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Photoprotection and high-light acclimation in semi-arid grassland lichens – a cooperation between algal and fungal partners

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Abstract

In lichens, each symbiotic partner cooperates for the survival of the symbiotic association. The protection of the susceptible photosynthetic apparatus is essential for both participants. The mycobiont and photobiont contribute to the protection against the damaging effect of excess light by various mechanisms. The present study investigated the effect of seasonality and microhabitat exposure on photoprotection and photoacclimation in the photo- and the mycobiont of six lichen species with different thallus morphology in inland dune system in the Kiskunság region (Hungary) with shaded, more humid and exposed, drier dune sides. High-Performance Liquid Chromatography, spectrophotometry, chlorophyll *a* fluorescence kinetic technique were used, and micrometeorological data were collected. The four years data series revealed that the north-east-facing side was characterized by higher relative humidity and lower light intensities compared to the south-west-facing drier and more exposed sides. The south-west facing side was exposed to direct illumination 3–4 hours longer in winter and 1–2 hours shorter in summer than the north-east facing side of the dune, influencing the metabolism of sun and shade populations of various species. Because rapid desiccation caused short active periods of lichens during bright and drier seasons and on exposed microhabitats, the rapid, non-regulated non-photochemical quenching mechanisms in the photobiont had a significant role in protecting the photosynthetic system in the hydrated state. In dehydrated conditions, thalli were mainly defended by the solar screening metabolites produced by the mycobiont and curling during desiccation (also caused by the mycobiont). Furthermore, the efficacy of light use (higher chlorophyll and carotenoid concentration) increased because of short hydrated periods. Still, a lower level of received irradiation was appropriate for photosynthesis in dry seasons and on sun exposed habitats. In humid seasons and microhabitats, more extended active periods lead to increased photosynthesis and production of solar radiation protectant fungal metabolites, allowing a lower level of photoprotection in the form of regulated non-photochemical quenching by the photobiont. Interspecific differences were more pronounced than the intraspecific ones among seasons and microhabitat types.

Keywords photoacclimation · seasonality · microhabitat · species-specific response · lichen secondary metabolites · plastid pigments

Abbreviations

A	arid
Fv / Fm:	maximum quantum yield of photosystem II photochemistry
H	humid
LSM	lichen secondary metabolite
NE	North-East
PAR	photosynthetically active radiation
PS	photosystem
RC	reaction centre
RH	relative humidity
ROS	reactive oxygen species
SPF	sun protection factor
SW	South-West
φNO	the yield of non-regulated excitation dissipation
φNPQ	non-photochemical quenching
φPSII	the yield of photochemical electron transport

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1 Introduction

Lichens are unique and complex ecosystems in which each symbiotic partner can contribute to the survival of extreme environmental conditions. The photobiont supplies the primary carbon source for the mycobiont; accordingly, the protection of the susceptible photosynthetic apparatus is essential for both participants (Sadowsky and Ott 2016). Light is indispensable to photosynthesis, although light can also cause irreversible photodamage in the algal photosystem (PS) II (Heber et al. 2000). In hydrated lichens, the excitation energy absorbed by the antenna system may be used for photochemical charge separation in the reaction centres (RCs). When the electron transport chain is saturated, the excitation energy can be re-emitted as fluorescence or dissipated as heat. Both non-photochemical quenching via zeaxanthin (Demmig-Adams 1990; Färber et al. 1997) and desiccation induced fluorescence quenching (Heber et al. 2001, 2006; Kopecky et al. 2005) are known in lichens. In the absence of effective thermal energy dissipation, the production of damaging reactive oxygen species (ROS) as by-products can cause irreversible damage in the PSII (Müller et al. 2001; Krieger-Liszkay 2005).

Both the mycobiont and photobiont can defend against solar radiation damage by various mechanisms (Beckett et al. 2021; Gasulla et al. 2012; Kranner et al. 2005; Nguyen et al. 2013; Sadowsky and Ott 2016). Lack of water is a main limiting factor for lichen metabolism. On the other hand, reversible drying out for a short period is one way of protecting poikilohydric organisms from excess light (Veerman et al. 2007). The lower transmittance (Dietz et al. 2000) or higher density (Gauslaa et al. 2017) of the cortex, the increased accumulation of solar radiation screening pigments (e.g. BeGora and Fahselt 2001; Singh et al. 2011; Solhaug and Gauslaa 1996; Solhaug et al. 2010), and curling during desiccation (Barták et al. 2006) are defence strategies offered by the mycobiont under high light exposure. The photobiont has also developed mechanisms to protect its photosynthetic apparatus, such as the aggregation and the change in shape during desiccation (de los Rios et al. 2007; Scheidegger et al. 1995). The enhanced non-photochemical quenching (ΔpH- and zeaxanthin dependent and desiccation induced) increases the thermal dissipation of excess light energy to protect the photosystem in the algae (Heber et al. 2001; Paoli et al. 2010; Vráblíková et al. 2006). Conformational change in the chlorophyll-protein complex is also an effective way to dissipate excess light energy due to desiccation (Heber et al. 2007). These protecting mechanisms require accurate coordination of both partners (Kranner et al. 2005), since a separated mycobiont and photobiont suffer from oxidative stress during desiccation. In the lichen thallus, the partners can regulate the photoprotective system of the other symbiotic component (Kranner et al. 2005; Solhaug and Gauslaa 2004).

Several studies have also demonstrated the seasonal change of solar radiation protectant lichen secondary metabolites (LSMs) and plastid pigments. The LSM and carotenoid concentration in lichens are higher, and the chlorophyll concentration is lower in brighter seasons in the northern or arctic-alpine region (Bjerke et al. 2005; Gauslaa and McEvoy 2005; Gauslaa et al. 2013; Vráblíková et al. 2006), which is contrary to the situation in continental, semi-arid (Farkas et al. 2020) and coastal areas (Higgins et al. 2015). The sun exposure of lichen microhabitats also influences the photoprotection mechanisms. Compared to shady microhabitats, higher sun exposure induces the production of UV protecting LSMs (BeGora and Fahselt 2001; Bjerke et al. 2002; Nybakken et al. 2007), and may also cause changes in the plastid pigment concentration (Czeczuga and Krukowska 2001). The concentration of photoprotective carotenoids in lichen populations is higher in the sun than in the shade (Demmig-Adams and Adams III 2006; Gautam et al. 2011; Paoli et al. 2010). According to some studies, shade-adapted thalli exhibit a higher concentration of chlorophyll than exposed ones (Pintado et al. 2005; Paoli et al. 2010; Pirintsos et al. 2011), but not always (Piccotto and Tretiach 2010; Pintado et al. 1997).

The main objective of the present study was to reveal the contributions of the photo- and mycobiont to light acclimation and photoprotection within the lichen thallus. We aimed to reveal the influence of the seasonal light conditions and exposed versus shaded microhabitats. We also focused on the responses of the various lichen species exhibiting different thallus structures to the changing environment. We hypothesized that because of the different anatomy and thallus structure, the investigated lichen species acclimate differently to the changing light conditions in space and time. We also assumed that both alga and fungi contribute equally to the protection of excessive solar radiation during the whole year.

The investigation extends the previous knowledge of terricolous lichens in semi-arid regions where they cover large areas between patches of vascular plants (Belnap and Lange 2003). Our results also contribute to the limited lichenological data on the proportion of absorbed excitation energy available in the literature.

2 Materials and methods

2.1 Study site

The study site is located in the Kiskunság region of Hungary near Fülöpháza (46° 52' 21.45" N, 19° 24' 18.29" E).

