

Effect of dehydration on spectral reflectance and photosynthetic efficiency in *Umbilicaria arctica* and *U. hyperborea*

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Abstract

In many polar and alpine ecosystems, lichens of genus *Umbilicaria* represent dominant species forming community structure. Photosynthetic and spectral properties of the lichens may change rapidly according to an actual hydration status of their thalli. In this study, we investigated responses of photochemical reflectance index (PRI), normalized difference vegetation index (NDVI), effective quantum yield of photosynthetic efficiency of photosystem (PS) II (Φ_{PSII}), and several photosynthetic parameters derived from fast induction kinetics of chlorophyll fluorescence (OJIP) to controlled dehydration. We used *U. arctica* and *U. hyperborea* collected close to Nuuk, Greenland. In both the species, PRI showed a curvilinear increase with dehydration, *i.e.*, a decreasing water potential (ψ_w). The increase was apparent within ψ_w range of 0 to -10 MPa. The PRI increase was less pronounced in *U. arctica* than in *U. hyperborea*. NDVI decreased with a progressive thallus dehydration in both the species, however, throughout ψ_w range of 0 to -30 MPa, *U. hyperborea* had lower NDVI values than *U. arctica*. The relationship between Φ_{PSII} and ψ_w resulted in a typical S curve. A critical ψ_w at which photosynthetic processes were fully inhibited was -30 MPa in both the species, however, species-specific differences in the S curve shape were found. Analyses of photosynthetic parameters derived from OJIPs revealed that the absorption of radiation energy and a trapping rate increased with dehydration in active reaction centres of PS II, the number of which decreased with a more pronounced lichen thallus dehydration. It is concluded that *U. arctica* and *U. hyperborea* possess effective physiological mechanisms to maintain an effective photosynthesis when partly dehydrated (the ψ_w range of 0 to -15 MPa). In spite of similar ecological niches that these two lichens occupy in nature, their spectral and photosynthetic properties differed.

Additional key words: chlorophyll fluorescence, lichens, NDVI, photosystem II, PRI, quantum yield, water potential.

Introduction

Indices derived from spectral reflectance measurements can be used to distinguish interspecific differences in higher plants and lichens as well (Bechtel *et al.* 2002). Within the last decades, several indices have been used in remote sensing for vegetation cover studies focused mainly on presence/absence of vegetation, species composition, and plant water relations and photosynthesis. Such approach allows a non-invasive evaluation of physiological status and the analysis of

limiting factors. Among the spectral indices used both in controlled experiments and in the field, the normalized difference vegetation index (NDVI), and the photochemical reflectance index (PRI) are most frequently used.

NDVI is defined as the ratio of reflectances measured at red and near infrared parts of spectrum. There are different equations to calculate NDVI exploiting slightly differing wavelengths: $(R_{750} - R_{705}) / (R_{750} + R_{705}) -$

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Abbreviations: F_s - steady-state chlorophyll fluorescence, F_v/F_m - variable to maximum fluorescence ratio; NDVI - normalized difference vegetation index; PRI - photochemical reflectance index; PS - photosystem; Φ_{PSII} - photosynthetic efficiency of photosystem II; ψ_w - leaf water potential.

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Gamon and Surfus (1999); $(R_{800} - R_{680}) / (R_{800} + R_{680}) -$ Gamon *et al.* (2013); $(R_{760-900} - R_{630-690}) / (R_{760-900} + R_{630-690}) -$ Yamano *et al.* (2006), or the whole sum of red (580 - 680 nm) and infrared (730 - 1100 nm) wavelengths (Bokhorst *et al.* 2012). In higher plants, NDVI reaches the highest value for green leaves, *i.e.*, those with an optimal amount of chlorophyll. Any decrease in chlorophyll content is demonstrated as a decrease in NDVI. Therefore, NDVI is widely used as indicator of stresses, such as low irradiance (Jiang *et al.* 2005), salinity (Naumann *et al.* 2008), ozone (Meroni *et al.* 2008), or leaf ageing (Letts *et al.* 2008). In many studies, NDVI is used as indicator of either water content or water potential in a leaf (Campi *et al.* 2008), water stress (Fabião *et al.* 2012), and evapotranspiration (Yebra *et al.* 2013). Such an approach, however, still suffers from insufficient accuracy because several interacting factors, *e.g.*, developmental stages of a leaf, are not included. That is why the use of NDVI for the estimation of leaf water content/potential is still limited (for review see Elsayed *et al.* 2011). In lichens, NDVI was shown to decrease with thallus dehydration, however, the decrease is species-specific (Neta *et al.* 2010), or as indicator of negative effects of heavy metals (*e.g.*, Garty *et al.* 2000). The study showed a relation between NDVI decrease and heavy metal-induced loss of photosystem (PS) II functioning expressed as a variable to maximum fluorescence ratio (F_v/F_m) decrease. The F_v/F_m ratio decrease is caused mainly by a partial disintegration of PS II (Garty *et al.* 2002).

