Photosynthesis of Three *Umbilicaria* Species from Lichen-Dominated Communities of the Alpine/Nival Belt of the Alps Measured Under Controlled Conditions

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With 4 Figures

Summary

REITER R., GREEN A. T. G., SCHROETER B. & TÜRK R. 2007. Photosynthesis of three *Umbilicaria* species from lichen-dominated communities of the alpine/nival belt of the Alps measured under controlled conditions. – Phyton (Horn, Austria) 46 (2): 247–258, 4 figures. – English with German summary.

The CO_2 exchange performances of three *Umbilicaria* species, *U. decussata*, *U. cylindrica* and *U. virginis*, were measured as part of a programme looking at adaptations of alpine lichens. Response curves of net photosynthesis (NP) to PPFD (photosynthetic photon flux density, 0 to 1500 μmol m^{-2} s^{-1}) and temperature (–5 to 30 °C) were generated under laboratory conditions. All species showed the typical saturation response of NP to PPFD with saturation being almost reached at 1500 μmol m^{-2} s^{-1}, the highest PPFD used. NP response to temperature had the same general form for all species with depressed values at low and high temperatures. Temperature optima were between 10.9 °C (*U. decussata*) and 12.2 °C (*U. virginis*). At 1500 μmol m^{-2} s^{-1}, NP was still positive, but low, at –5 °C, and for one species even at 30 °C giving a

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very broad temperature range with substantial NP for all the species. The species fitted the general pattern of lower maximal NP for alpine and antarctic *Umbilicaria* species and higher for montane species with the exception of *U. virginis* which behaved more like a montane species. It is possible that this is a result of it being a more shade-adapted species and its exceptional behaviour emphasizes the importance of microclimate in these extreme environments.

Zusammenfassung

REITER R., GREEN A. T. G., SCHROETER B. & TÜRK R. 2007. Photosynthesemessungen unter kontrollierten Bedingungen von drei *Umbilicaria*-Arten flechtendominierter Gesellschaften der alpinen/nivalen Zone der Alpen. – Phyton (Horn, Austria) 46 (2): 247–258, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Im Rahmen eines Programmes über Anpassungen alpiner Flechten wurde der CO_2-Austausch von drei *Umbilicaria*-Arten, *U. decussata*, *U. cylindrica* und *U. virginis* gemessen. Die Abhängigkeitskurven der Nettophotosynthese (NP) von PPFD (photosynthetisch active Strahlungsdichte von 0 bis 1500 µmol m^{-2} s^{-1}) und Temperatur (–5 bis 30 °C) wurden unter Laborbedingungen bestimmt. Alle Arten zeigten die typische Sättigungskurve von NP gegen PPFD, wobei die Sättigung bei der höchsten verwendeten Lichtstärke von 1500 µmol m^{-2} s^{-1} fast erreicht war. Die Temperaturkurve von NP zeigte für alle Arten eine Optimumskurve mit Temperaturoptima zwischen 10.9 °C (*U. decussata*) und 12.2 °C (*U. virginis*). Bei 1500 µmol m^{-2} s^{-1} war NP auch bei –5 °C und bei einer Art sogar bei 30 °C noch immer positiv (wenn auch gering), was einen weiten Temperaturbereich für photosynthetische Produktion bei allen Arten ergab. Die Flechten passten in das allgemeine Bild, das niedrige maximale NP Werte für alpine und antarktische, jedoch höhere für montane *Umbilicaria* Arten erwarten lässt. Nur *U. virginis* verhielt sich eher wie eine montane Species. Dies könnte mit dem Schattencharakter dieser Art zusammenhängen und dieses Ausnahmeverhalten betont die Bedeutung des Mikroklimas unter diesen extremen Umweltbedingungen.

