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PhD Thesis

The bright and shaded side of duneland life from lichens' point of view

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By

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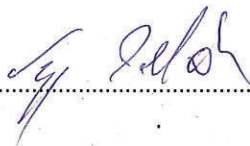
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BACKGROUND AND THE AIMS OF THE INVESTIGATION

Inland dune ecosystems are rich in terricolous lichen species. However, these communities are sensitive to human activities, both locally and globally. Terricolous lichens are relevant associates of biological soil crusts in arid and semi-arid environments. The function of lichens is affected by the changing seasons and different microhabitat conditions. Dunes are inhabited by ecosystems of high conservation interest because of their unique, vulnerable and threatened features. At the same time, inland dunes are less investigated from the terricolous lichens point of view. Because of the low amount ($n = 10$) of investigations carried out between inland dunes, we still have limited information on terricolous lichen assemblages and the main drivers, especially soil surface variables, that shape the community in these ecosystems in Europe. Since only two studies (Jüriado *et al.* 2016, Gheza *et al.* 2020) were known about the lichen communities of calcareous sandy grasslands between inland dunes in Europe, the description of these communities from Hungary can significantly contribute to our knowledge. The effect of environmental conditions caused by human activities (disturbance history at a site scale) or the topography (at a landscape scale) and micro-environments (at dune scale) of inland dunes on the composition of the lichen communities is poorly known in Pannonian semi-arid sandy grasslands.

Lichens could adapt and acclimate their photosynthesis and photoprotection to changing environments differently. However, the investigations mainly were carried out on epiphytic or saxicolous lichens. Only a few works focused on exploring the acclimation of terricolous lichens to the changing environment in semi-arid grasslands (e.g. Kalapos & Mázsa 2001;

Tuba *et al.* 2008). And the continuous micrometeorological monitoring of the environment of lichens was also rare (e.g. Lange 2003a).

In lichens, each symbiotic partner cooperates to survive the symbiotic association. The protection of the 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 (Nash 2008). The fungal partner, which makes up the main mass of the thallus, is responsible for the drying out and the production of UV-protectant lichen metabolites. Regulated and non-regulated non-photochemical quenching mechanisms help remove the extra excitation energy from the photochemical system to prevent damage to proteins and membranes in the algae. However, there is less information on the extent of contribution in partners or the changes during seasons and between microhabitats with different light conditions.

1. The main goal of the PhD work was to explore the lichen community of an inland duneland ecosystem on calcium-rich sand, the main factors influencing the community at different scales (disturbance history, microclimate, soil surface variables), and the habitat preference of the species.

2. The second goal was to reveal the acclimation of the photosynthetic activity and photoprotection to the changing environment in space (microhabitat) and time (seasonality) combined in the seven most abundant terricolous species of the lichen community.

3. The third goal was to describe the changing proportion of absorbed light between photosynthesis and the different photoprotective quenching mechanisms in terricolous lichens.

4. Usually, only one species is grabbed from the lichen community of a given area and point in time for a study object. We intended to expand the

circle of research objects deriving from the same habitat in different seasons to get closer to the entire picture of the mechanisms working in lichens.

MATERIALS AND METHODS

Study sites

The two investigated sites were located in the Kiskunság National Park near Bugacpusztaháza ('BU') and near Fülöpháza ('FH') in Central Hungary. The climate is moderately continental with a sub-Mediterranean influence on both study sites (Péczely 1967). The region is mainly covered by calcareous sand from the deposits of the Danube River. As a secondary effect, the wind reshaped the landscape resulting in North-East (NE) and South-West (SW) facing dune sides with interdune depressions between them (Pécsi 1967). The natural vegetation has been exposed to intensive human impacts for at least two millennia in the region (Biró & Molnár 1998; Molnár *et al.* 2012). The dominant plant association was semi-arid sandy grassland (*Festucetum vaginatae* 'danubiale' Rapaics ex Soó em. Borhidi association) at the investigation sites. Most of the terricolous lichen species found here are members of the 'Bunte Erdflechten-Gesellschaft' (Gams 1938), also known as the complex of *Fulgensietum fulgentis* Gams and *Cladonietum symphyrcarpiae* Doppelb. associations, typical for this region (Büdel 2001).