The photochemical reflectance index (PRI) is calculated according to the equation $PRI = (R_{570} - R_{531}) / (R_{570} + R_{531})$. In some studies, the equation is different, *e.g.*, $PRI = (R_{550} - R_{530}) / (R_{550} + R_{530})$ (Peñuelas *et al.* 1994) or even reverse $PRI = (R_{531} - R_{570}) / (R_{531} + R_{570})$ (Peñuelas *et al.* 1997). Although most reflectance indices are derived from wavelengths belonging to red and infrared parts of spectrum, the PRI calculation exploits shorter wavelengths that are related to photosynthetic pigments. The reflectance at the wavelength of 531 nm evaluates the amount of xanthophyll cycle pigments which are closely linked to radiation use efficiency. Specifically, the reflectance at 531 nm is associated with the de-epoxidation of violaxanthin to zeaxanthin *via* antheraxanthin (Gamon *et al.* 1990). The reflectance at the wavelength of 570 nm is unaffected by xanthophyll cycle pigments. It can, therefore, be used as reference value. In higher plants, PRI is used for many purposes at different scales ranging from a single leaf level to remote sensing of large areas covered by vegetation. It is well related to the xanthophyll cycle pigments interconversion (Ripullone *et al.* 2011) and may thus be used as indicator of changes in functioning PS II under a variety of stresses. According to Gamon *et al.* (1997), PRI is highly correlated with F_v/F_m and CO_2 uptake (research done on higher plants). The same study reports a decrease of PRI in nutrient deficient plants. Also in CAM plants, PRI correlates with F_v/F_m (Peñuelas *et al.* 1995). Yamano *et al.* (2006) suggest a correlation between PRI and F_v/F_m in

soil crusts (partially formed by lichens) as well, and this correlation is stronger than between NDVI and F_v/F_m . Recently, there is a trend in field-grown plants to correlate PRI airborne data with those observed by direct measurements on leaf level in order to provide a deeper insight into a water supply-dependent seasonal variation of photosynthetic activity (Zarco-Tejada *et al.* 2012). For vegetation of subpolar and polar regions, airborne spectral data are correlated with results from land observation as well (Rees *et al.* 2004). For lichen-dominated tundra ecosystems, such an approach is applied in complex studies, *e.g.*, in North America and Eurasia Arctic transects, specifically at Isachsen Island and Krenkel Island (*see* Walker *et al.* 2012). The authors focused on NDVI and its changes during an arctic summer season with a special respect to climate change effects. Generally, the estimation of changes of NDVI and PRI in lichen vegetation has a potential to be used in future ecophysiological studies from subpolar and polar regions combining field and satellite data. The time courses and patterns of NDVI and PRI, however, would be interpreted carefully because the changes might be driven by a variety of local factors, such as durability of snow cover, precipitation pattern, microrelief-dependent differences in desiccation of lichens, *etc.*

It is well established for lichens that a spectral reflectance (Neta *et al.* 2010) and photosynthetic parameters of their photobionts are dependent on an actual hydration of a thallus (Jupa *et al.* 2012) and an osmotic stress of a photobiont (Vácz and Barták 2006). There are, however, interspecific differences depending mainly on optical properties of a particular lichen, intrathalline content and composition of pigments and secondary metabolites. In lichens of *Umbilicariaceae* family, earlier studies focused on a water limitation pointed out species-specific responses of photosynthetic parameters that are well documented by gazometric (*e.g.*, Larson 1980), and fluorometric (*e.g.*, Hájek *et al.* 2006, Jupa *et al.* 2012) methods. The knowledge of species-specific responses of spectral characteristics of *Umbilicariaceae* family lichens to dehydration is still insufficient. Therefore, the main objective of the present study was to assess the ability of two species of the *Umbilicariaceae* family from Greenland to resist to a gradual dehydration of their thalli using spectral reflectance and chlorophyll fluorescence measurements. Earlier study (Van der Veen and Csatho 2005) focused on spectral properties of Greenland lichens did not consider the water status of lichen thalli. Therefore, we focused on the responses of 1) photosynthetic parameters measured by two chlorophyll fluorescence techniques, and 2) spectral reflectance indices as affected by a loss of water potential caused by thallus desiccation. Since dehydration-induced changes in the photosynthetic performance of lichen thalli and their spectral properties take place simultaneously, we correlated these changes in order to find the water potential at which first signs of limitations of primary photochemical processes of photosynthesis occur, as well as a critical water potential

at which photosynthesis is fully inhibited. The other objective was to find interspecific differences between

the two *Umbilicaria* species.

Materials and methods

Plant species, treatments, and anatomical characteristics: *Umbilicaria hyperborea* (Ach.) Hoffmann is a lichen species reported from the Canadian Arctic, Greenland, Scandinavia, the Russian Arctic, and several mountain ranges in North America, Europe, Central and Eastern Asia (see Byazrov 2012 for details). *U. arctica* (Ach.) Nylander range is similar to *U. hyperborea* covering mainly Arctic regions of the Northern hemisphere and several locations in North America mountain ranges. Both the species are frequent in SW Greenland and in dominating lichen communities in a neighbourhood of Nuuk and Kobbefjord (for more details see Hansen 1995, 2011).