The moderately continental climate with a submediterranean influence (Péczely 1967) provides habitats for semi-arid sandy grasslands (*Festucetum vaginatae danubiale* association Rapaics ex Soó 1929 em. Borhidi 2012). The landscape is characterized by an inland dune system with calcareous sand derived from the deposit of the Danube River. The wind, as a secondary effect, reshaped the landscape resulting in a dune system (Pécsi 1967). The prevailing wind has a northwest direction, and the yearly average wind speed is between 2.5–3 m s^{-1} (Péczely 1967).

The investigation was completed with micrometeorological data deriving from two micrometeorological stations. The stations were situated at Bugacpusztaháza, a similar duneland system, 28 air km from the present study site and had been already in operation during the present study. According to macrometeorological data (National Meteorological Service), landscape structure and soil surface variables at microenvironmental scale (Veres et al. 2021), the conditions at Bugacpusztaháza seemed to be representative of Fülöpháza. The method for micrometeorological data recording is specified in Veres et al. (2020). Changes in microclimate were recorded during the investigation period, including the main differences between the two microhabitat types (humid: northeast-facing (NE) and arid: southwest-facing (SW)). Two HOBO Micro Station H21-002 (Onset Computer Corporation, U.S.A.) with sensors (Onset Computer Corporation, U.S.A.) measuring photosynthetically active radiation (PAR) and relative humidity (RH) were placed at 0.5 m height. Data were continuously recorded each minute. PAR data were aligned with the seasonal change of angle in light incidence and the dune side inclination and exposition. Only the PAR and RH data are reported in the present study. We also estimated a hypothetically active period during nights (PAR = 0 mmol m^{-2} s^{-1} and RH > 80%), and a period when weather conditions could be suitable for photosynthesis (30 µmol m^{-2} s^{-1} < PAR <1,000 µmol m^{-2} s^{-1} and RH > 80%, based on Lange (2003). PAR data of the arid dune side are lacking because of some wire damage caused by wild animals in the spring.

2.2 Sampling method

Samples were taken from both sun populations on SW-facing side and shade populations on NE-facing side of foliose *Cladonia foliacea* (Huds.) Willd., the fruticose *Cladonia furcata* (Huds.) Schrad., the cup *Cladonia magyarica* Vain. and the crustose *Diploschistes muscorum* (Scop.) R. Sant. Additionally, populations of placodioid *Gyalolechia fulgens* (Sw.) Søchting, Frödén and Arup and foliose *Xanthoparmelia pokornyi* (Körb.) O. Blanco, A. Crespo, Elix, D. Hawksw. and Lumbsch were collected but found only in the exposed SW-facing microhabitats. The species hosted eukaryotic green algae: various species of *Asterochloris* in *Cladonia* species (Smith et al. 2009; Škaloud et al. 2015), and *Trebouxia* species in *G. fulgens* and *X. pokornyi* (Škaloud and Peksa 2008; Stenroos et al. 2011; Leavitt et al. 2015). *Diploschistes muscorum* switches photobiont during its lifespan (Friedl 1986, Piercey-Normore and DePriest 2001, Škaloud et al. 2015, Wedin et al. 2015). In the early stage, it has *Asterochloris* captured from *Cladonia* species; later replaced by various species of *Trebouxia*. These six lichen species are members of the "Bunte Erdflechten-Gesellschaft" (Gams 1938), also known as the *Fulgensietum fulgentis* Gams and *Cladoniaetum symphycarpae* Doppelb. associations, typical for this region (Büdel 2001). Thalli were collected in four seasons (July and November of 2014, February and May of 2015).

Samples were taken from one SW- and one NE-facing side (= microhabitats) of a dune. In every season, new thalli were collected from the same dune sides during the investigation period. After collection, thalli were transported to the laboratory, where they dried out under semi-natural conditions (i.e. seasonal temperature, humidity and light regime) (Csintalan et al. 1999) and then cleaned from plant and moss debris. The samples were stored for a maximum of 14 days at room temperature (Tair = 20–22 °C, RH = 23% all year) in darkness before measuring chlorophyll fluorescence kinetics and 21 days before plastid pigment analysis. LSMs were quantified after all samplings had been completed in October 2017. Samples were stored at room temperature (Tair = 20–22 °C, RH = 23% all year) in the darkness.

Ten samples per species per season per microhabitat were measured during plastid pigment and HPLC analysis. Because of its low abundance, *G. fulgens* was sampled in 5 replicates only. Twenty samples per species per season per microhabitat were measured by chlorophyll fluorescence kinetic technique, except for *G. fulgens* with only ten samples. *Gyalolechia fulgens* and *X. pokornyi* occurred only in the SW-facing microhabitat, and only seasonal changes were investigated.

2.3 Extraction and measurement of lichen secondary metabolite concentration

Quantification of lichen secondary metabolites in the three *Cladonia* species from each microhabitat type and season was performed with a high-performance liquid chromatography (HPLC, Alliance e2695, Waters Corporation, Milford, MA, U.S.A.) system including a Photodiode Array Detector (2998 PDA Detector, Waters Corporation, Milford, MA, U.S.A). Ten thalli were chosen from the randomized material of each microhabitat type sampled in four seasons. Lichen material was pulverized with liquid nitrogen. 50 mg of the homogenized material were dissolved in 10 ml pure acetone and sonicated for 10 min. in an ultrasonic water bath. Samples were centrifuged for 20 min. After

separation, the supernatant was filtered through a Cronus Ø 25 mm PTFE syringe filter (0.22 µm). For calibration, standard stock-solutions (1 mg ml^{-1}) were prepared from reference standards dissolved in acetone. Usnic acid, fumarprotocetraric acid and atranorin were quantified based on a five-point (5, 10, 20, 50, 100 µg ml^{-1}) calibration. The chromatographic design of Ji and Khan (2005) was modified for the application. A Phenomenex Luna 5 µm C18, 150 × 4.6 mm, column was used for chromatographic separation. The sample injection volume was 10 µl. The temperature was 40 °C in the column oven and 5 °C in the sample cooler. Baseline separation of the compounds investigated was achieved with a gradient elution program where solvent A consisted of ortho-phosphoric acid and deionized (Milli-Q ultrapure) water (0.5 : 99.5), and solvent B contained ortho-phosphoric acid and acetonitrile (0.5 : 99.5). All the chemicals used were HPLC grade. The linear gradient started with 60% of solvent A after the volume decreased to 10% within 20 min. and then to 0.5% in 30 sec., it remained constant for 9.5 min. The volume of solvent A was changed back to 60% within 1 min. The flow rate of solvents was 1 ml min^{-1}. Lichen metabolites were detected at 280 nm (usnic acid), 240 nm (fumarprotocetraric acid) and 233 nm (atranorin).