Introduction

Polar regions and the alpine/nival belts of high mountains are extreme environments in terms of temperature, radiation, water availability and wind (for review see FRANZ 1979, KÖRNER 1999). The vegetation of these zones is dominated by cryptogams, especially lichens. In the Alps, for example, there are more than 150 lichen species present in the subnival and nival belts (FREY 1968/69). Arctic-alpine lichens must be adapted to the prevailing severe climatic conditions and the species present do seem to share some characteristics. Dark pigmentation increases with altitude (FREY 1933, 1960) and not only protects against strong light but may also accelerate the melting of a light snow cover by heat absorption (KAPPEN 1988). However, dark coloured lichen thalli do occur elsewhere and this adaptation is not confined to the alpine or polar environment (LONGTON 1988).

The lichen genus *Umbilicaria* is particularly predominant and conspicuous on most siliceous mountains above the summer snowline (GAMS

1960). *Umbilicariaceae* are, for instance, well known from the highest peaks of the Austrian Alps; 3739 m, Weißkugel, Ötztaler Alpen, Austria (PITSCHMANN & REISIGL 1955) and between 3700–3795 m, Großglockner, Hohe Tauern, Austria (FREY 1968/69). *Umbilicaria* thalli also have a particular advantage for ecophysiological studies. Whereas many other lichen thalli might be formed by anastomosis of adjacent individuals, individual *Umbilicaria* plants are easily recognised because of their monophyllous growth form and single central holdfast (LARSON 1979). They also show possible adaptations such as a resistant epinecral layer (POELT 1976). As a first step in an investigation of the in situ performance of alpine lichens it was decided to measure the photosynthetic response of three *Umbilicaria* species, *U. cylindrica*, *U. decussata* and *U. virginis*, under controlled laboratory conditions. It has been reported that this type of study is a good predictor of lichen performance in the field (LANGE & al. 2001). Previous studies have shown that lichens can be active in the alpine zone (BLISS & HADLEY 1964, REITER & TÜRK 2000a,b), that the net photosynthesis rate (NP) of *Umbilicaria* species can be positive and substantial below the freezing point [*Umbilicaria aprina* in continental Antarctic (SCHROETER & al. 1994)], and that alpine species tend to have much lower NP and optimal temperatures for NP than montane species (SANCHO & KAPPEN 1989, SANCHO & al. 2000). It was anticipated that the species studied here would fit this pattern but would also give different responses of NP to light and temperature that reflected their particular habitats and geographical distributions.

Umbilicaria cylindrica (L.) Delise is a polymorphic, circumpolar species also present in temperate areas of the southern hemisphere in Tasmania and New Zealand (NIMIS & POELT 1987, PURVIS & al. 1992). *U. cylindrica* has a wide ecological amplitude; it can be found in very different habitats and is very common in high mountain ecosystems. In Europe it occurs from the arctic to the Middle European zone with a wide altitudinal range from the montane to the nival belt in the Alps, and also in the alpine mediterranean steppe (NIMIS 1993, POELT & VĚZDA 1981, SUPPAN & al. 2000, WIRTH 1995). *U. cylindrica* is part of the alpine achionophytic and weakly chionophytic lichen communities in sun exposed sites, but is not found on overhangs (CREVELD 1981). Well developed *U. cylindrica* was reported from the summit of Finsteraarhorn in Switzerland at 4270 m a. s. l. by FREY 1936.

U. decussata (Vill.) Frey has a bipolar, arctic alpine and boreal distribution, but is restricted more to the alpine/nival belt (POELT 1969, POELT & VĚZDA 1981). In the Alps *U. decussata* is never found at altitudes below the timberline, but occurs frequently 300–400 m higher including the highest peaks e. g. Mt. Rosa at 4350 m (FREY 1936). *U. decussata* is common on high mountains where it grows on wind exposed rocks (SANTESSON 1993) and is mostly found on very steep slopes to slightly overhanging rock faces (CREVELD 1981).

