

Interspecific differences in photosynthetic efficiency and spectral reflectance in two *Umbilicaria* species from Svalbard during controlled desiccation

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Abstract

This study aimed to evaluate the effective photosynthetic quantum yield (Φ_{PSII}) and the Photochemical Reflectance Index (PRI) for assessment of photosynthetic performance of two *Umbilicaria* lichens during gradual desiccation of their thalli. *U. cylindrica* and *U. decussata* exhibited curvilinear relationship (S-shape curve) of decreasing Φ_{PSII} values with decreasing water potential (WP) of thalli. During initial phase of desiccation (WP from 0 to -10 MPa), no decrease of Φ_{PSII} was apparent, further desiccation (WP from -10 to -20 MPa) led to fast Φ_{PSII} decrease from 0.6 to 0.1 indicating strong inhibition of photosynthetic processes. Critical WP at which photosynthetic processes are fully inhibited was found below -25 MPa in both lichen species. Photochemical Reflectance Index (PRI) exhibited curvilinear increase with thalli desiccation (decreasing WP). At full thallus hydration, the PRI reached the value of -0.18 in both species. Under strong dehydration (WP from -20 to -30 MPa), however, *U. cylindrica* showed somewhat lower value (-0.04) than *U. decussata* (-0.02 MPa). PRI to WP relationship is discussed and compared to existing evidence from higher plants and poikilohydric organisms.

Key words: Quantum yield, water potential, chlorophyll fluorescence, Photochemical Reflectance Index, lichen, water stress

Abbreviations: F_v/F_m - potential photosynthetic quantum yield of photosystem II, Φ_{PSII} - effective photosynthetic quantum yield of photosystem II, NDVI - normalized differentiate vegetation index, NPQ - non-photochemical quenching, PPFD - photosynthetic photon flux density, PRI - Photochemical Reflectance Index, PS II - photosystem II, WP - water potential

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Introduction

Lichens are poikilohydric symbiotic organisms exhibiting maximum photosynthetic rate at optimum hydration that is species-specific. If hydration of lichens decreases below such optimum due to progressive desiccation, photosynthetic processes are gradually inhibited. During desiccation of lichen thallus, several biochemical and biophysical mechanism are activated to minimize damages to photobionts (Kranner *et al.* 2008) and their photosynthesizing pigments (Zorn *et al.* 2001). Initial phase of desiccation is typical by partial water loss from a thallus but no reduction of photosynthetic rate is apparent. More pronounced water loss, however, leads to fast decrease of photosynthetic processes. At severe dehydration of thalli, full inhibition of photosynthesis occurs. Within last couple of years, the dependence of photosynthesis of numerous Arctic and Antarctic lichens on thallus dehydration expressed as water potential has been investigated in our laboratory (see *e.g.* Barták *et al.* 2005). Representatives of genus *Umbilicaria* typically show substantial photosynthesis even at strong dehydration, *i.e.* within water potential (WP) range from -15 to -20 MPa. In this study, we investigated two lichens from Svalbard (*Umbilicaria cylindrica* and *Umbilicaria decussata*) during gradual desiccation using measurements of chlorophyll fluorescence, effective quantum yield of photosynthetic processes in photosystem II (Φ_{PSII}) of symbiotic alga in particular. The other aim of this study was to evaluate critical water potential (WP) at which photosynthetic processes are fully inhibited and compare to existing data from other lichen species.

The Photochemical Reflectance Index (PRI) is based on a reflectance measure-

ment developed by Gamon (1992). The PRI uses two wavelengths, 531 nm and 570 nm, respectively.

$$PRI = (R_{531} - R_{570}) / (R_{531} + R_{570})$$

Reflectance at 531 nm is mostly affected by the changes in carotenoid pigments, especially xanthophyll-cycle pigments. Therefore, numeric value of the PRI is sensitive to zeaxanthin formation which is activated under high light conditions and water stress in photosynthesizing tissue. PRI is thus used as an effective indicator of photoinhibitory and water stress in higher plants (*e.g.* Liu *et al.* 2012). In most studies, PRI is well related to non-photochemical quenching of access light energy absorbed by photosynthetic pigments in chloroplasts. It is because of substantial involvement of light- or drought-induced zeaxanthin formation into protective mechanisms of non-photochemical nature activated during initial and the following phases of stress in plants. The PRI is generally used for the assessment of changes in carotenoid content (Sims *et al.* 2002), interconversion of xanthophyll-cycle pigments in particular. Some of recent studies, however, pointed out that PRI might be used also as an indicator of water stress in plants (Thenot *et al.* 2002). For lichens, no such study investigating PRI in relation to the hydration status of thallus has been performed since NDVI index is generally used much more frequently than PRI (Gloser *et al.* 2007). Moreover, the use of NDVI is recently devoted to large scale studies exploiting remote sensing approach with the main emphasis given to the identification of components of vegetation cover (*e.g.* Rees 2012).