2.4 Extraction and measurement of photosynthetic pigments

The concentration of plastid pigments was measured by spectrophotometry (Shimadzu UV-1601) according to Pfeifhofer et al. (2002). A cooled mortar and a pestle were used to grind c. 100 mg of clean, air dry (max. 23% RH in the laboratory) thalli of each sampled lichen with c. 7–8 mg of L-sodium ascorbate to prevent chlorophyll degradation (Calatayud et al. 2000). Then liquid nitrogen was added, and the samples were pulverized. The material was mixed with 500 µl pure acetone (HPLC grade) in the mortar then poured quickly into cold centrifuge tubes. The rinse of the remnant was performed by adding 500 µl pure acetone and pouring it into the sample. The last step was repeated two times. The homogenate was stored on ice in darkness (in an isolated box with a lid) until the analysis. The samples were centrifuged at 20,000 g for 10 min. at 4 °C. After separation, the supernatant was decanted into clean, cold centrifuge tubes. The pellet was re-suspended with 1,000 µl acetone and vortexed. Then the centrifuge procedure was repeated, and the supernatants were combined. Spectrophotometrical quantification of pigments in the acetone extracts was conducted following Lichtenthaler and Buschmann (2001). Preliminary investigations showed that two extraction steps were adequate for quantitative extraction. The samples were filtered through Ø 13 mm PTFE syringe filter (0.45 µm) and measured in a glass cuvette on 470, 645, 662, 710 nm against a blank (100% acetone). The chemicals used were of analytical grade quality. The concentration was calculated from the recorded absorbance (A) on specified wavelengths completed with A710 (presence of sediment in the samples):

chlorophyll *a* (µg g^{-1}) = (11.24 * A662 - A710) - 2.04 * (A645 - A710)) * extract volume/thalli weight

chlorophyll *b* (µg g^{-1}) = (20.13 * A645 - A710) - 4.19 * (A662 - A710)) * extract volume/thalli weight

carotenoids (µg g^{-1}) = (1,000 * (A470 - A710) * extract volume/thalli weight - 1.9 * chlorophyll *a* - 63.14 * chlorophyll *b*) / 214

2.5 Chlorophyll *a* fluorescence kinetic measurements

After specimens were dried out and cleaned, they were rehydrated by spraying with distilled water twice a day (in the morning and the afternoon). Thalli were kept under low light (about 10 µmol m^{-2} s^{-1}) at seasonal ambient temperature for 1–2 days until the photosynthetic system regenerated (i.e. until Fv / Fm became constant). In summer samples, this preparation process required more time (3 days) than for thalli collected in other seasons. Chlorophyll *a* fluorescence kinetics were measured (described by Jensen 2002) on fully water-saturated lichen thalli after 30 min. of dark adaptation at room temperature (T = 20–22 °C) with a portable pulse amplitude modulated fluorometer (FMS 2 Hansatech Instruments Ltd. U.K.; Modfluor software) in the laboratory.

After dark adaptation, minimum fluorescence yield in dark-adapted state (Fo) was obtained, using a weak measuring beam for 3 sec. The maximum fluorescence yield of the dark-adapted sample (Fm) was determined with a saturation pulse of 7,500 µmol m^{-2} s^{-1} light intensity for 800 msec. From these parameters, maximum variable chlorophyll fluorescence yield in dark-adapted state (Fv = Fm - Fo) and maximum quantum yield of PSII photochemistry (Fv / Fm = (Fm - Fo) / Fm; Kitajima and Butler 1975) was calculated. The maximum fluorescence yield of the light-adapted sample (Fm') was determined with a saturation pulse of 7,500 µmol m^{-2} s^{-1} light intensity at actinic light 500 µmol m^{-2} s^{-1}. Before the maximum (Fm') and the steady-state (Ft) fluorescence yields were determined, two saturating pulses were added for 800 msec. The yield of photochemical electron transport (φPSII), non-photochemical quenching (φNPQ), and the yield of non-regulated excitation dissipation (φNO) were calculated according to Klughammer and Schreiber (2008) (the last Ft and Fm' values were used for calculations):

$$\varphi PSII = \left(Fm' - Ft\right)/Fm'$$
$$\varphi NPQ = Ft/Fm' - Ft/Fm$$
$$\varphi NO = Ft/Fm$$

Measurement of chlorophyll fluorescence is a non-invasive method, and the measured data can give important information on energy dissipation. Fv / Fm provides information about the condition of the photosynthetic systems within the thalli and shows how efficiently the photochemical reaction is proceeding. φPSII gives insight into the effective photochemical quantum yield of PSII and shows the proportion of use excitation energy for charge separation. φNPQ represents the quantum yield of light-induced (ΔpH- and zeaxanthin-dependent) non-photochemical fluorescence quenching. The φNO describes the combined pathways of radiative and non-radiative deexcitation reactions, which do not lead to photochemical energy conversion and are not involving the NPQ-mechanisms (Klughammer and Schreiber 2008). These are competitive processes, and their sum is equal to 1 (Kramer et al. 2004).

2.6 Statistical analysis

A pairwise t-test was performed to compare the means of micrometeorological data (PAR, RH), taking the average of every 10 min. between the SW- and NE-facing sides of the investigated dune (R Core Team 2020). For seasonal means, the average of a month preceding sample collection was taken using the *dplyr* package (Wickham et al. 2018). For the calculation of direct illumination reaching the dune sides during a year, the geographical characteristic (latitude, longitude), angle of the slopes and solar coordinates were used. 'Sunrise' time means when the direct radiation first reaches the dune side, and 'sunset' is when the last direct beam reaches the side. These are the possible light conditions that can be still affected by humidity and clouds. For the calculation of the seasonal duration of direct illumination and the hypothetical active periods, a 1-month average preceding the sampling was used. The period when relative humidity is higher than 80% is regarded as a hypothetical active period for lichens. The daily activity was calculated after sunrise.

The effect of seasons (summer, autumn, winter, spring) and microhabitats (SW, NE) on plastid pigment concentration, solar radiation screening LSMs and values of quenching mechanisms (response variables) were statistically evaluated. All statistical analyses were carried out with the R software version 3.6.3 (R Core Team 2020). The influence of species, seasons and microhabitats was tested by the three-way ANOVA followed by a Tukey HSD test with 'TukeyHSD' in *agricolae*. The combination of six species, four seasons and two microhabitats resulted in 40 groups. During the analysis, each group were compared to each group. Normality of data distribution was checked visually by Q-Q plot (quantiles of the residuals are plotted against the quantiles of the normal distribution with a 45° degree reference line) with 'qqnorm' and 'qqline' functions of *car* package and by Shapiro-Wilk normality test using 'shapiro.test' of *dplyr*. Our data followed a normal distribution. Levene's test was used to check the homogeneity of variances with 'leveneTest' in *car*. The variances across groups were homogeneous. A level of $p < 0.05$ was considered for a significant difference. Graphs were prepared in R environment (Fig. 3) and MS Excel (Fig. 1 and Fig. 2).

3 Results

3.1 Micrometeorology

According to the four years data series, the microclimatic conditions differed significantly between the NE- and