For experiments, these species were sampled in April 2011 from rocks at several locations near Nuuk, Greenland (64°11' N, 53°44' W). Thanks to a 3 d period of a warm, sunny, and windy weather preceding the date of collection, the thalli were collected in a dry state. After the collection, the thalli were placed into a portable desiccator and transferred to Brno, the Czech Republic, and stored in the dry state in darkness and at the temperature of 5 °C. Two days before the experiments, the samples were rewetted by demineralized water and kept in the hydrated state at 10 °C. During that period, the lichens were exposed to a photosynthetic photon flux density (PPFD) of 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during a 16-h photoperiod.

To estimate interspecific differences in the distribution of photobiont in a thallus, microscopical observations of cross-sections were made. Fully-hydrated thalli were cross cut (an average thickness of a section was 120 μm) and anatomical structures of a thallus were observed by a microscope *Olympus BX41* (Tokyo, Japan) and photographed by a camera (*Olympus 140*, Tokyo, Japan). Then, the images were analyzed using the *UTHSCSA ImageTool* (Informer Technologies, Dominican Republic) software. The following parameters were measured: 1) thallus thickness, 2) algal layer thickness, and 3) ratio of algal layer to thallus thickness. The three parameters were evaluated for central and marginal parts of thalli in both the species. Average values were calculated for at least 20 individual measurements.

Measurements of lichen thalli dehydration, NDVI, and PRI: During spectral reflectance and photosynthetic measurements, lichen thalli were let desiccate at a temperature of 25 °C (room temperature) and a relative humidity of 40 %. During a gradual dehydration, changes in the water potential (ψ_w) of 10 individual thalli were measured repeatedly until a full dehydration was reached (about 8 h). For a single ψ_w measurement, a thallus was equilibrated in a chamber of a dew point water potential

meter (*WP4T*, Decagon Devices, Pullman, USA) for 10 - 20 min, and then ψ_w was measured for at least 20 min using an automated method described by Jupa *et al.* (2012). This measurement was immediately followed by NDVI and PRI measurements after a 5 min dark adaptation. In addition, the desiccation was measured by a loss of mass (electronic scales *Mettler AE 100*, Switzerland), so that the relative water content (RWC) of lichen thalli could be evaluated.

NDVI was measured by *PlantPen NDVI 300* and PRI by *PlantPen PRI 200* (*Photon System Instruments*, Drásov, Czech Republic). Both instruments use a particular spectral reflectance for the calculation of the indices using the equations: $\text{NDVI} = (R_{740} - R_{660}) / (R_{740} + R_{660})$ (Gamon and Surfus 1999) and $\text{PRI} = (R_{570} - R_{531}) / (R_{570} + R_{531})$ (Peñuelas *et al.* 1997). The NDVI and PRI data were then plotted against ψ_w measured simultaneously. For NDVI data fitting, the two-parameter Gompertz model, a curve having equation $f(x) = \exp[-\exp B(x-E)]$, where B represents a slope and E an inflection point, was used. For PRI, the three parameters log-logistic model was used $f(x) = D / [1 + (x/E)^B]$, where B is a slope, D is the upper limit of PRI values, and E is an inflection point.

Photosynthetic parameters were measured by two fluorometric approaches: 1) fast chlorophyll fluorescence kinetics (OJIP) and 2) measurements of Φ_{PSII} . The fast fluorescence kinetics (OJIP) was measured by a *FluorPen FP 100* (*Photon System Instruments*). On dark-adapted thalli, records of a polyphasic rise of chlorophyll fluorescence during the first 3 s were done and analysed using the *FluorPen 1.0.4.0* software. On a curve resulting from such a measurement (OJIP), typically four important chlorophyll fluorescence levels can be distinguished. They represent points O, J, I, and P, numeric values of which reflect processes of light absorption and efficiency of energy flow through PS II and through a plastoquinone pool (Lazár *et al.* 2003, 2006). A set of OJIP-derived parameters characterizes the functioning PS II and the redox state of the plastoquinone pool (for review, see Strasser *et al.* 2000). Time courses of the OJIP-derived parameters as dependent on dehydration were constructed as plots of individual parameters against the water potential.

Photosynthetic efficiency of PS II (Φ_{PSII}) was measured by a fluorometer *PAM-2000* (Walz, Effeltrich, Germany). Before the measurement, the thalli ψ_w was measured and then the thalli were exposed to PPFD of 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 5 min. Then a saturation pulse (2 s, 5 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was applied and Φ_{PSII} calculated as $\Phi_{\text{PSII}} = \Delta F / F_m'$, where ΔF is the difference between a maximum chlorophyll fluorescence reached after a saturation pulse applied on light (F_m') and a steady-state

chlorophyll fluorescence on light (F_s). Then, Φ_{PSII} values were plotted against ψ_w and a mutual relationship

calculated. The above mentioned three-parameter log-logistic model was used for the construction of S-curves.