U. virginis Schaerer is an arctic-alpine lichen with a circumpolar distribution and is strictly confined to the nival belt. *U. virginis* is the nival lichen in the Alps par excellence (POELT & VĚZDA 1981) and has never been found below 2700 m in the Alps (FREY 1947). FREY 1933 emphasizes that *U. virginis* always grows in niches and fissures and never in wind exposed habitats. *U. virginis* and *U. decussata* are very achionophytic and less tolerant of late-lying snow (CREVELD 1981, BENEDICT 1990).

More information about the ecological relationships of the three *Umbilicaria* lichens and other alpine nival lichens from the Tauern chains and a comparison with those from other regions in the Alps can be found in FREY 1968/69. A list of lichens which were also found at the collection sites is given in REITER & TÜRK 2001.

Only little is known about the photosynthetic performance of alpine lichens. It is not easy, possibly not justifiable, to extrapolate to the alpine situation from polar studies.

The main objective of this work is to prepare response curves linking net photosynthesis with photosynthetic photon flux density (PPFD) and temperature as a first step to gaining an understanding of the performance of the three selected *Umbilicaria* species. Thus the response of three species from different habitats to light intensity, temperature, thallus water content and humidity is determined under fully controlled conditions in the laboratory, to interpret the daily patterns of *Umbilicaria* species obtained in the field (see REITER & al. unpublished).

A b b r e v i a t i o n s : Chl: chlorophyll, DW: dry weight, LCP: light compensation point, NP: net photosynthesis, PPFD: photosynthetic photon flux density, TCP: temperature compensation point.

Material and Methods

Similarly sized samples of the three *Umbilicaria* species were collected from acidic rocks in the nival belt of the Hohe Tauern, Central Alps of Austria. *Umbilicaria cylindrica* (L.) Delise and *U. decussata* (Vill.) Frey were collected at 3100 m from the east ridge of the Hoher Sonnblick, close to the Meteorological Observatory (Goldberggruppe, 47°03′N, 12°57′E, 8th of September 1999) and *U. virginis* Schaerer at 3400 m from the south ridge of the Kleinvenediger (Venedigergruppe, 47°07′N, 12°21′E, 7th October 1999). After removal from the substrate the samples were transported in an air-dry state to the laboratory at the University of Salzburg, Austria, and then kept frozen in the dark at –15 °C. Three days before measurements, the lichens were reactivated in a climate chamber with a 12/12 h light/dark cycle at 5 °C and 200 µmol m^{-2} s^{-1} PPFD. Every morning the thalli were moistened with deionized water. CO_2 exchange of the lichens was measured with an open flow minicuvette system (CMS-400, Walz, FRG) with the infrared gas analyser (BINOS 100 4P, Rosemount, FRG) operated in the differential mode. The measurements were carried out at optimal water content of the lichens (determined before with separate water content experiments) and under partial pressure of 240 ppm CO_2 (the estimated value for

