Phototolerance of lichens, mosses and higher plants in an alpine environment: analysis of photoreactions. *Planta*, 211: 770–780.
- Gold, W. G., Glew, K. A., and Dickson, L. G., 2001: Functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains, Washington, USA. *Northwest Science*, 73: 315–326.
- Green, T. G. A., 2008: Lichens in Arctic, Antarctic and alpine ecosystems. In Beck, A., and Lange, O. L. (eds.), *Ökologische Rolle der Flechten. Rundgespräche der Kommission für Ökologie*, Volume 36. Munich, Germany: Verlag Dr. Friedrich Pfeil, 45–66.
- Green, T. G. A., and Broady, P. A., 2003: Biological soil crusts of Antarctica. In Belnap, J., and Lange, O. L. (eds.), *Biological Soil Crusts: Structure, Function, and Management*. Ecological studies, Vol 150, Second edition. Heidelberg, Berlin: Springer, 141–154.
- Kappen, L., 1988: Ecophysiological relationships in different climatic regions. In Galun, M. (ed.), *Handbook of Lichenology*, Volume 2. Boca Raton, Florida: CRC Press, 37–100.
- Kappen, L., 1990: Carbon dioxide exchange of Antarctic crustose lichens in situ measured with a CO₂/H₂O porometer. *Oecologia*, 82: 311–316.
- Kappen, L., 1993: Plant activity under snow and ice, with particular reference to lichens. *Arctic*, 46: 297–302.
- Kappen, L., 2000: Some aspects of the great success of lichens in Antarctica. *Antarctic Science*, 12: 314–324.
- Kappen, L., and Breuer, M., 1991: Ecological and physiological investigations in continental Antarctic cryptogams, 2: moisture relations and photosynthesis of lichens near Casey Station, Wilkes Land. *Antarctic Science*, 3: 273–278
- Kappen, L., and Redon, J., 1987: Photosynthesis and water relations of three maritime Antarctic lichen species. *Flora*, 179: 215–229.
- Kappen, L., Breuer, M., and Bölter, M., 1991: Ecological and physiological investigations in continental Antarctic cryptogams. 3. Photosynthetic production of *Usnea sphacelata*: diurnal courses, models, and the effect of photoinhibition. *Polar Biology*, 11: 393–401.
- Kappen, L., Schroeter, B., Green, T. G. A., and Seppelt, R. D., 1998: Microclimatic conditions, meltwater moistening, and the distributional pattern of *Buellia frigida* on rock in a southern continental Antarctic habitat. *Polar Biology*, 19: 101–106.
- Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115: 445–459.
- Lange, O. L., 1965: Der CO₂-Gaswechsel von Flechten bei tiefen Temperaturen. *Planta*, 64: 1–19.
- Lange, O. L., 2003a: Photosynthesis of soil-crust biota as dependent on environmental factors. In Belnap, J., and Lange, O. L. (eds.), *Biological Soil Crusts: Structure, Function, and Management*. Ecological Studies, Volume 150, Second edition. Heidelberg, Berlin: Springer, 217–241.
- Lange, O. L., 2003b: Photosynthetic productivity of the epilithic lichens *Lecanora muralis*: long-term field monitoring of CO₂ exchange and its physiological interpretation: II. Diel and seasonal patterns of net photosynthesis and respiration. *Flora*, 198: 55–70.
- Lange, O. L., Tenhunen, J. D., Harley, P. C., and Walz, H., 1985: Method for field measurements of CO₂ exchange. The diurnal changes in net photosynthesis and photosynthetic capacity of lichens und mediterranean climatic conditions. In Brown, D. H. (ed.), *Lichen Physiology and Cell Biology*. New York, London: Plenum Press, 23–39.
- Lange, O. L., Kilian, E., and Ziegler, H., 1986: Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia*, 71: 104–110.
- Lange, O. L., Büdel, B., Heber, U., Meyer, A., Zellner, H., and Green, T. G. A., 1993: Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO₂ exchange. *Oecologia*, 95: 303–313.
- Lange, O. L., Meyer, A., Zellner, H., and Heber, U., 1994: Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Functional Ecology*, 8: 253–264.
- Lange, O. L., Green, T. G. A., Reichenberger, H., and Meyer, A., 1996: Photosynthetic depression at high thallus water contents in lichens: concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera* species. *Botanica Acta*, 109: 43–50.
- Lange, O. L., Green, T. G. A., Melzer, B., Meyer, A., and Zellner, H., 2006: Water relations and CO₂ exchange of the terrestrial lichen *Teloschistes capensis* in the Namib fog desert: measurements during two seasons in the field and under controlled conditions. *Flora*, 201: 268–280.
- Liengen, T., 1999: Conversion factor between acetylene reduction and nitrogen fixation in free-living cyanobacteria from High Arctic habitats. *Canadian Journal of Microbiology*, 45: 223–229.
- Øvstedal, D. O., and Smith, R. I., 2001: *Lichens of Antarctica and South Georgia. A Guide to Their Identification and Ecology*. Cambridge: Cambridge University Press.
- Pannewitz, S., Schlenzog, M., Green, T. G. A., Sancho, L., and Schroeter, B., 2003: Are lichens active under snow in continental Antarctica. *Oecologia*, 135: 30–38.
- Peer, T., Türk, R., Gruber, J. P., and Tschalkner, A., 2010: Species composition and pedological characteristics of biological soil crusts in a high alpine ecosystem, Hohe Tauern, Austria. *eco.mont—Journal on Protected Mountain Areas Research*, 2/1: 23–30.

- Pérez, F. L., 1997: Microbiotic crusts in the high equatorial Andes, and their influence on paramo soils. *Catena*, 31: 173–198.