Results

U. arctica and *U. hyperborea* differed in thallus anatomy (Table 1). Generally, the thallus thickness reached higher values in *U. arctica* than in *U. hyperborea*, both in central and in marginal parts. A similar interspecific difference was found for the photobiont layer thickness that was about 70 and 31 % larger in central and marginal parts, respectively, in thalli of *U. arctica* than *U. hyperborea*. The proportion of the photobiont layer thickness to the thallus thickness was comparable for both the species reaching, however, higher values in marginal than central thallus parts.

The relation between PRI and ψ_w was curvilinear and PRI increased with a ψ_w decrease (Fig. 1). At the full hydration, values of PRI in *U. hyperborea* ranged from -0.18 to -0.01 and in *U. arctica* between -0.09 and -0.15. As the value of PRI in *U. hyperborea* was generally rising with desiccation, the variability of values decreased and finally ranged between -0.05 and -0.01. The increase of PRI in *U. arctica* was less pronounced than in *U. hyperborea*. Between the full hydration and ψ_w of -10 MPa, PRI rose within an interval between -0.1 and -0.06 and remained more or less stable during a further desiccation.

In spite of a similar trend of NDVI decrease with decreasing ψ_w values during desiccation (Fig. 1), the values of NDVI differed between the species. The fully hydrated thalli of *U. arctica* showed NDVI between 0.55 - 0.75 and much lower values were found in fully hydrated *U. hyperborea* (0.30 - 0.55). However, the values of NDVI in dehydrated *U. arctica* ranged between 0.55 and 0.30 and between 0.30 and 0.15 in dehydrated *U. hyperborea*.

The maximum values of Φ_{PSII} were found at the full hydration state. *U. arctica* showed slightly higher values than *U. hyperborea* (Fig. 2). In both species, no

Table 1. Photobiont layer thickness, thallus thickness, and their ratio in two *Umbilicaria* species. Means \pm SD, $n = 80$.

Species		Photobiont layer thickness	Thallus thickness	Ratio
<i>U. hyperborea</i>	margin	43.2 \pm 15.29	200.8 \pm 57.51	0.215
<i>U. hyperborea</i>	centre	51.2 \pm 12.53	268.6 \pm 51.06	0.191
<i>U. arctica</i>	margin	56.7 \pm 11.89	254.6 \pm 53.55	0.223
<i>U. arctica</i>	centre	87.5 \pm 19.80	466.1 \pm 116.91	0.188

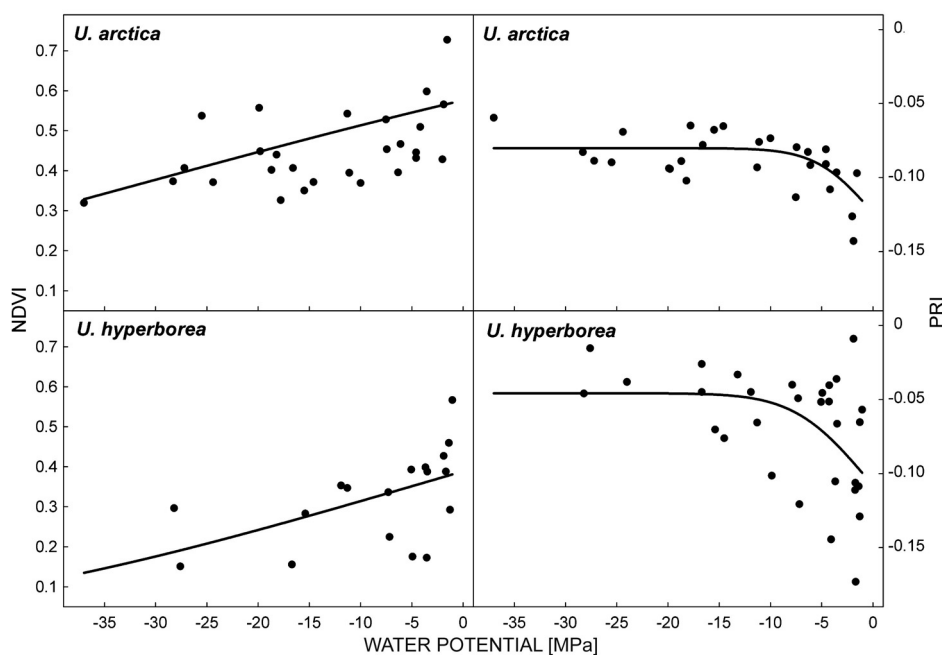


Fig. 1. Spectral indices of lichen thalli (*Umbilicaria arctica* and *U. hyperborea*) recorded during a decrease of water potential from a fully hydrated ($\psi_w = 0$ MPa) to dehydrated state (ψ_w below -30 MPa). For NDVI, the best fit is a two-parameter non-linear Gompertz equation: $NDVI = \exp[-\exp B (\psi_w - E)]$, where $B = -0.019$ and -0.020 , and $E = 5.601$ and 34.211 for *U. arctica* and *U. hyperborea*, respectively. For PRI, the three-parameter-log-logistic model was used, where $B = 12.459$ and 9.313 , $D = 0.093$ and 0.127 , and $E = 37.372$ and 37.194 for *U. arctica* and *U. hyperborea*, respectively (for details see Materials and methods).

hypersaturation effect was observed. Within the ψ_w range between 0 and -7 MPa, only a mild decrease of Φ_{PSII} was found in both the species. A further dehydration (ψ_w between -7 and -25 MPa) led to a rapid decrease of Φ_{PSII} from 0.6 to zero in both the species. In absolutely dry thalli (ψ_w below -30 MPa), Φ_{PSII} reached 0, which means that photosynthetic processes were fully inhibited in both the species.