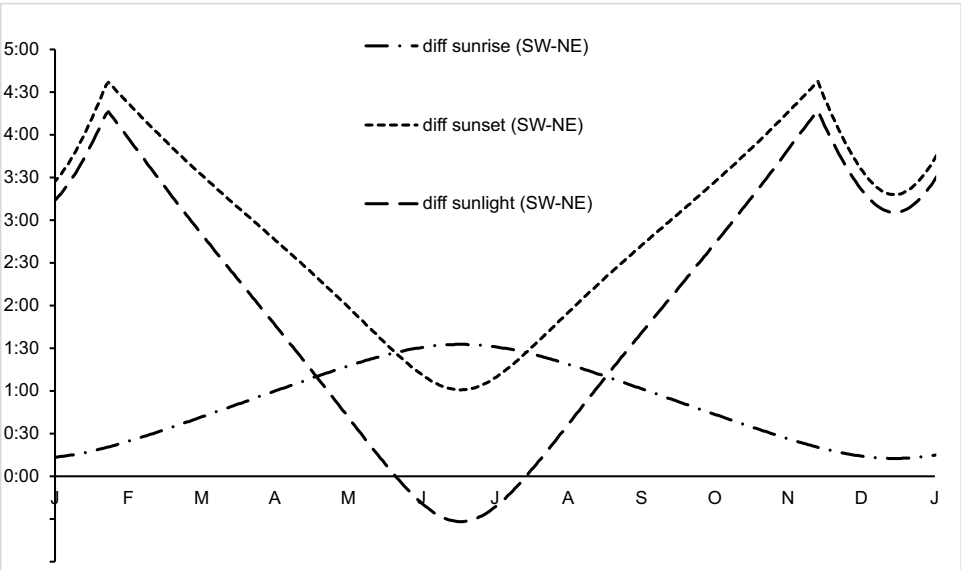

Fig. 1 The mean difference in direct illumination time between the two, exposed south-west (SW) facing and shaded north-east (NE) facing dune sides from January to December corrected with the seasonal solar coordinates and inclination of the slopes. Difference (SW-NE) between 'sunrise' of direct light (diff sunrise) and 'sunset' of direct light (diff sunset) and the difference between the direct illumination length (diff sunlight) between the dune sides.

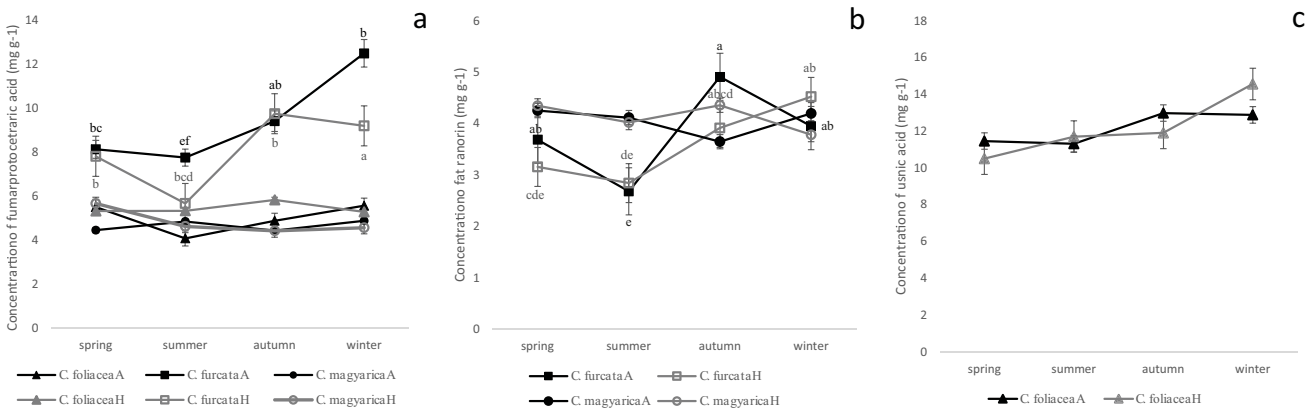

Fig. 2 **a-c** The seasonal and microhabitat variation in mean concentrations of fumarprotocetraric acid (a), atranorin (b) and usnic acid (c) in three *Cladonia* species during a one year investigation period. Populations of *C. foliacea*, *C. furcata* and *C. magyarica* were investigated from exposed arid (A) and shaded humid (H) microhabitats. sd = standard deviation of means, n = 10 / species / season / microhabitat. The different letters sign significant differences (season * microhabitat interaction) in *C. furcata*.

SW-facing sides over the long term. The NE-facing sides were characterized by higher relative humidity ($p < 2e^{-16}$) and lower light intensities ($p < 2e^{-16}$) compared to the drier and more exposed SW-facing sides. Hence, lichen thalli at NE sides are regarded as shade/humid (H) and as sun/arid (A) populations at SW sides (Veres et al. 2020). A clear difference in direct illumination was recorded between the exposed (annual average 11 h 30 min) and shaded (9 h 30 min) dune sides on a long term scale.

The quality and quantity of incoming irradiation varied among the seasons (Table 1). In the winter and autumn months, the direct illumination lasted 3–4 h longer on the exposed than on the opposite side because there was a remarkable difference between 'sunset' time, while there was no significant difference in 'sunrise' time (Fig. 1). During the summer months, the direct illumination reached the shaded side 1–2 hours longer because of the significant difference between 'sunrise' time (Fig. 1). The direct illumination reaching the dune side was ca. 90% of the total irradiation on the arid and 93% on the humid slope during summer, 97% (A) and 57% (H) during winter and 96% (A) and 56% (H) autumn. In spring, no significant difference was detected in direct illumination between arid and humid sides: 91% (A) and 88% (H).

The incoming irradiation varied among the seasons (Table 1) from 14 h 35 min in summer to 4 h 55 min in winter. The average time when the relative humidity rose above 80% (when the water content of lichen thalli shows a significant increase, Blum 1973) also varied among seasons both during the day and at night (Table 1). The average daily

Table 1 Average length (hours) of direct illumination and the length of the hypothetical active period during a year in different seasons in the two humid (NE) and arid (SW) microhabitat types on a dune. Lenght of active period: the period when lichens could be metabolically active (RH > 80% during nights and by 30 µmol m^{-2} s^{-1} < PAR < 1000 µmol m^{-2} s^{-1} (Lange 2003) during days). diff. Start: the difference (SW-NE) in the direct illumination starts between the dune sides (NE = humid, A = arid); diff. End = difference between the direct illumination ended on the dune side. Seasons (1 month periods preceding sampling): summer = 17.07–17.06. 2014, autumn = 23.11–22.10. 2014, winter = 02.02–02.01. 2015, spring = 27.05–27.04. 2015.

	diff. Start	diff. End	Duration of direct illumination		Lenght of active period	
Season			NE	SW	NE	SW
summer day	-1:31	1:09	14:36	14:12	3:07	3:15
summer night					5:18	4:58
autumn day	0:25	4:19	5:31	9:21	4:31	4:48
autumn night					13:02	13:03
winter day	0:19	4:14	4:56	8:46	4:10	7:05
winter night					12:26	14:44
spring day	1:23	1:41	13:03	13:30	3:53	0:39
spring night					6:52	NA

*NA: data are lacking because of wire damage on PAR sensor caused by wild animals

time when photosynthesis may occur was remarkably lower in spring (mean arid: 39 min, mean humid: 3 h 53 min) and summer (mean arid: 3 h 15 min, mean humid: 3 h 7 min) than in autumn (mean arid: 4 h 48 min, mean humid: 4 h 31 min) and winter (mean arid: 7 h 5 min, mean humid: 4 h 10 min). The overnight rehydration lasted twice as long in winter (mean arid: 14 h 44 min, mean humid: 12 h 26 min) and autumn (mean arid: 13 h 3 min, mean humid: 13 h 2 min) than in spring (mean arid: no data, mean humid: 6 h 52 min) and summer (mean arid: 4 h 58 min, mean humid: 5 h 18 min).

3.2 Lichen secondary metabolites

Compared to *C. furcata*, *C. magyarica* showed higher concentration of atranorin (Fig. 2b, Table S.1). Atranorin showed significant seasonal variation only in *C. furcata* ($p = 6.2e^{-10}$) (Fig. 2b, Table S.1), being lower in summer and spring than in winter and autumn. In *C. magyarica* atranorin did not vary across microhabitats ($p = 0.58$) or seasons ($p = 0.32$) (Table S.1). The microhabitat had a remarkable effect on the amount of atranorin in *C. furcata* ($p = 0.007$, Table S.1). Atranorin was usually higher in arid than humid microhabitats in spring and autumn and vice versa in summer and winter.