Micrometeorological data collection

Two micrometeorological stations were placed at the Bugacpusztaháza site, on the opposite sides of a dune with NE and SW expositions. Later the data served as a basis of distinction according to the aridity of dune sides. It was hypothesised that the conditions on the selected dune represent the prevailing

conditions on other dunes of similar morphology and aspects found in the territory. Two micro stations were used with sensors of air temperature (T_{air}), relative humidity (RH), and photosynthetically active radiation (PAR, 400–700 nm) at 0.5 m height and soil temperature (T_{soil}) and soil water content (WC_{soil}) at 5 cm deep in the sand. Data were continuously recorded each minute during the four years investigation period. Vapour pressure deficit (VPD) was also calculated from measured data. We also used meteorological and precipitation data of the meteorological station of the Department of Plant Physiology and Plant Ecology of the Hungarian University of Agriculture and Life Sciences at Bugacpusztaháza and the Centre for Ecological Research at Fülöpháza. We also estimated a hypothetically metabolically active period of lichens during nights ($PAR = 0 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $RH > 80\%$) and a period when weather conditions could be suitable for photosynthesis ($30 \mu\text{mol m}^{-2} \text{s}^{-1} < PAR < 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $RH > 80\%$) during the daytime, based on Lange (2003) and Verseggy (1971).

Lichen material

The most abundant species have been collected for physiological measurements: *Cladonia foliacea* (Huds.) Willd., *Cladonia furcata* (Huds.) Schrad., *Cladonia magyrica* Vain., *Diploschistes muscorum* (Scop.) R. Sant., *Gyalolechia fulgens* (Sw.) Søchting, Frödén and Arup, *Thalloidima physaroides* (Opiz) Opiz. and *Xanthoparmelia pokornyii* (Körb.) O. Blanco, A. Crespo, Elix, D. Hawksw. and Lumbsch. Lichens were identified according to Smith *et al.* (2009), Verseggy (1994) and Wirth *et al.* (2013). The nomenclature follows the Index Fungorum CABI (2020) and Farkas & Lőkös (1994). After measurements, voucher specimens were deposited in Lichen Herbarium VBI, Hungary. The species hosted eukaryotic green algae: various species of *Asterochloris* in *Cladonia* species, and *Trebouxia* species in *G. fulgens* and

X. pokornyi. *Diploschistes muscorum* switches photobiont during its lifespan: *Asterochloris* in the early stage, *Trebouxia* later. In the early stages, the photosynthetic partner of *T. physaroides* is a cyanobacterium switched to coccoid green algae over time.

Sampling method

Coenology

At Bugacpusztaháza six, Fülöpháza four, overall ten stands were located on randomly selected SW and NE aspects of different dunes, representing the duneland vegetation of the area. On each stand (i.e. dune side), one 1 m × 1 m sampling quadrat was placed (10 quadrats in total). The quadrats had 10 × 10 sections (100 micro-quadrats per quadrat). In each micro-quadrat, the coverages of lichen growth forms (% fruticose, foliose and crustose), moss (%), vascular plant (%), litter (%) and bare soil (%) were evaluated with Braun-Blanquet method (1964). The average height of vascular plants (mm) was also measured. The presence or absence of each lichen species was also recorded. Many lichen species were identified in the field, while others were transported to the laboratory and then examined with thin-layer chromatography (HPTLC) using the method of Arup *et al.* (1993). Lichen species that fell out of the sampling units were also recorded and added to a complete species list of the area.

Physiological measurements

Thalli were collected from populations living on both the SW and NE oriented microsites in each of four seasons (spring, summer, autumn, winter) when possible. Ten replicates per season per stand were measured in each species. Because of the low abundance, only five *G. fulgens* samples per

season per stand were analysed. Altogether almost 1200 specimens were collected during the investigation period. *Gyalolechia fulgens* and *X. pokornyi* occurred only on the SW sides of the dunes. After sample collection, thalli were transported to the laboratory and dried out under seasonal temperature, humidity, and light regime. After that, thalli were cleaned from plant and moss particles.