Recently, there is trend to use several biophysical methods to measure photosynthesis in plants in order to identify limiting factors of photosynthesis of particular species. Over last few decades, chlorophyll fluorescence technique has been used frequently in the assessment of the extent of stress in photosynthetic apparatus in plants. That was why we decided to measure water limitation of photosynthesis in desiccating lichens by chlorophyll fluorescence and ongoing changes in PRI indicating the extent of water stress. Recently, simultaneous measurements of Chl fluorescence data and PRI are used to evaluate the effect of leaf development stage (Rahimzadeh-Bajgiran et al. 2012), radiation and temperature variation during growing season (Weng et al. 2006), actual leaf temperature (Inamullah et Isoda 2005), and exposure to ozone (Meroni et al. 2008) on functioning of photosynthetic apparatus of higher plants. In poikilohydric plants and organisms, however, such approach is used only to a limited

extent. In our study, we focused on simultaneous measurements of PRI and effective quantum yield of photosynthetic processes in photosystem II (Φ_{PSII}). Close correlation is found between PRI and Φ_{PSII} (e.g. Gamon et al. 1997) in higher plants. However, in poikilohydric autotrophic organisms, lichens at different level of hydration in particular, the PRI to Φ_{PSII} relationship, has not yet been investigated. Only scarce data are available on PRI and potential yield of photochemical reactions in PS II (F_v/F_m) in desiccating lichens. Yamano et al. (2006) found linear relationship between PRI and F_v/F_m in lichens forming desert soil crust. We therefore hypothesized, that reasonable correlation should be found between Φ_{PSII} and PRI when measured on gradually desiccating lichen thalli. Combination of the two biophysical methods is beneficial because it brings a deeper insight into functioning of chloroplastic photosynthetic apparatus under stress.

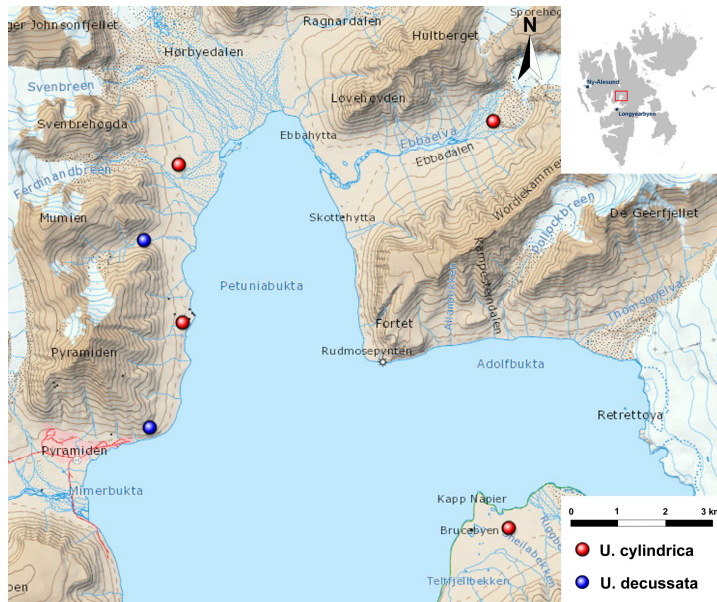


Fig. 1. Map of Central Svalbard with the indication of the plots at which thalli of *U. cylindrica* and *U. decussata* were collected during field campaign in Arctic summer 2012. Modified map extract (source: NPI: <http://toposvalbard.npolar.no/>).



Fig. 2. One of collection plots with high occurrence of *U. cylindrica* and *U. decussata*. The thalli of both species were abundant mainly on rock surfaces, several centimeters above ground level where the upper margin of snow cover occurs.