Cladonia furcata showed approx. two times higher fumarprotocetraric acid concentration compared to the other two *Cladonia* species (Fig. 2a, Table S.2). A seasonal change in fumarprotocetraric acid concentration was detected in samples of *C. furcata* ($p = 7.55e^{-12}$) (lower concentration in summer and spring than in winter and autumn) and *C. foliacea* ($p = 0.03$), unlike in *C. magyarica* ($p = 0.44$) (Table S.2). Sun thalli showed higher fumarprotocetraric acid concentration compared to shade thalli in *C. furcata* ($p = 0.02$) and *C. foliacea* ($p = 0.04$), while microhabitat did not affect the amount of fumarprotocetraric acid in *C. magyarica* ($p = 0.36$) (Table S.2).

A significant seasonal change in usnic acid concentration was found in *C. foliacea* ($p = 0.0004$) (Fig. 2c, Table S.3), being lower in summer and spring than in winter and autumn. Meanwhile, usnic acid did not differ between sun and shade thalli ($p = 0.98$, Table S.3).

3.3 Photosynthetic / plastid pigment concentration

The seasonal change of plastid pigment concentrations differed among the species (Fig. 3a–d, Table S.4–7). Usually, the chlorophyll $a + b$ concentration was lower in *G. fulgens* and *D. muscorum* than in other species (Fig. 3a, Table S.4). *Cladonia foliacea* ($p = 1.58e^{-6}$), *C. furcata* ($p = 0.003$), *G. fulgens* ($p = 0.05$), and *X. pokornyi* ($p = 0.05$) showed significant differences among the seasons (Table S.4). Usually, the minimum values occurred during winter (on average 155–326 µg g^{-1} in *Cladonia* species and *D. muscorum*), except for *G. fulgens* showing maximum (204 µg g^{-1}) during winter. *Gyalolechia fulgens* and *X. pokornyi* occurred only in SW-facing microhabitats; therefore, the comparison was only possible between sun and shade populations of *Cladonia* species and *D. muscorum* (Fig. 3a–d). The concentration of chlorophylls was significantly higher in sun than in shade populations in *C. furcata* ($p = 0.0006$), *C. magyarica* ($p = 0.002$) and *D. muscorum* ($p = 0.04$) (Table S.4).

The chlorophyll a / b showed higher values in *G. fulgens* and lower ones in *C. foliacea* than in the other species (Fig. 3b, Table S.5). There was a seasonal trend in the mean chlorophyll a / b ratio of *C. foliacea* ($p = 3.0e^{-12}$), *C. furcata* ($p = 0.01$), *D. muscorum* ($p = 9.6e^{-5}$), and *X. pokornyi* ($p = 0.02$) (Table S.5). There was no significant difference between arid and humid dune sides in any of the species (Table S.5).

The carotenoid concentration was lower in *D. muscorum* and higher in *G. fulgens* than in the three *Cladonia* species or *X. pokornyi* in each season (Fig. 3c, Table S.6). A significant seasonality of the carotenoid concentration occurred in *C. foliacea* ($p = 6.41e^{-9}$), *C. furcata* ($p = 0.001$), *D. muscorum* ($p = 0.03$) and *X. pokornyi* ($p = 0.006$) (Table S.6). Usually, the highest mean carotenoid concentration was detected in summer (43–145 µg g^{-1}), whereas the lowest values occurred in winter (71–105 µg g^{-1}) for *Cladonia* species and in autumn for the other three species (36–44 µg g^{-1} in *D. muscorum*; 106 µg g^{-1} in *X. pokornyi*; 222 µg g^{-1} in *G. fulgens*). The sun populations contained significantly more carotenoids than shade populations, in *C. foliacea* ($p = 4.29e^{-6}$), *C. furcata* ($p = 4.74e^{-10}$), *C. magyarica* ($p = 2.44e^{-5}$) and *D. muscorum* ($p = 0.002$) (Table S.6).

The ratio of chlorophylls to carotenoids was the lowest in *G. fulgens* and the highest in *D. muscorum* (Fig. 3d). The mean chlorophylls / carotenoids ratio usually peaked in autumn (2.12–4.74) and was the lowest in spring (0.59–4.01). Significant seasonal differences were detectable in *C. furcata* ($p = 1.80e^{-7}$), *C. magyarica* ($p = 4.2e^{-5}$) and *D. muscorum* ($p = 1.9e^{-7}$) (Table S.7). Significant differences were detected in the ratio of chlorophylls / carotenoids between sun and shade populations (shade > sun) of *C. foliacea* ($p = 1.48e^{-6}$), *C. furcata* ($p = 6.07e^{-8}$), *C. magyarica* ($p = 0.02$) and *D. muscorum* ($p = 1.68e^{-7}$) (Table S.7).

3.4 Partition of photochemical, regulated and non-regulated non-photochemical quenching in the different seasons and microhabitat types

The Fv / Fm values of the species (Table 2) provide information about the state of PSII. In general, Fv / Fm was higher in autumn, spring, and in shade thalli than in