Laboratory measurements

Chlorophyll a fluorescence kinetics

After rehydration and dark adaptation, lichen thalli were measured using portable pulse amplitude modulated fluorometer as Jensen (2002) described. The maximum quantum yield of PSII photochemistry (F_v/F_m), Stern-Volmer non-photochemical quenching (NPQ), the yield of photochemical electron transport (ϕ_{PSII}), non-photochemical quenching (ϕ_{NPQ}), and the yield of non-regulated excitation dissipation (ϕ_{NO}) were calculated. The ϕ_{PSII} gives insight into the effective photochemical quantum yield of PSII and shows the proportion of use excitation energy for charge separation. When the electron transport chain is saturated, the excitation energy can be re-emitted as fluorescence or dissipated as heat. The ϕ_{NPQ} represents the quantum yield of light-induced (ΔpH - and zeaxanthin-dependent) non-photochemical fluorescence quenching. The ϕ_{NO} 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 & Schreiber 2008). The parameters ϕ_{PSII} , ϕ_{NPQ} , and ϕ_{NO} are competitive processes, and their sum equals 1 (Kramer *et al.* 2004).

Photosynthetic pigments and lichen secondary metabolite concentration

The concentration of plastid pigments was measured by spectrophotometry according to Pfeifhofer *et al.* (2002) with minor modifications based on Lichtenthaler & Buschmann (2001). The concentrations of lichen secondary metabolites (LSMs) were measured by high-performance liquid chromatography based on Ji & Khan (2005). The amount of atranorin and fumarprotocetraric acid in *C. furcata* and *C. magyarica*, and usnic acid and fumarprotocetraric acid in *C. foliacea* were analysed.

Data analysis

Micrometeorological data

The Shapiro-Wilk test was applied to test the normality of the data. A pairwise t-test was performed to compare the means of micrometeorological data, taking the average of every 10 minutes between the SW and NE facing sides of the investigated dune. In the case of seasonal means of parameters, the average of the month preceding sample collection was taken. 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.

Coenological data

We compiled a detailed species list of the two study sites, where the previous (Lőkös & Verseggy 2001) and present occurrences were combined and compared. Only lichen and soil surface variables data collected in micro-quadrats were used for quantitative analyses. The effects of the site ('BU' or 'FH') and dune side (SW facing = arid or NE facing = humid side) on the environment (cover of bryophytes, vascular plants, soil, litter and height of vascular

plants) and lichen related (species number, total lichen cover, cover of three growth forms) variables were evaluated. First, Non-metric Multidimensional Scaling (NMDS) using Jaccard-dissimilarity was applied to unfold the species composition among sites and dune sides based on all sampled micro-quadrats; additionally, Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to test the separation using the Manhattan metrics on pooled (i.e. quadrat-level) frequency data. Then species richness and cover of lichen growth forms, as well as the different substrate forms as potential drivers of lichen species, were further investigated by generalised mixed-effects models (GLMMs), where site and dune side were set as fixed effects and quadrat as a random term. Finally, the relationships between the presence of the eight most abundant lichen species, the site, the dune side and the environmental variables were tested by separate logistic mixed-effects models. Prior to these analyses, all tested fixed factors were centred and scaled ('z-score standardisation').

Chlorophyll a fluorescence kinetic parameters, LSMs and plastid pigment concentrations

The effect of seasons and exposition of microhabitats on plastid pigment and solar radiation screening LSMs concentration and values of quenching mechanisms (response variables) were statistically evaluated. The influence of species, seasons and microhabitat exposition to response variables were tested by the three-way analysis of variance followed by a paired comparison by Tukey HSD test. The 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) and by Shapiro-Wilk normality test. Levene's test was used to check the homogeneity of variances. A level of $p < 0.05$ was considered for a significant difference.

RESULTS AND DISCUSSION

Micrometeorological data

According to the four-year data series, the microclimatic conditions differed significantly between the NE- and SW-facing sides over the long term. The T_{air} , PAR (corrected with slope and orientation), T_{soil} and VPD values were significantly higher ($p < 0.001$) on the SW than on the NE oriented side, where the RH and WC_{soil} proved to be significantly higher ($p < 0.001$). The daily fluctuation of differences for every micrometeorological parameter changed seasonally. The highest daily fluctuation was observed in summer. A balanced difference in light and humidity conditions between dune sides was detected in winter. According to our results, the SW facing sides were considered as arid, the NE facing dune sides as humid microhabitats.

A clear difference in direct illumination was recorded between the arid (annual average 11 h 30 min) and humid (9 h 30 min) dune sides at a long term scale. The quality and quantity of incoming irradiation varied among the seasons. In the winter and autumn months, the direct illumination lasted 3–4 h longer on the arid than on the opposite side because there was a remarkable difference between 'sunset' time. During the summer months, the direct illumination reached the humid side 1–2 hours longer because of the significant difference between 'sunrise' time. The length of incoming irradiation varied among the seasons from 14 h 35 min in summer to 4 h 55 min in winter.