the Hoher Sonnblick at 3107 m [KÖRNER 1999]) produced by means of a CO_2/N_2 gas mixing unit (GMA–2, Walz, FRG). The light source was a halogen lamp with fibre optics (FL–400, Walz, FRG) with neutral density filters used to alter PPFD. Three replicate thalli were measured for each lichen species and the results averaged. The chlorophyll content for each species was determined as the mean of 5 replicates after 24 h extraction with 80 % acetone and measured by spectrophotometry (Beckmann DU-50 Spectrophotometer, USA) with calculations according to BROWN & HOOKER 1977.
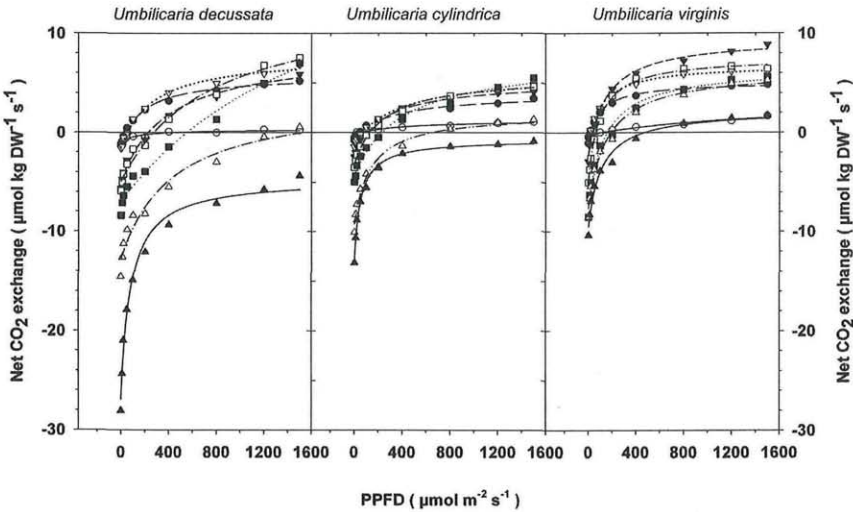
Fig. 1. Dependency of net CO_2 exchange on PPFD at various temperatures (dry weight basis) for *U. decussata*, *U. cylindrica* and *U. virginis* (left, centre and right panels, respectively). Net photosynthesis was measured at optimal water content and each data point represents the mean of 3 replicates. The different temperatures are represented by the following symbols: –5 °C (○), 0 °C (●), 5 °C (▽), 10 °C (▼), 15 °C (□), 20 °C (■), 25 °C (△), 30 °C (▲). SigmaPlot 5.0 (Jandel, USA) was used to create the graphs (all $R^2 > 0.93$).

Results

The response of NP to increase in PPFD for all three species followed the expected saturation curve that is typical for lichens (Fig. 1). Net photosynthesis for all three species were close to light saturation at a PPFD of 1500 µmol photons m^{-2} s^{-1}, the highest PPFD at which measurements were possible, and there was no evidence of any photoinhibitory depression under the experimental conditions. Light compensation point for NP (LCP) showed the expected increase with thallus temperature due to the rise in respiration rate. For *U. cylindrica*, it rose from 50 µmol m^{-2} s^{-1} PPFD at 0 °C to 243 µmol m^{-2} s^{-1} PPFD at 20 °C. The change was 42 to 542 µmol m^{-2} s^{-1} and 19 to 159 µmol m^{-2} s^{-1} PPFD for *U. decussata* and

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U. virginis, respectively over the same temperature range. Overall, *U. decussata* always had the highest LCP and *U. virginis* the lowest over the measured temperature range from –5 to 30 °C.

The response of net photosynthesis to increase in temperature showed a similar pattern for all three species (Fig. 2). All had a clear optimal temperature for NP which rose with increase in PPFD (Fig. 3). For *U. virginis* and *U. cylindrica* this increase was rapid at low temperatures (1.3 °C at 50 µmol m^{-2} s^{-1} PPFD) and tended to a maximum of 11 to 12 °C at around
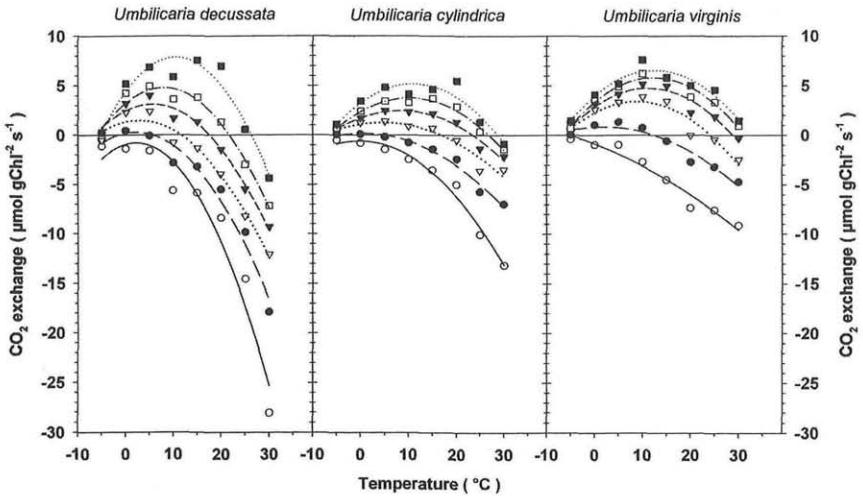