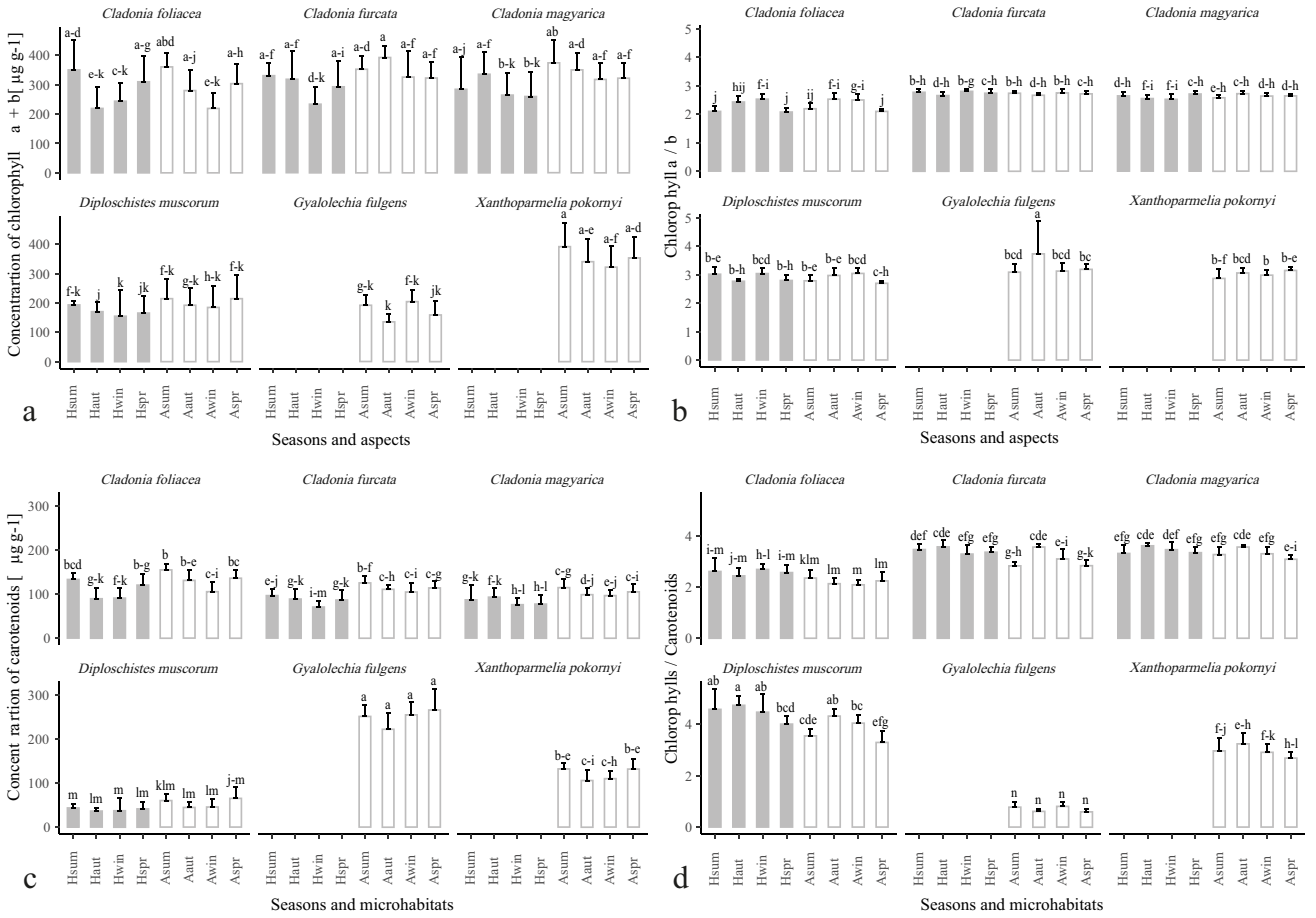

Fig. 3 **a-d** The mean concentration of photosynthetic pigments in six terricolous lichen species. Chlorophyll *a* + *b* (a), chlorophyll *a* / *b* (b), the total concentration of carotenoids (c), chlorophylls / carotenoids (d) of shade (H) and sun (A) populations were investigated from two sides (microhabitat = arid, humid) of a dune in different seasons (sum = summer, aut = autumn, spr = spring, win = winter). The standard deviation of means is also depicted. The columns (groups = species / season / population) with different letters are significantly different within one variable. n = 10 / species / season / microhabitat, except *G. fulgens*, n = 5 / season / microhabitat

Table 2 The seasonal average values (± standard deviation of means) of maximum quantum yield of photosystem II photochemistry (Fv / Fm) measured in the sun and shade population of different lichen species during a year. (n = 20 / species / season / microhabitat, *Gyalolechia fulgens* n = 10 / season / microhabitat). *Gyalolechia fulgens* and *Xanthoparmelia pokornyi* occurred only on arid dune sides.

	ARID				HUMID			
Species	spring	summer	autumn	winter	spring	summer	autumn	winter
Cladonia convoluta	0.69 ± 0.03	0.51 ± 0.07	0.66 ± 0.03	0.65 ± 0.06	0.73 ± 0.03	0.63 ± 0.05	0.72 ± 0.03	0.64 ± 0.09
Cladonia furcata	0.67 ± 0.05	0.51 ± 0.05	0.67 ± 0.06	0.61 ± 0.09	0.71 ± 0.05	0.64 ± 0.09	0.73 ± 0.02	0.7 ± 0.06
Cladonia magyarica	0.67 ± 0.04	0.54 ± 0.06	0.59 ± 0.14	0.59 ± 0.1	0.68 ± 0.05	0.6 ± 0.07	0.72 ± 0.02	0.65 ± 0.06
Diploschistes muscorum	0.64 ± 0.03	0.52 ± 0.06	0.58 ± 0.11	0.56 ± 0.13	0.66 ± 0.04	0.56 ± 0.06	0.66 ± 0.02	0.6 ± 0.06
Gyalolechia fulgens	0.63 ± 0.02	0.53 ± 0.03	0.71 ± 0.02	0.45 ± 0.11				
Xanthoparmelia pokornyi	0.63 ± 0.06	0.6 ± 0.05	0.69 ± 0.02	0.64 ± 0.05				

summer, winter and sun thalli of most species (see also Veres et al. 2020).

The proportion of absorbed excitation energy transformed to photochemical quenching (φPSII) was significantly lower ($p < 0.00001$) in summer than in autumn or winter in each species, except for *G. fulgens* (Table 3, Table S.8). The photochemical quenching was also considerably higher during wintertime compared to summer and spring in *C. furcata* ($p < 0.00001$) and *X. pokornyi* ($p < 0.00001$) (Table 3, Table S.8). The photochemical

Table 3 Mean partition (%) of photochemical (φPSII), regulated non-photochemical quenching (φNPQ) and non-regulated non-photochemical quenching (φNO) (%) in the different species, seasons and microhabitat types (A = arid, H = humid). Standard errors (%) are also shown. The sum of cells with the same background (white for A and grey for H) in a row is 100%. * = different letters indicating a significant difference between seasons within each species (n = 20 / species / season / microhabitat, *Gyalolechia fulgens* n = 10 / species / season / microhabitat)

	φPSII				φNPQ				φNO			
Species	A	*	H	*	A	*	H	*	A	*	H	*
Cladonia convoluta												
springing	21±4%	de	23±5%	cde	46±1%	ab	52±6%	a	33±1%	c	25±6%	cde
summer	13±5%	f	18±5%	e	17±9%	d	32±14%	c	70±13%	a	32±16%	b
autumn	31±5%	ab	32±6%	a	49±5%	ab	51±6%	a	20±02%	e	50±2%	e
winter	27±7%	abc	26±7%	bcd	42±1%	b	51±9%	a	32±12%	cd	23±11%	de
Cladonia furcata												
spring	18±5%	d	22±4%	cd	34±12%	bcd	45±13%	a	48±12%	b	32±11%	cd
summer	19±6%	d	20±8%	d	18±11%	e	28±13%	d	64±15%	a	34±17%	ab
autumn	39±6%	a	37±9%	a	39±5%	abc	44±7%	ab	22±4%	d	52±3%	d
winter	28±1%	bc	35±6%	ab	29±15%	cd	43±6%	ab	44±23%	bc	22±5%	d
Cladonia magyarica												
spring	22±7%	b	22±6%	bc	36±07%	bcd	42±1%	abcd	42±07%	ab	36±13%	bc
summer	16±5%	c	19±7%	bc	32±13%	d	44±13%	ab	52±14%	a	31±11%	bc
autumn	31±5%	a	33±7%	a	33±11%	cd	46±8%	a	36±16%	bc	37±3%	d
winter	22±5%	b	29±7%	a	33±12%	d	43±9%	abc	45±15%	ab	28±7%	cd
Diploschistes muscorum												
spring	24±5%	cd	23±4%	cd	33±8%	bc	37±5%	ab	43±09%	bc	40±6%	bcd
summer	19±4%	d	19±3%	d	26±13%	c	36±14%	ab	55±14%	a	36±14%	abc
autumn	33±4%	b	39±4%	a	31±7%	bc	35±6%	ab	35±1%	cde	45±4%	e
winter	25±1%	c	27±5%	c	28±9%	bc	42±8%	a	47±18%	ab	31±9%	de
Fulgensia fulgens												
spring	20±5%	b			47±6%	a			34±7%	b		
summer	15±4%	b			17±12%	b			67±13%	a		
autumn	32±2%	a			42±6%	a			25±2%	b		
winter	14±12%	b			08±18%	b			78±28%	a		
Parmelia pokornyi												
spring	14±7%	c			26±12%	b			60±14%	a		
summer	17±3%	c			18±12%	b			65±14%	a		
autumn	35±5%	a			42±8%	a			23±4%	b		
winter	27±7%	b			42±8%	a			30±11%	b		

quenching differed significantly between the sun and shade populations in only a few cases. However, the response of photochemical quenching to seasonal environmental changes seemed to be species-specific (Table 3, Table S.8).