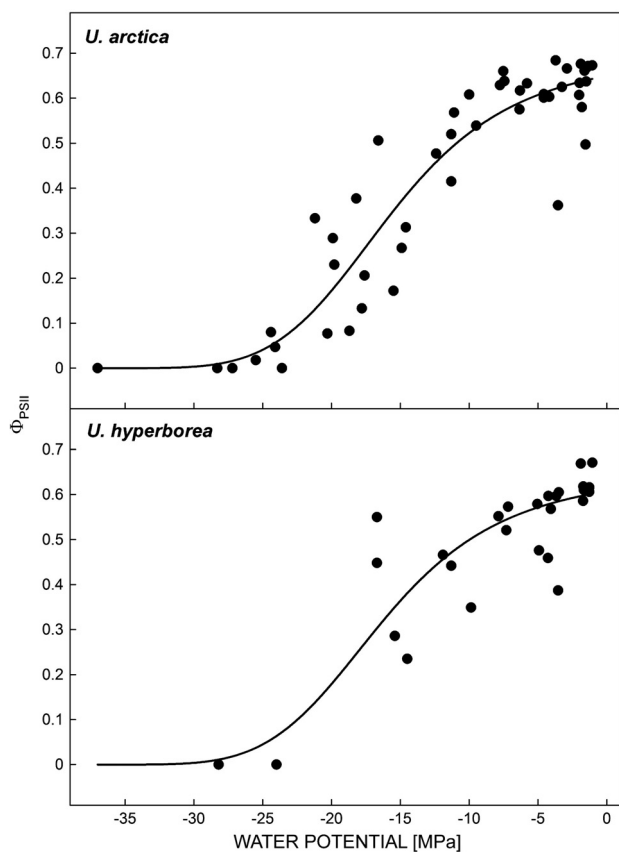


Fig. 2. Dependence of Φ_{PSII} on water potential. The log-logistic model was used to construct best-fit S-curves with the following parameters: B = -4.769 and -4.693, D = 0.698 and 0.649, and E = 21.479 and 20.875 for *U. arctica* and *U. hyperborea*, respectively.

With a progressive dehydration, OJIPs showed a decrease in an overall chlorophyll fluorescence signal, which resulted in „flattening“ their shapes (Fig. 3). As a result of that, Area over the curve delimited by a horizontal line at a maximum fluorescence value showed a dehydration-dependent decrease (Fig. 4). In spite of the

fact that much higher Area values were found in *U. arctica* than in *U. hyperborea* at the full thalli hydration, Area showed a similar rate of decrease with thallus dehydration in the two species. At ψ_w of about -15 MPa, Area reached its minimum and did not change with a further thallus dehydration.

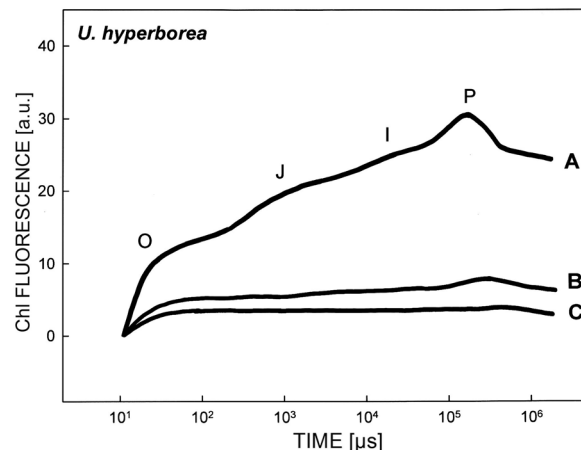


Fig. 3. Fast chlorophyll fluorescence curves (OJIPs) recorded at different water potentials: A - a fully hydrated thallus ($\psi_w = 0$ MPa), B - a partially dehydrated thallus ($\psi_w = -12$ MPa), and C - a dehydrated thallus ($\psi_w = -22$ MPa).