Fig. 2. Dependency of net CO_2 exchange on temperature at various PPFD (dry weight basis) for *U. decussata*, *U. cylindrica* and *U. virginis* (left, centre and right panels, respectively). Net photosynthesis was measured at optimal water content and each data point represents a mean of 3 replicates. The different PPFD are represented by the following symbols: 0 µmol m^{-2} s^{-1} (○), 50 µmol m^{-2} s^{-1} (●), 200 µmol m^{-2} s^{-1} (▽), 400 µmol m^{-2} s^{-1} (▼), 800 µmol m^{-2} s^{-1} (□), 1500 µmol m^{-2} s^{-1} (■). SigmaPlot 5.0 (Jandel, USA) was used to create the graphs (all $R^2 > 0.91$).

up to 800 to 1500 µmol m^{-2} s^{-1}. The situation was probably similar for *U. decussata* but the temperature response results were not so stable. The temperature optima for NP at 1500 µmol m^{-2} s^{-1} were very similar (from 10.9 to 12.2 °C) for all three species with *U. decussata* the lowest and *U. virginis* the highest. All species show substantial depression of maximal NP at 5 °C with *U. decussata* scarcely achieving positive values but, at zero degrees, maximal rates were substantial and above 50% of the absolute maxima usually achieved between 10 °C and 20 °C. The low NP at subzero temperatures was due to inhibition of the photosynthetic pathways however, the depressed NP found for all species at temperatures above around 20 °C were a result of the greatly increased respiration rates at high tem-

peratures. Respiration rates were so high at 30 °C for *U. decussata* and *U. cylindrica* that NP became negative. The upper temperature compensation point for NP (TCP) rose with increasing PPFD and was reached at ca. 30 °C. Over the PPFD range from 50 to 1500 µmol m^{-2} s^{-1}, TCP increased from 4.9 to 26.5 °C for *U. decussata* and from 5.0 to 28.6 °C for *U. cylindrica*. *U. virginis* did not reach TCP at 1500 µmol m^{-2} s^{-1} (the highest PPFD used) but it is calculated to be ca. 32.5 °C. The lower TCP was always below –5 °C and calculated to be around –7.7 °C at 1500 µmol m^{-2} s^{-1} PPFD for all species.
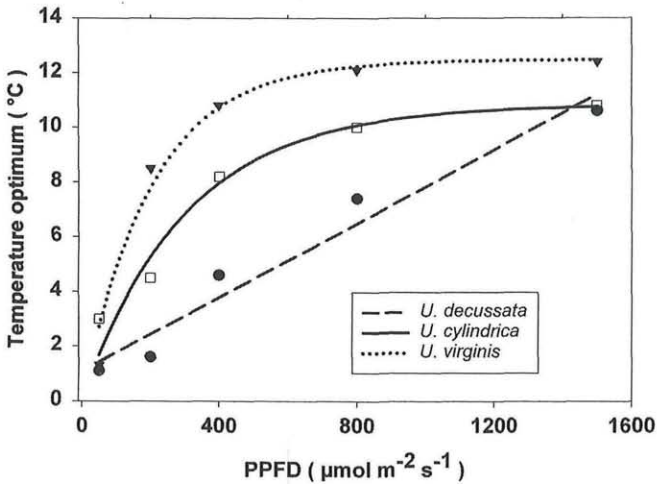

Fig. 3. Relationship between optimal temperature for NP and the temperature at which it was determined for *U. decussata* (●),*U. cylindrica* (□) and *U. virginis* (▼). The data is derived from the fitted curve shown in Fig. 2.