A significantly lower ($p < 0.00001$) amount of the absorbed excitation energy could be dissipated in a regulated way (φNPQ) in summer than in other seasons for *C. foliacea*, *C. furcata* and *X. pokornyi* (Table 3, Table S.9). Meanwhile, *C. magyarica* ($p = 0.87$) did not show remarkable differences among the seasons, whereas *G. fulgens* and *D. muscorum* exhibited the opposite seasonal pattern (Table 3, Table S.9). Generally, the φNPQ was higher in the shaded (mean 28–52%) compared to the exposed (mean 17–49%) microhabitats ($p < 2e^{-16}$). This difference was always significant during winter in each species, whereas a species-specific response was characteristic for the other seasons (Table 3, Table S.9).

The proportion of absorbed excitation energy transformed to φNO was significantly higher in summer ($p < 0.01$) than in other seasons in each species except for *G. fulgens*, where winter samples showed the highest values (Table 3, Table S.10). The φNO was usually higher in the exposed (mean 20–70%) than in the shaded (mean 18–52%) microhabitats (Table 3).

4 Discussion

4.1 Seasons

A significant seasonal trend was detectable in the concentration of lichen secondary metabolites, plastid pigments and the proportion between ways of excitation energy absorbed by the antenna complex. Higher irradiation and lower relative humidity (RH) characterized the climate in summer and late spring (Veres et al. 2020). In bright and warm seasons, thallus WC can reach even 90% at dawn, but the fast dehydration after sunrise (1–1.5 hours, Verseghy 1971) can partly protect the lichen thalli against the harmful effects of the high irradiation (Heber et al. 2001; Veerman et al. 2007). During hydration periods in the morning, repair of damage from the previous day may occur (Weissman et al. 2005). Low RH after sunrise shortens the rehydrated state, and therefore the duration of active metabolism in summer. During drought periods, RH does not exceed the critical level for active metabolism even at dawn (Verseghy 1971). Without nocturnal hydration, the damage could slowly accumulate (Mayaba and Beckett 2001). Besides, the water uptake of the species is also lower in summer in the region (Verseghy 1971). During the night, dew and high RH (e.g. Lange et al. 1990; Lange 2003; Raggio et al. 2014) can provide a water source for active metabolism including synthesis of solar radiation protectant LSMs. Moisture conditions were not favourable for both metabolite synthesis and repairing mechanisms during nights in drier seasons. The results of Rajczy (1982) supports our findings revealing that *C. furcata* and *C. foliacea* became wet between 22–23 p.m. and took up water until 1 a.m. between dunes at Fülöpháza in the middle of summer. One hour before sunrise, they took up water again. The morning dew was formed at sunrise (4.15 a.m.), and from that time, lichens lost water until 6–7 a.m. when the critical hydration level was reached. Because the lichen can only produce solar radiation protectant substances in the hydrated state (Solhaug et al. 2003), the decreased level of these metabolites in the dry summer may result from short active periods insufficient to provide required amounts of photosynthates for LSM synthesis (Solhaug and Gauslaa 2004) in summer. Our results showed that despite the fact that the highest amount of precipitation was measured in summer, only 13–19% of incoming radiation was used for photochemical quenching. Verseghy (1976) pointed out that lichens exhibited the lowest biomass production during summer in the Kiskunság region. The lowest biomass increase occurs in summer and the highest in autumn (Lange 2003b; Verseghy 1976). Days with dew and nocturnal rain contributes more to the annual net primary production than heavy rain (Lange 2003a, 2003b; Veste et al. 2001).

Furthermore, the short hydrated periods can increase the need for more efficient use of light due to the higher amount of chlorophylls and carotenoids (Demmig-Adams and Adams 1992; Pintado et al. 1997). However, the seasonal changes in chlorophyll concentrations could also reflect fluctuations in the photobiont populations (Tretiach et al. 2013). Vráblíková et al. (2006) and MacKenzie et al. (2001) also demonstrated seasonal variation in the content of lichen chlorophyll and xanthophyll which was related to seasonally changing light conditions. Our lichens were mostly dehydrated during summer. The protection of PSII is critical since photodamage can also occur in an air-dry thallus (Gauslaa and Solhaug 1999; Heber et al. 2010; Solhaug et al. 2003), when the RCs are also active (PSI is not or partially inhibited by desiccation). The dissipation of excess light energy is essential since excitation energy flow used for charge separation is not possible (Heber et al. 2006). It seems that in summer, the φNPQ was less involved in dissipating excess light energy (φNO > φNPQ), especially in arid microhabitats. Combined pathways of radiative and non-radiative deexcitation reactions were probably dominant in the form of heat and fluorescence, mainly due to closed PSII reaction centres (Klughammer and Schreiber 2008). Lichens probably possess mechanisms to protect PSII while desiccated or they can repair it upon rehydration. Lichens can protect the PSII due to reversible desiccation of the thallus. In the desiccated state, the energy quenching is mainly through non-regulated non-photochemical quenching mechanisms rather than by conformation changes in the chlorophyll-protein complex (Flores-Bavestrello et al. 2016). Furthermore, in summer, there were nights (8 days before sampling) when RH could not reach 80%, significantly reducing the chance for rehydration and starting active metabolism, and thus the regeneration of the PS, recovery of NPQ or the antioxidant enzyme production responsible for the deactivation of ROS (Aoussar et al. 2018; Veerman et al. 2007).

During winter and autumn, high and more stable air humidity and lower irradiation frequently occur (Lange 2003b; Veres et al. 2020), creating a more extended favourable environment for lichen metabolism and photosynthesis. The temperature dropped below the freezing point for only two days during the whole measuring period, one month before the winter sampling, allowing higher net photosynthesis than in harsh winters (Lange 2003b; Tuba et al. 2008). These may require a smaller chlorophyll antenna size for effective light-harvesting (Jin et al. 2001). In the hydrated

state, the cortical transmittance (Dietz et al. 2000) and the production of light screening fungal metabolites increase (Solhaug et al. 2003). Similar results for *C. foliacea* were found by Farkas et al. (2020): the amount of usnic acid and fumarprotocetraric acid showed higher concentrates in winter than summer. The concentration of usnic acid in *Cladina mitis* was also significantly higher in autumn and winter (BeGora and Fahselt 2001). Gauslaa and McEvoy (2005) observed the reverse seasonal courses for the cortical solar radiation screening pigment, parietin in *Xanthoria parietina* peaked in summer. Furthermore, φNPQ was higher than φNO in our study, indicating that the antenna complex had safely dissipated the excessive light as heat and the energy flux of the photosynthetic apparatus worked efficiently during winter and autumn. Heber et al. (2006) also showed that the desiccation-induced quenching decreased in humid seasons and increased in late spring and summer. During autumn, on average, more than one-third of the excitation energy was utilized by photochemical processes leading to the most productive period of the year in semi-arid sandy grasslands, as also found by MacKenzie et al. (2001), Raggio et al. (2014) and Verseghy (1976). Tuba et al. (2008) pointed out that temperature had a significant role for the chlorophyll content of lichens and mosses. Our results suit to the measured values of Tuba et al. (2008) in *C. foliacea* and *C. furcata*. The temperature data originating from our measurements justify that there was a mild winter during the study period (Veres et al. 2020).