Material and Methods

Samples of lichen *Umbilicaria cylindrica* were collected in the first half of July 2012 on several field locations of central part of Spitsbergen Island (16°E, 78°N; Svalbard), in the vicinity of Petuniabukta (*see* Fig. 1). All samples grew on stones and rocks near the coast in the elevation to 100 m above sea level. Typical thalli of *Umbilicaria cylindrica* are round-shaped. It is grey or brownish-grey and often divided into multiple lobes. For the experiment, we selected thalli sized at least 3 cm in diameter (*see* Fig. 3). *Umbilicaria decussata* has more or less round-shaped thallus, typically 1 to 5 cm in diameter. Thallus upper surface is light gray to dark gray or brownish gray, with sharp ridges radiating from the central point. Lower surface of thallus is white (*see* Fig. 3). Thalli, typically attached at

central point (umbilicus), were cut off by sharp blade from surface of stones (Fig. 2) and hydrated for 24 hours. Fully hydrated thalli were placed in plastic dishes and subjected to slow desiccation at room temperature (25°C, 40% RH). Dependence of quantum yield of photochemical reactions in photosystem II (Φ_{PSII}) on water potential (WP) of thalli was determined using PAM-2000 modulated fluorometer (Walz, Germany) connected to a portable computer and a dew point water potential meter WP4T (Decagon Devices, USA) with programmed temperature control. Determination of WP by the device was based on chilled-mirror dewpoint technique. The instrument enables the measurement of samples up to 40 mm in diameter and 10 mm in height with an accuracy of 0.1 MPa.