- Raggio, J., Green, T. G. A., and Sancho, L. G., 2015: In situ monitoring of microclimate and metabolic activity in lichens from Antarctic extremes: a comparison between South Shetland Islands and the McMurdo Dry Valleys. *Polar Biology*, doi <http://dx.doi.org/10.1007/s00300-015-1676-1>.
- Reiter, R., and Türk, R., 2000a: Investigations on the CO₂ exchange of lichens in the alpine belt. I. Comparative patterns of net CO₂ exchange in *Cladonia mitis*, *Thamnolia vermicularis* and *U. cylindrica*. In Schroeter, B., Schlenso, M., and Green, T. G. A. (eds.), *New Aspects in Cryptogamic Research*. Contributions in Honour of Ludger Kappen. *Bibliotheca Lichenologia* 75: 333–351.
- Reiter, R., and Türk, R., 2000b: Investigations on the CO₂ exchange of lichens in the alpine belt. II. Comparative patterns of net CO₂ exchange in *Cetraria islandica* and *Flavocetraria nivalis*. *Phyton*, 40: 161–177.
- Reiter, R., Green, T. G. A., Schroeter, B., and Türk, R., 2006: Photosynthesis of three lichens *Umbilicaria* species from lichen-dominated communities in the alpine/nival belt of the Alps measured under controlled conditions. *Phyton*, 46: 247–258.
- Reiter, R., Höftberger, M., Green, T. G. A., and Türk, R., 2008: Photosynthesis of lichens from lichens dominated communities in the alpine/nival belt of the Alps—2: laboratory and field measurements of CO₂ exchange and water relations. *Flora*, 203: 34–46.
- Robinson, S. A., Wasley, J., and Tobin, A. K., 2003: Living on the edge—plants and global change in continental and maritime Antarctica. *Global Change Biology*, 9: 1681–1717.
- Sancho, L. G., Pintado, A., Valladares, F., Schroeter, B., and Schlenso, M., 1997: Photosynthetic performance of cosmopolitan lichens in the maritime Antarctic. *Bibliotheca Lichenologia*, 67: 197–210.
- Sancho, L. G., Green, T. G. A., and Pintado, A., 2007: Slowest to fastest: extreme range in lichen growth rates supports their use as an indicator of climate change in Antarctica. *Flora*, 202: 667–673.
- Schlenso, M., Pannewitz, S., Green, T. G. A., and Schroeter, B., 2004: Metabolic recovery of continental Antarctic cryptogams after winter. *Polar Biology*, 27: 399–408.
- Schlenso, M., Green, T. G. A., and Schroeter, B., 2013: Life form and water source interact to determine active time and environment in cryptogams: an example from the maritime Antarctic. *Oecologia*, 173: 59–72.
- Schmidt, S. K., Lynch, R. C., King, A. J., Karki, D., Robeson, M. S., Nagy, L., Williams, M. W., Mitter, M. S., and Freeman, K. R., 2011: Phylogeography of microbial phototrophs in the dry valleys of the high Himalayas and Antarctica. *Proceedings of the Royal Society*, 278: 702–708.
- Schroeter, B., Green, T. G. A., Pannewitz, S., Schlenso, M., and Sancho, L. G., 2010: Fourteen degrees of latitude and a continent apart: comparison of lichen activity over two years at continental and maritime Antarctic sites. *Antarctic Science*, 22: 681–690.
- Schroeter, B., Green, T. G. A., Pannewitz, S., Schlenso, M., and Sancho, L. G., 2011: Summer variability, winter dormancy: lichen activity over 3 years at Botany Bay, 77°S latitude, continental Antarctica. *Polar Biology*, 34: 13–22.
- Schroeter, B., Green, T. G. A., Kulle, D., Pannewitz, S., Schlenso, M., and Sancho, L. G., 2012: The moss *Bryum argenteum* var. *muticum* Brid. is well adapted to cope with high light in continental Antarctica. *Antarctic Science*, 24: 281–291.
- Theurillat, J. P., 1995: Climate change and the alpine flora: some perspectives. In Guisan, A., Holten, J. I., Spichiger, R., and Tessier, L. (eds.), *Potential Ecological Impacts of Climate Change in the Alps and Fennoscandinavian Mountains*. Geneva: Conservatoire at Jardin Botaniques, 121–127.
- Türk, R., and Gärtner, G., 2003: Biological soil crusts of the subalpine, alpine and nival areas in the alps. In Belnap, J., and Lange, O. L. (eds.), *Biological Soil Crusts: Structure, Function, and Management*. Ecological Studies, Volume 150, Second edition. Heidelberg, Berlin: Springer, 67–74.
- Veste, M., Littmann, T., Friedrich, H., and Breckle, S. W., 2001: Microclimatic boundary conditions for activity of soil lichen crusts in the sand dunes of the north-western Negev desert, Israel. *Flora*, 196: 465–474.
- Williams, L., Borchardt, N., Colesie, C., Baum, C., Komsic-Buchmann, K., Rippin, M., Becker, B., Kartsen, U., and Büdel, B., 2016: Biological soil crusts of Arctic Svalbard and of Livingston Island, Antarctica. *Polar Biology*: doi <http://dx.doi.org/10.1007/s00300-016-1967-1>.
- Yoshitake, S., Uchida, M., Koizumi, H., and Nakatsubo, T., 2010: Production of biological soil crusts in early stage of primary succession on a High Arctic glacier foreland. *New Phytologist*, 186: 451–460.
- Zheng, L. J., Maier, S., Grube, M., Türk, R., Gruber, J. P., and Peer, T., 2014: Alpine biological soil crusts on the Hochtor (Grossglockner high alpine route, Hohe Tauern, Austria): soils, functions and biodiversity. *Acta Zoo Bot Austria*, 150: 175–196.

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