4.2 Aspect (microhabitats)

A more contrasting environmental difference may be required, for example, different forest stands (Gauslaa et al. 2006), to induce a clear difference between sun and shade lichen populations. The detected significant differences in photoacclimation and -protection between the sun and shade populations could be explained by factors characterizing arid and humid seasons (see the section on 'Seasons' above). However, the proportion of φNPQ was significantly impacted by the exposure of thalli, particularly in summer and winter. Less time is available for photosynthesis in sun populations during summer and in shade populations during winter. In winter, the direct illumination lasts longer on the exposed than on the shaded side of the dune because of later sunset time. In summer, the direct illumination on the arid side is shorter than that on the humid side because of the later sunrise. An effective light-harvesting (Pintado et al. 1997) and excess light dissipation (Vráblíková et al. 2006), mainly via φNO (Flores-Bavestrello et al. 2016), is required in both seasons. The higher level of φNPQ (and lower proportion of φNO) on humid microhabitats indicates a longer active period. The more variable weather conditions (clear and overcast) result in a less contrasting difference between the sun and shade populations in spring and autumn. Our results also showed that the non-photochemical quenching parameters are more affected by the microhabitat conditions than that the photochemical quenching in most seasons.

4.3 Species-specific response

The seasonal variations of investigated parameters showed species-specific differences. Lichens are poikilohydric organisms that cannot actively regulate their water content. However, they can extend or shorten their metabolically active period and protect themselves due to different long term adaptation strategies (e.g. morphological traits). *Cladonia furcata* exhibits a thin cortical layer allowing rapid water uptake and fast water loss (Colesie et al. 2017; Dietz et al. 2000; Verseghy 1971). A thin cortex rapidly becomes more translucent during rehydration than a thick cortex. A thin cortex presumably contains less solar radiation protectant atranorin than a thicker cortex (needs further evidence). Therefore, a higher protection of PSs against the harmful excess light energy reaching the photobiont layer is needed (Heber et al. 2006), which may explain the high concentration of fumarprotocetraric acid accumulating on the surface of the hyphae in the photobiont layer (Honegger 1986). The moderate proportion of φNPQ and φNO (less non-photochemical quenching needed) supports the efficiency of absorbing light (Nguyen et al. 2013) of the metabolite. On the other hand, *C. furcata* can benefit from the thin cortex due to rapid air moisture uptake in humid periods (Verseghy 1971), explaining the highest φPSII among the species.

Cladonia magyarica showed a constant high atranorin concentration during the year compared to the seasonally changing level in *C. furcata*. The more stable humidity conditions beneath *C. magyarica* thalli due to the water retention ability of moss cushions (Colesie et al. 2012) and the higher water retention capacity of the species (Verseghy 1971) may allow a continued high level of solar radiation screening in the upper cortex (Heber et al. 2006; Solhaug et al. 2003).

Among the cortical solar radiation protective pigments, usnic acid in *C. foliacea* exhibited approximately four times higher concentrates than those measured for atranorin (*C. magyarica*, *C. furcata*). Furthermore, the species can avoid photoinhibition due to curling during desiccation (Barták et al. 2006). Usnic acid plays a significant role when the species is rehydrated and hence unfolded since the thalli have only a dense, upper cortex; otherwise, the thick, white medulla covers them (Verseghy 1971). The thicker cortex may contain a higher amount of cortical pigment (needs further evidence). Meanwhile, during the extended dehydrated period, long-lasting protection is required against harmful excess light indicated by the highest level of φNPQ.

The working mechanisms of the two LSMs are also different. Atranorin is a more labile metabolite, reflects the incoming light (Nguyen et al. 2013) and has a low or moderate SPF (sun protection factor) (Nguyen et al. 2013); however, usnic acid absorbs light and functions as a very effective solar radiation screening pigment (Rancan et al. 2002) that also protects against PAR (McEvoy et al. 2007). Färber et al. (2014) also pointed out the difference in the efficiency of cortical pigments in pendulous lichen species.

The concentration of carotenoids can indicate both the size of the antenna complex and the xanthophyll pool as they could participate both in light-harvesting and in photoprotection (Demmig-Adams 1990; Müller et al. 2001). Although our investigation did not cover the qualitative analysis of the carotenoid composition, it did acquire useful information on the proportion of excessive light energy. In *D. muscorum*, the relatively low chlorophyll, the lowest carotenoid concentration among the species, and the relatively high proportion of φPSII suggest that this species can receive enough photons for assimilation due to the prolonged hydration period on moss cushions (Colesie et al. 2012). This lichen can protect itself by mechanisms other than φNPQ and φNO. The pale colour (high albedo) and the pruinose surface likely increase in light reflectance, thus protecting the thallus from excessive light. The highest chlorophyll / carotenoid ratio among the investigated species suggests that the mycobiont in this species provides strong screening pigments (Gauslaa and Goward 2020) or structure (Gauslaa et al. 2017) to protect the photobiont, which likely is adapted to the low light conditions inside the thallus (Demmig-Adams and Adams 1992).

Gyalolechia fulgens showed the lowest proportion of φPSII, φNPQ and chlorophyll concentration and the highest proportion of φNO and carotenoid level, suggesting that this species experiences a shorter period in the wet state compared to other species (Pintado et al. 1997). The highest carotenoid level likely contributes more to photoprotection due to the direct defence of the thylakoid membrane (Müller et al. 2001) than the anthraquinone compound or whitish pruina in the cortex.

Xanthoparmelia pokornyi, occurring only in arid microhabitats, showed the highest chlorophyll concentration and relatively high carotenoid concentration as well. Since the φNPQ was relatively low, the carotenoids could participate mainly in an effective light-harvesting caused by the rapid desiccation in the exposed microhabitats. The species-specific acclimation mechanisms were also confirmed by earlier studies on plastid pigment concentrations across different habitat types (Balarinová et al. 2014; Cempírková and Večeřová 2018; Dymova and Kuzivanova 2018; Paoli et al. 2010, 2017) and seasons (Higgins et al. 2015).

5 Conclusions

The different species can acclimate to the changing environmental conditions (humidity, light) by taking advantage of each season in various ways, as formerly documented by Paoli et al. (2017). During drier and brighter seasons, the mycobiont (by fungal screening in the cortex and fungal induced curling) in *C. furcata* and *C. foliacea*, has a significant role in the protection of the photosynthetic system. Meanwhile, in wetter seasons, under lower light intensity, the protecting role of the photobiont increases. Since the synthesis of light screening LSMs requires more time (days, Solhaug and Gauslaa 2004; Verma et al. 2012) than is necessary for the activation of non-photochemical quenching mechanisms (e.g. VAZ cycle 5–10 minutes, Müller et al. 2001), the latter seems to be a more efficient process during the short metabolically active period in drier and brighter seasons. In other species (e.g. *C. magyarica*), the mycobiont and photobiont increase the production of these substances simultaneously to achieve a more effective excess energy dissipation. The regulated non-photochemical quenching showed the highest variance among the species and the highest difference between sun and shade populations (compared to seasonal changes) and is thus the most species- and microhabitat-specific protection mechanism. Our results showed that only c. 25% of the absorbed light energy was utilized in photochemical processes. It confirms that the balance between energy conservation and dissipation is shifted towards dissipation in poikilohydric organisms compared to vascular plants (Heber et al. 2006).

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Data availability Data are available on request. Lichen specimens are deposited in the Lichen Herbarium VBI (Vácrátót, Hungary).

Code Availability Not applicable

Declarations

Conflicts of interest We have no conflicts of interest to disclose.

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