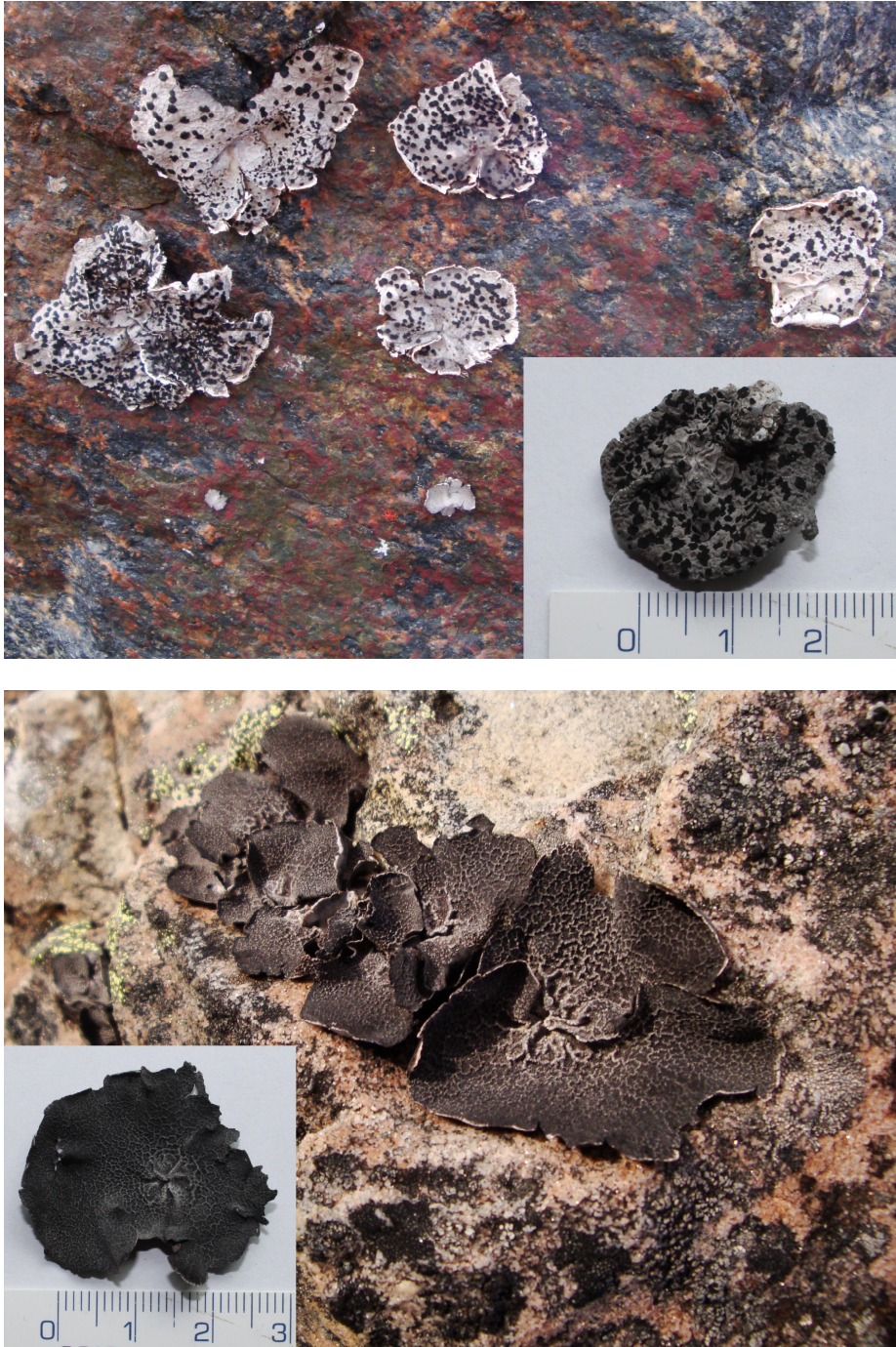


Fig. 3. Typical thallus of *U. cylindrica* (upper) and *U. decussata* (lower). The photographs were taken with dry thalli.

For WP determination, samples were placed into a measuring chamber of the device and equilibrated to constant relative humidity. After measuring of WP, the same sample was exposed for 5 min to constant artificial irradiance of $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon fluence density (PPFD) and then the Φ_{PSII} was immediately measured. LED was used as the source of PPFD and the value of PPFD

was determined using radiometer EMS-12 (Photon System Instruments, Czech Republic). After Φ_{PSII} measurement, Photochemical Reflectance Index (PRI) was determined. For PRI measurements, a PlantPen PRI 200 (Photon System Instruments, Czech Republic) was used. The whole cycle of measurements was repeated during the desiccation period until Φ_{PSII} reached zero.

Results

At full thallus hydration, supra-saturation effect on photosynthesis was observed in *U. cylindrica* but not in *U. decussata* (see Fig. 4, the Φ_{PSII} values at WP=0). Either no or mild decrease of Φ_{PSII} was observed in both species within the WP range of 0 to -10 MPa which reflects initial phase of thallus dehydration. Further decrease of water potential (below -10 MPa) led to substantial and rapid decrease of Φ_{PSII} in both experimental lichen species. Significant limitation of photochemical processes in PS II appeared at WP below -20 MPa. Critical WP at which Φ_{PSII} was close to zero differed between species. Full inhibition of photosynthetic processes was reached at about -25 MPa in *U. decussata* while the same was apparent at lower values of about -30 MPa in *U. cylindrica*.

Relation between PRI and WP was curvilinear and exhibited PRI increase with WP decrease (Fig. 5). The relationship was similar in both investigated species. At full thallus hydration, PRI values reached the values between -0.19 and -0.17. When very limited loss of water

from lichen thallus occurred (WP decrease from 0 to -2 MPa), PRI increased up to the values about -0.07 (*U. cylindrica*) and -0.05 (*U. decussata*). There were also some minor interspecific differences found in bending of the PRI to WP relationship as well as the maximum PRI values found at heavily desiccated thalli (see data points in Fig. 4). While in *U. cylindrica* the PRI maximum was about -0.04, it reached slightly higher values in *U. decussata* (-0.03 to -0.02). Slight differences, however, were found in the PRI to Φ_{PSII} relation (Fig. 6). The relation was of curvilinear shape. Under full hydration and initial phases of water loss, *i.e.* at Φ_{PSII} ranging from 0.7 to 0.6, PRI values increased rapidly, typically from -0.18 to -0.06. This was found in *U. cylindrica* while the increase was much less pronounced in *U. decussata* (from -0.10 to -0.06). Further decrease in the intrathalline water content led to the decrease in Φ_{PSII} (from 0.4 to 0.1), however, PRI values showed only minor increase from -0.06 to -0.04 in *U. cylindrica* and -0.06 to -0.02 in *U. decussata*.