Maximal NP was always found at the highest PPFD (1500 µmol m^{-2} s^{-1}; Fig. 1) and, on a dry weight basis, ranged from 3.5 µmol CO_2 kg DW^{-1} s^{-1} (*U. decussata*) to 6.0 and 8.9 µmol CO_2 kg DW^{-1} s^{-1} (for *U. cylindrica* and *U. virginis* respectively). Variation in maximal NP were less when calculated on a chlorophyll basis, 5.5 µmol CO_2 g Chl^{-1} s^{-1} (*U. cylindrica*) and 7.6 µmol CO_2 g Chl^{-1} s^{-1} (*U. decussata* and *U. virginis*). The measured respiratory rates were all highest, 10.4, 12.8 and 14.4 µmol CO_2 kg DW^{-1} s^{-1} for *U. virginis, U. decussata* and *U. cylindrica*, respectively, at 30 °C, the highest temperature used.

Chlorophyll contents were similar for *U. cylindrica* and *U. virginis* at 1.10 and 1.17 g Chl kg^{-1}, respectively, and lower at 0.46 g Chl kg^{-1} for *U. decussata* and bore little relationship with thallus nitrogen contents which were 1.0, 1.7 and 1.1 %, respectively. Because of differences in thallus densities there was a much greater difference in chlorophyll contents

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when expressed on an area basis (0.42, 0.29 and 0.17 g Chl m^{-2} for *U. cylindrica* and *U. virginis* and *U. decussata*, respectively). Although other alpine species have similar chorophyll contents (0.71 and 0.41 g Chl kg^{-1} for *U. havaasii* and *U. cinereorufescens*, respectively), the content for *U. decussata* appears to be low in comparison with the 1.49 g Chl kg^{-1} for the same species from SANCHO & KAPPEN 1989.
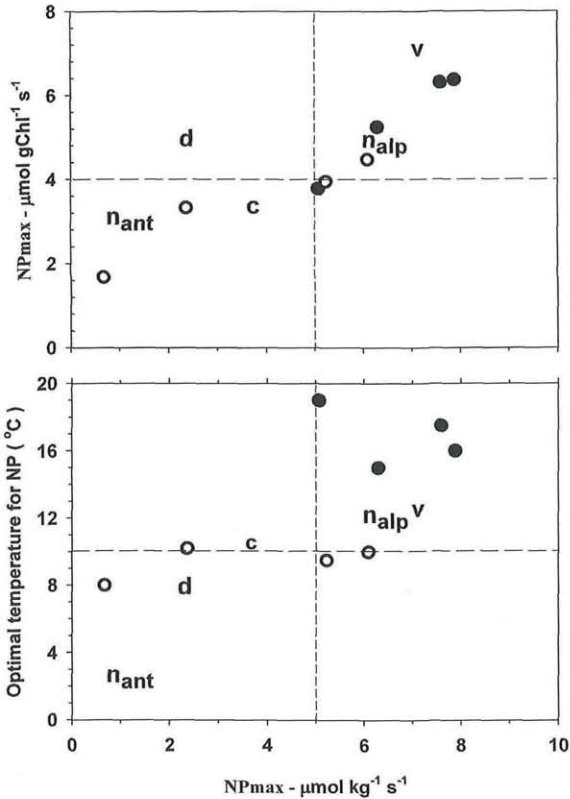

Fig. 4. Comparison between the photosynthetic performance of *Umbilicaria* species from alpine, montane and antarctic environments. Upper panel: relationship between net photosynthesis on a chlorophyll basis and on a dry weight basis; Lower panel, relationship between optimal temperature for NP and NP (dry weight basis). In both graphs the symbols represent: (●) montane and (○) alpine species from SANCHO & KAPPEN 1989; n$_{ant}$ and n$_{alp}$ are *U. nylanderiana* from antarctica and an alpine site in Spain, respectively, from SANCHO & al. 2001; species from this investigation are d, *U decussata*, c, *U. cylindrica* and v, *U. virginis*. All rates have been adjusted to the PPFD (620 µmol m^{-2} s^{-1}) used by SANCHO & KAPPEN 1989.