A gradual dehydration of a thallus brought a reduction in a number of reaction centres of PS II capable to transfer an absorbed energy and thus participate in a photosynthetic linear electron transport. In those centres that remained active, however, the absorption of light energy (Abs/RC, Fig. 5) as well as a trapping rate (TR_0/RC , Fig. 5) increased with a progressive thallus dehydration. No interspecific difference was found in Abs/RC and TR_0/RC to ψ_w relations. This indicates that active RCs, a number of which declined with thallus dehydration, increased trapping energy and its absorption in a similar manner in both the lichen species. The effectivity of absorbed energy transfer (Φ_{Pav}) showed a curvilinear relationship with ψ_w , however, it was slightly higher in *U. arctica* than in *U. hyperborea* within the whole range of ψ_w . The Φ_{Pav} to ψ_w relationship showed a more or less similar trend during desiccation in both the species. However, Φ_{Pav} values were generally smaller in *U. hyperborea* than *U. arctica*. Capacity for photosynthetic energy transfer through PS II (F_m/F_0) showed a decrease with ψ_w decline in both the species. Interspecific differences, however, were not found.

Discussion

Thallus and algal layer thicknesses are in a good agreement with data of Valladares *et al.* (1996), who studied anatomical features of several species of the *Umbilicariaceae* family. Our data on thallus thickness were recorded for central and marginal parts of *U. arctica*

and *U. hyperborea*, whereas the above study of Valladares *et al.* (1996) presented mean values for three different thallus zones: marginal, close to the umbilicus, and intermediate. Our results indicate a great intrathalline variability of thallus and algal layer thicknesses of

U. arctica and *U. hyperborea* similarly to earlier studies focused on other species of the *Umbilicariaceae* family (Larson 1983, Barták *et al.* 2004). The differences in thallus thickness found in our study might be attributed mainly to a variation in the medulla thickness since large intraspecific differences exist throughout the *Umbilicariaceae* family (Valladares and Sancho 1995). Such anatomic features have implications for interspecific differences in water storage capacity in *Umbilicariaceae* (Valladares *et al.* 1997).

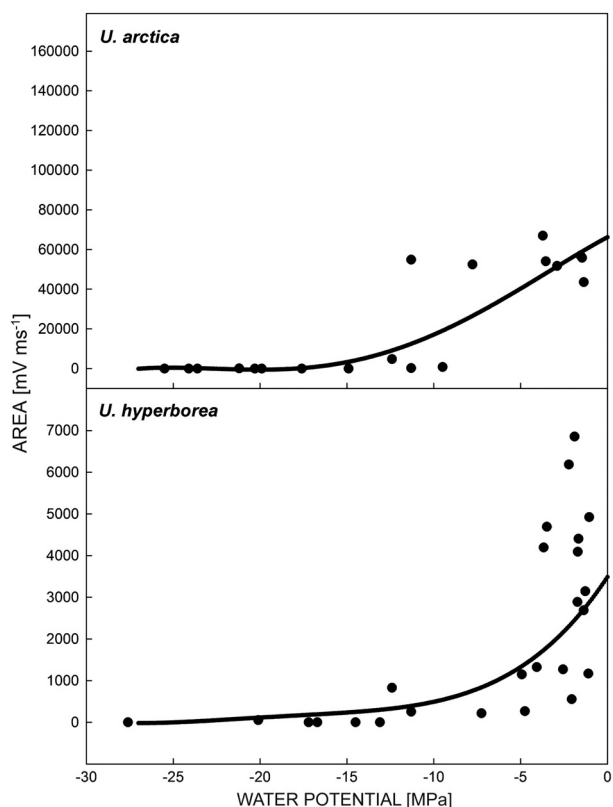


Fig. 4. Area above OJIP curves delimited by the curve, the vertical line at the beginning of the curve, and the horizontal line at the point P of chlorophyll fluorescence, as dependent on thallus dehydration from a fully-hydrated ($\psi_w = 0$ MPa) to dehydrated state (ψ_w below -30 MPa).

During desiccation, the values of Φ_{PSII} in *U. arctica* showed a sigmoidal decrease. The Φ_{PSII} remained high (0.6 - 0.7) at decreasing ψ_w until the value of about -8 MPa was reached. With a more pronounced dehydration, Φ_{PSII} started to decrease and reached zero at ψ_w of about -28 MPa. The relationship between Φ_{PSII} and ψ_w was similar in *U. hyperborea*, but a much higher variability of values was apparent probably due to a lower chlorophyll fluorescence signal caused by a black colour of the upper cortex. From the fitted data (Fig. 2), it is clear that the decrease of Φ_{PSII} started at a higher ψ_w (about -5 MPa). Earlier studies reported a similar Φ_{PSII}/ψ_w relationship: Barták *et al.* (2005) found a maximum Φ_{PSII} ranging between 0.5 and 0.6 and a similar curve shape in

Xanthoria elegans. Relations of Φ_{PSII} to decreasing ψ_w found in this study are in a good agreement with data presented by Jupa *et al.* (2012) for other representatives of the *Umbilicariaceae* family from polar regions (*U. cylindrica*, *U. decussata*). Similarly to his study, we found slight interspecific differences for Φ_{PSII} in the ψ_w range of -10 to -18 MPa indicating that *U. arctica* might perform a higher rate of primary photosynthetic processes than *U. hyperborea* in partially dehydrated thalli. Such an interspecific difference might be important in the field since many lichens from polar regions are not optimally supplied with water during a substantial part of vegetation season. In the field, however, many factors affect photosynthetic lichen performance in response to thallus hydration. Among them, intrathalline heterogeneity, hydration/dehydration status (Barták *et al.* 2000), a species-specific rate of dehydration for specific microclimate conditions, and a difference in the ratio between Φ_{PSII} and a net photosynthesis rate are of a major importance. Therefore, differences in photosynthesis performance between *U. arctica* and *U. hyperborea* at a ψ_w range between -10 to -18 MPa should be supported by simultaneous CO_2 exchange and chlorophyll fluorescence measurements in follow-up studies.