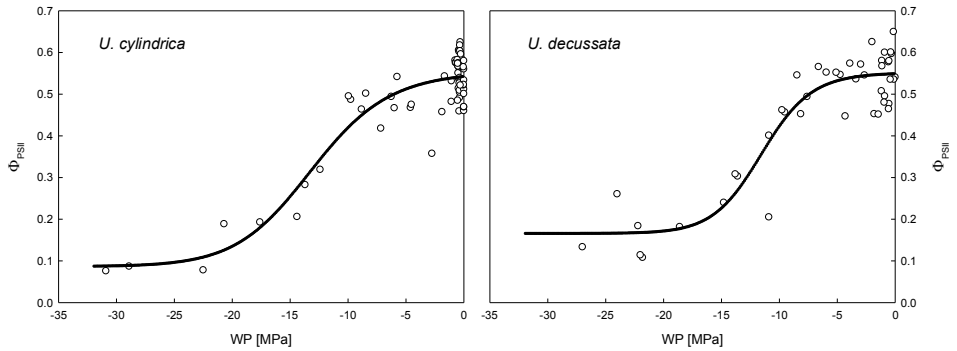


Fig. 4. Relation between the effective quantum yield of photosystem II (Φ_{PSII}) and water potential (WP) recorded during desiccation of lichen thalli from wet (WP = 0 MPa) to dry (WP below -25 MPa) state. The curve is the best fit of log-logistic S-curve.

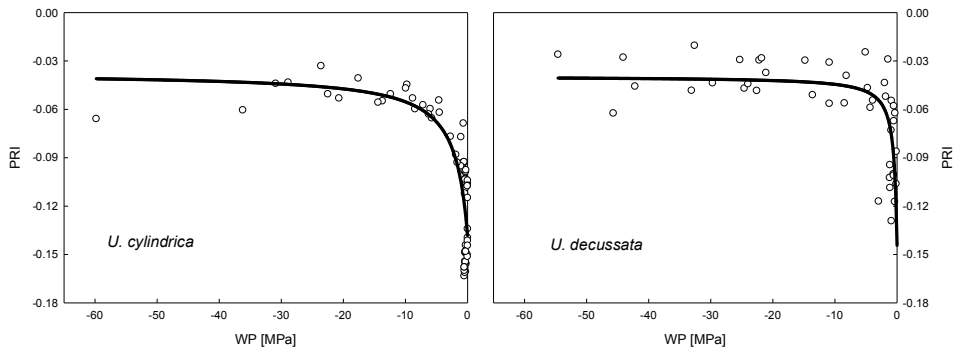


Fig. 5. Relation of Photochemical Reflectance Index (PRI) to water potential (WP) recorded in *U. cylindrica* and *U. decussata* during gradual desiccation from full thalli hydration (WP=0 MPa) to fully dehydrated thalli.

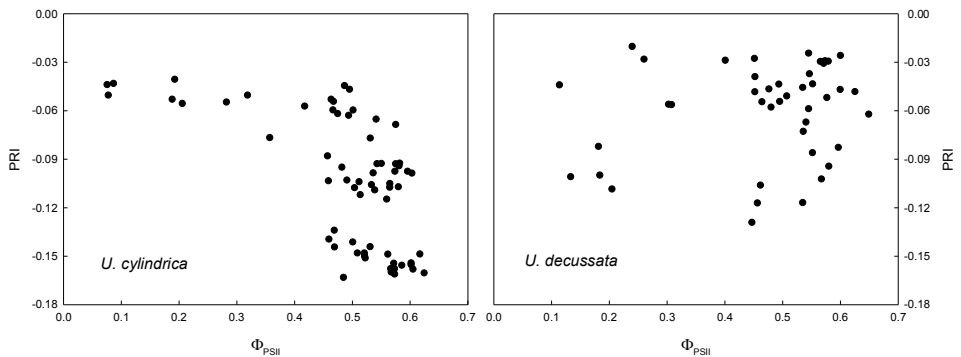


Fig. 6. Relation of effective quantum yield of photosynthetic processes (Φ_{PSII}) to Photochemical Reflectance Index (PRI). Data points were recorded during gradual desiccation of *U. cylindrica* and *U. decussata* thalli.

Discussion

Critical WP ranged between -25 and -30 MPa for both investigated *Umbilicaria* species. This was well comparable to the WP values found in the earlier studies done on Antarctic species. Critical WP was found -25 MPa in *Xanthoria elegans* (Barták *et al.* 2005) and -30 MPa for lichenized *Nostoc* (Moudrá *et al.* 2009). There are, however, indications that interspecific differences exist in critical WP of lichen species growing in polar regions. Results obtained for lichen species collected at Galindez Island (Antarctica) and measured by the same method showed that *Umbilicaria antarctica* had critical WP of about -40 MPa, while much higher values were found for *Stereocaulon* (-30 MPa) – Barták *et al.* Gloser (2004).