Discussion

The response curves linking net photosynthesis with PPFD and temperature as a first step to gaining an understanding of the performance of the three selected *Umbilicaria* species are due to the different habitats and the diverse species specific reactions. Previous studies have suggested that, for lichens, the results obtained in the laboratory under controlled conditions are actually good predictors of the lichens performance in the field (LANGE & al. 2001). SANCHO & KAPPEN 1989 and SANCHO & al. 2000 have suggested that the maximal NP of *Umbilicaria* species is dependent on their habitat and that species from alpine and Antarctic habitats have lower NPmax than those from lower, montane areas. This does seem to be generally correct (Fig. 4) when all the *Umbilicaria* species [from SANCHO & KAPPEN 1989, SANCHO & al. 2000 and this investigation] are compared on the basis of their maximal NP (dry weight versus chlorophyll basis). Alpine and Antarctic species tend to have lower rates on both bases although there is a region of overlap at approximately 5.0 µmol kg^{-1} DW^{-1} s^{-1} and 4.0 µmol g^{-1} Chl^{-1} s^{-1}. Two species from this study, *U. decussata* and *U. cylindrica*, fall into the alpine group as might be anticipated. However, *U. virginis* falls well outside the alpine sector and behaves more like the species from the montane grouping. When an alternative comparison is made between maximal NP (dry weight basis) and optimal temperature the result is very similar. Antarctic, especially, and alpine lichens have lower optimal temperatures for NP, below 12 °C. Once again *U. virginis* is the exception with a higher, albeit only slightly higher, optimal temperature of around 12.5 °C.

Although the overall trend found by previous researchers seems to be of general application, it appears that *U. virginis* is an exception because it behaves much more like a montane lichen than its nival habitat would suggest. A possible explanation for the apparent aberrant behaviour can be found by considering both its typical habitat and its photosynthetic performance reported here. Although it is the only species of the three studied that is confined to the nival zone it does not grow on exposed surfaces but occurs in crevices, a habitat that would be expected to be better protected from wind and high light. The NP response curves suggest that it is more shade adapted than the other species. It has more chlorophyll (DW basis) than the other species, is less dense and, in particular, has lower PPFD for compensation at all temperatures. In higher plants shade adaptation is associated with lower maximal rates of NP but this is not always the case for mosses and lichens where adaptation to high PPFD can be due to the presence of strong filter pigments with consequently lower NP (GREEN & LANGE 1995). Both *U. decussata and U. cylindrica* possess a dark pigmented cortex to protect the photobionts against excessive radiation (BÜDEL & LANGE 1994, KAPPEN & al. 1998, RIKKINEN 1995). The slightly

higher optimal temperature for *U. virginis* may be an artefact of the measurement systems used in all the investigations reported here because none used saturating PPFD. At non-saturating PPFD the shade adapted species would actually perform better.

The species have a broad range of temperature over which they maintain positive NP. The upper TCP was just below (*U. decussata* and *U. cylindrica*) or above 30 °C (*U. virginis*) at 1500 µmol m^{-2} s^{-1} PPFD. At the other extreme calculations from the regression analysis show that the lower TCP is around 7.7 °C at 1500 µmol m^{-2} s^{-1} PPFD which further confirms the known ability of *Umbilicaria* species to maintain positive NP at below freezing temperatures (KAPPEN 1988). Positive NP of *Umbilicaria aprina* was detected down to –8 °C in the laboratory (SCHROETER & SCHEIDEGGER 1995) and to –17 °C during field measurements in continental Antarctic (SCHROETER & al. 1994). Thus, with a temperature range of at least more than 30 °C the response curve of NP to temperature is very broad.

The response curves obtained are valuable because they not only indicate the need for field studies to clarify the exact habitats of these species and their daily and seasonal performance but also provide guidance to the possible important factors to measure. Altitude alone is probably only of general importance in predicting the behaviour and the alpine species are more similar to Antarctic species where microclimate is of great importance (GREEN & al. 1999).

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