A curvilinear increase in PRI with decreasing ψ_w was similar to relations reported by Jupa *et al.* (2012) for two *Umbilicaria* species. Similarly to our study, PRI has negative values throughout the whole range of ψ_w . Other lichen species as well as mosses may, however, exhibit a decreasing trend of PRI with thallus dehydration, *i.e.*, decreasing ψ_w . This is particularly valid for dehydrating lichen *Stereocaulon foliosum* (Singh *et al.* 2013, Nayaka and Saxena 2014). A similar response, *i.e.*, decreasing positive values of PRI with dehydration, was found for *Parmelia* sp. by Gates (1965). It is, therefore, no general response of PRI to thallus dehydration in lichens since both negative and positive PRI values may be found at a full thallus hydration as well as both an increase and a decrease of PRI with dehydration (Barták *et al.* 2014, *Usnea antarctica*, *Xantoria elegans*, *Leptogium puberulum*). Specificity of the response might be attributed to optical properties of a particular lichen species, thallus colour and its change with thallus desiccation, the presence of secondary compounds in a thallus, and an algal/cyanobacterial photobiont and its physiological characteristics. To compare our PRI data, we used spectral reflectance curves presented by several authors for lichens and mosses (Bubier 1997, Mohammed 2000, Bechtel 2002, Van Galen *et al.* 2007, Peters 2011, Jupa *et al.* 2012), respectively, and calculated PRI values. Across species, PRI in wet lichens vary between -0.17 and 0.06, whereas a different range was found for mosses (-0.02 to 0.10). We calculated PRI values (not shown here) for *U. rigida*, *U. spodochlora*, and *U. velela*. We found an increase of PRI values in dry thalli, which support a general trend found for *U. cylindrica* and *U. decussata* in our previous study (Jupa *et al.* 2012). PRI may, therefore, be recommended as a promising parameter to monitor in

future ecophysiological studies in lichen-dominated polar and tundra habitats, especially when field ground measurements are combined with small-scale aerial spectral data (e.g., quadcopter).

NDVI decreased with thallus dehydration (ψ_w decreasing from 0 to -30 MPa) similarly as reported by Gloser and Gloser (2007). Similar results were reported by Yamano *et al.* (2006) for lichen components forming a soil crust in a cold desert in China. The authors showed an increase in NDVI and PRI with an increasing dose of water used for lichen thalli rehydration. They also reported a linear increase in NDVI and PRI with an increasing value of F_v/F_m . In our study, we found a positive relation of NDVI and PRI with Φ_{PSII} . Singh *et al.* (2013) reported a NDVI decrease in a dehydrated lichen

Stereocaulon foliosum. It reaches the values of 0.515 at RWC 93 % and 0.433 at RWC 37 %. Our data presented in Fig. 1, if recalculated for the above RWCs, gave NDVI values of 0.614 (*U. arctica*) and 0.413 (*U. hyperborea*) at 93 % RWC and 0.514 (*U. arctica*) and 0.332 (*U. hyperborea*) at 37 % RWC. It indicates that NDVI decreases not only with thallus dehydration (a general trend in the below-specified three species) but also with the thallus colour in the sequence: green (*U. arctica*) – reddish-brown (*S. foliosum*) – brownish-black (*U. hyperborea*).

The shape of OJIP curves recorded on fully hydrated thalli exhibited a P step followed by a decrease in chlorophyll fluorescence (a dip according to Ilík *et al.* 2006). The dip is attributed to a fast activation of