Our data supports the evidence from literature, that gradual loss of water from lichen thalli leads to decrease in rate of photochemical processes of photosynthesis, Φ_{PSII} in particular. Dehydration-dependent decrease in photochemistry leads to the decline biochemical part of photosynthesis as proven by numerous gas exchange studies in desiccating lichens in a laboratory (*e.g.* Lange *et al.* 2001) or in the field (Reiter *et al.* 2008). Such dehydration-dependent decrease in photosynthesis is accompanied by the activation of protective mechanisms that protect components of photosystem II from damages. These mechanisms are similar to those activated in lichens during photo-inhibition and include interconversion of xanthophyll cycle pigments (Calatayud *et al.* 1997, Vrábliková *et al.* 2005). They comprise several pathways of thermal energy dissipation (Heber *et al.* 2007, 2010) that act in reaction centers of PS II during lichen dehydration. To protect themselves from overenergization, reaction centers of PS II are converted from energy absorbing centers to energy dissipating centers at certain level of dehydration (Heber *et al.* 2011). Presence

of strong quencher in core of PS II and/or PS II antennae is reported from lichens desiccating on light (Veerman *et al.* 2007), however its chemical structure is not known. Recent studies showed, that the association of fungal and algal partners plays also important role since the lichen association showed higher resistance to dehydration stress than isolated photobionts (Kosugi *et al.* 2006).

In higher plants, positive relation between PRI and Φ_{PSII} has been reported for a variety of species and experimental treatments. The relation, however, differs from what we found in *U. cylindrica* and *U. decussata*. Inamullah *et al.* Isoda (2005) showed that different irrigation regimen of *Gossypium hirsutum* and *Glycine max* resulted in a decrease of Φ_{II} with water limitation. In these plants, PRI was positively correlated with Φ_{PSII} , *i.e.* PRI declined with pronounced water limitation. Similar response was found by Stylinski *et al.* (2000) who reported that an increase in photosynthetic electron rate brought an increase in PRI in *Quercus pubescens* leaves exposed to natural and elevated CO₂ concentrations. Positive relation between Φ_{PSII} and PRI was also found in grasses (Weng *et al.* 2012) as well as two shrubs *Baccharis halimifolia* and *Myrica cerifera* exposed to salt stress (Zinnert *et al.* 2012).

For poikilohydric autotrophic organisms, relation between PRI and Φ_{PSII} has been investigated only exceptionally. In mosses, Van Gaalen *et al.* (2007) showed decreasing values of non-photochemical quenching (NPQ) with increasing PRI in desiccating *Sphagnum sp.* The same authors reported linear increase of PRI with *Sphagnum* dehydration expressed as relative water content. We may, therefore, conclude that reasonable agreement exists between our findings of PRI to WP relationship and available data from poikilohydric moss, because both

they show the PRI increase with water loss from thalli. The PRI to WP relationship found in this study showed, however, curvilinear shape. This might be explained either by optical properties of desiccating *Umbilicaria* sp. thalli that differ from those of *Spagnum* ones. The other explanation is that relation of WP to relative water content is curvilinear in *U. cylindrica* (our data, not shown). General conclusion from our data is that PRI increases with decreasing WP in both *Umbilicaria* species investigated in this

study. This conclusion can be supported also by the data presented by Gauslaa (1984). In his paper, spectral reflectance curves are given for several species of *Umbilicaria* genus. We used the data derived from the curves that he recorded for wet and dry thalli. We calculated PRI values (not shown here) for several *Umbilicaria* species. In *U. rigida*, *U. spodochlora* and *U. vellea*, we found an increase of PRI values in dry thalli which support the general trend found for *U. cylindrica* and *U. decussata* in Fig. 5.

Conclusion

The results indicated high degree of tolerance of genus *Umbilicaria* species to water stress and their ability to photosynthesize even under substantial water loss from their thalli. Moreover, critical water potential values were below -25 MPa which indicates the ability of the two lichen species to perform photochemical

processes of photosynthesis at strongly desiccated state of a thallus as well (Jupa et Barták 2012). We may, therefore, conclude that *U. cylindrica* and *U. decussata* may thrive well in polar ecosystems with limited water availability and short period of thallus hydration.

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