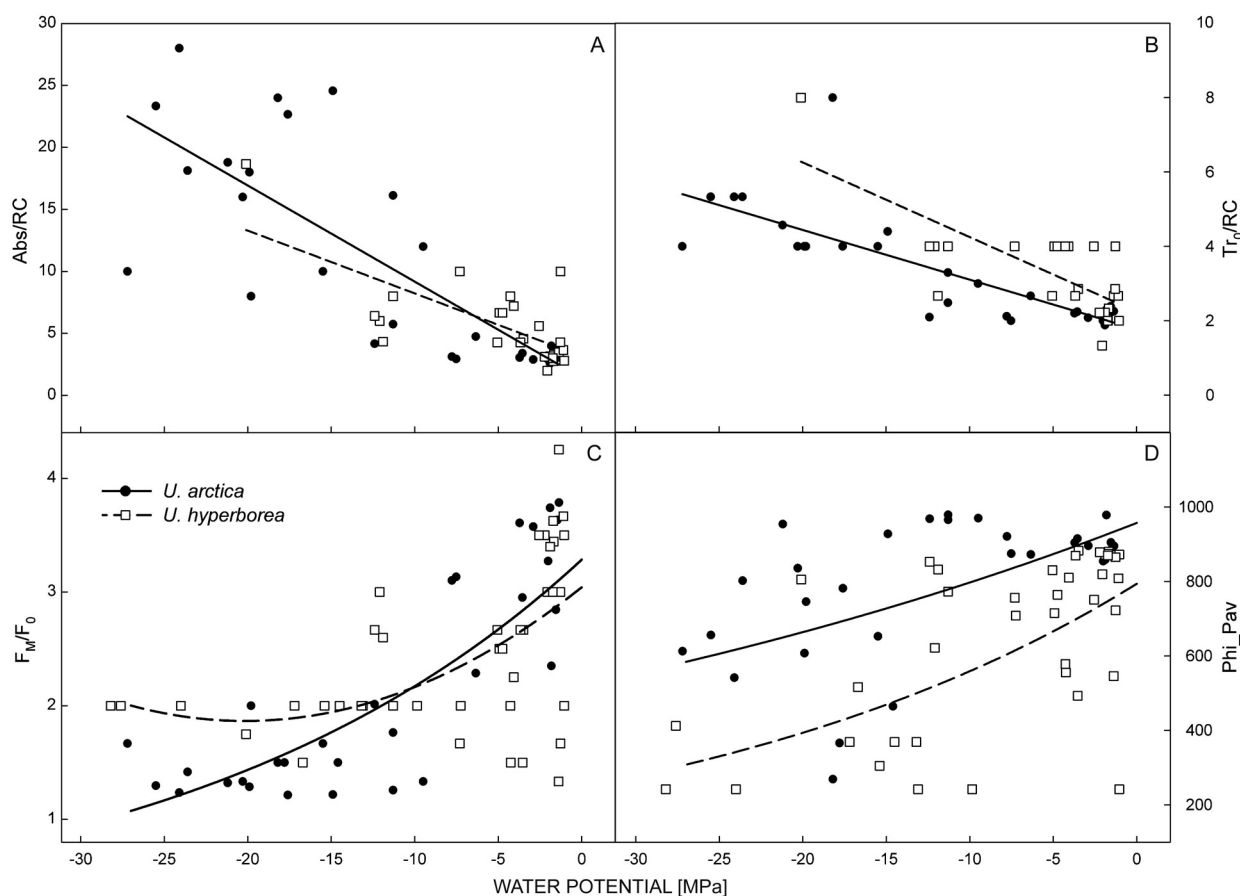


Fig. 5. Photosynthetic chlorophyll fluorescence parameters derived from OJIP curves during a decrease of thallus water potential. Relations of absorption per reaction centre – A, trapping rate per reaction centre – B, F_m/F_0 (the ratio of maximum to background chlorophyll fluorescence) – C, Φ_{Pav} (the effectivity of absorbed energy transfer in PS II – D, to water potential of thalli of *U. arctica* and *U. hyperborea*.

photosynthetic electron transport on the acceptor side of PS II and a light-induced activation of ferredoxin-NADP oxidoreductase (Lazár 2006). The dip is followed by a local maximum (denoted as G step) caused by a plastoquinone (PQ) pool and quinone (QA) re-reduction. Ilík *et al.* (2006) reported that the plastoquinone re-reduction is not associated with a cyclic electron flow around PS I and is probably caused by inability of the

cytochrome b6/f complex to rapidly reoxidise the PQ pool.

The OJIP curves recorded in our study showed a decrease in absolute values with a progressive dehydration. A stress-induced decrease in chlorophyll fluorescence values forming „flattened“ OJIPs is a general phenomenon documented in lichens and their photobionts. Our earlier data recorded on *U. arctica*

(unpublished) showed a photoinhibition-dependent decrease of OJIPs, *i.e.*, variable chlorophyll fluorescence values recorded between O and P steps. Decreased values between the O and P steps result in a decrease in Area, which is an equivalent for absorbed energy transfer to the photosynthetic linear electron transport chain. The same limitation of photosynthetic processes is, therefore, apparent in *U. arctica* and *U. hyperborea* exposed to a gradual dehydration in our study.

Similarly to photoinhibitory effects investigated in a former study, the dehydration led to increases in Abs/RC and TR_o/RC but a decrease in Area. This indicates that the dehydration stress led to an inactivation of chlorophyll molecules in light harvesting complexes and to a reduction in a number of functioning reaction centres

of PS II. Those active centres, however, exhibited an increase in the trapping rate, *i.e.*, in the reduction of pheophytine *a* and quinone, and the absorption of light energy per single reaction centre with a progressive thallus dehydration in both the lichen species. It represents an important mechanism that contributes to PS II functioning in lichen algal photobionts at suboptimal conditions. Highly effective active reaction centres are essential also during the activation of photosynthesis in wetted dry lichens. Soni and Strasser (2008) showed that an accumulation of fully active photosynthetic centres of a qualitatively similar conformation and a high integrity are the main factors affecting OJIP shapes during the reactivation of photosynthesis in rewetted lichens.

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