The average time lichens could spend in a metabolically active state also varied among seasons during the day and at night. The average daily time when photosynthesis may occur was remarkably lower in late spring and summer (from 39 min to 3 h 53 min) than in autumn and winter (from 4 h 10 min to 7 h 5 min). The overnight rehydration lasted twice as long in winter

and autumn (between 12 h 26 min and 14 h 44 min) than in spring and summer (between 4 h 58 min and 6 h 52 min).

Inland duneland terricolous lichen community

Soil surface variables on the two investigated sites and dune sides and their influences on the species appearance

The average moss cover was higher ('FH': $p < 0.05$), but the vascular plant cover ('FH': $p < 0.01$) and height ('BU': $p < 0.01$, 'FH': $p < 0.001$) was lower on arid than on humid dune sides. Almost all abundant species (found in > 50 micro-quadrats and at both sites) were negatively influenced by a higher moss cover. The cover of disturbed topsoil negatively affected the abundance of *C. magyarica*, *Cladonia pyxidata* (L.) Hoffm. ($p < 0.001$) and *D. muscorum* ($p = 0.041$). *Cladonia foliacea* was negatively affected by higher vegetation ($p = 0.001$). Higher coverage of leaf litter had a strong association with *P. canina*. *Diploschistes muscorum*, on the other hand, preferred growing in and on moss patches. The presence of *C. foliacea*, *C. furcata*, *C. rangiformis*, *Xanthoparmelia* species, *Squamrina lentigera* (Weber) Poelt and the crustose *D. muscorum* and *G. fulgens* were more abundant in patches where vascular plant height was lower. The position of the species in the ordination space indicated that the species has heterogeneous preferences. However, the degree of segregation by site and exposition was significant.

The revealed difference in herb height and cover between sides could cause a difference in the light level reaching lichen thalli, resulting in different microclimatic conditions where lichens with different environmental needs could find their preferred niche resulting in different lichen communities on the opposite sides. Our results agreed with the observation that vegetation generally becomes more open with increasing aridity (Walter & Breckle

1984) and lichens compete with mosses for free patches (Ketner-Oostra & Sýkora 2000).

Lichen communities of the two investigated sites and dune sides

Twenty terricolous lichen taxa were recorded at the Bugacpusztaháza and 19 at the Fülöpháza site (in total 22 taxa). Five of them were new to the sites from this investigation, and eight formerly reported species were not confirmed during the present study. Nine species were only found on humid dune sides (e.g. *Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng., *Endocarpon pusillum* Hedw., *Peltigera canina* (L.) Willd.). Nine other species occurred only on arid sides of the dunes (e.g. *G. fulgens*, *X. pokornyi*). Nine species occurred on both dune sides. The core lichen species composition of Fülöpháza arid dune sides is much different from the arid core species of Bugacpusztaháza. In contrast, humid core lichen species composition showed a notable overlap between the sites. The Bugacpusztaháza site appears to have had a higher lichen species turnover and less species retention than Fülöpháza.

The site, dune side exposition and environmental factors were important factors determining terricolous lichen assemblages. The site had higher explanatory power than the aspect of the dunes in species composition ($p < 0.0046$ and $p = 0.0231$, respectively). The NMDS (stress = 0.102) showed a separation among dune sides and sites. The ordination using two orthogonal dimensions cumulatively represented 59.61% of the variation of species composition (Mantel tests; NMDS 1: $r^2 = 0.349$, $p < 0.001$; NMDS 2: $r^2 = 0.247$, $p < 0.001$). The species richness was more affected by the site than the side. Species richness was significantly higher at 'FH' than at 'BU' ($p < 0.001$). At the 'FH' site, the total species richness was significantly higher ($p < 0.001$) in arid micro-quadrats (mean: 3.66; range: 0–9) compared to humid

micro-quadrats (1.55 [0–4]). The opposite was detected at BU, where the humid sides (1.69 [0–4]) hosted more species ($p = 0.056$) than arid ones (1.16 [0–4]). The cover of fruticose species was higher on humid than on arid sides. The site had a high explanatory power explaining community composition in our study. Since we could not find any significant difference in the climate between the two study sites, and the investigated soil surface variables differed significantly only in open soil cover according to the literature data, we hypothesise that the disturbance history played an important role in developing different lichen communities suiting the results of Leppik *et al.* (2013).

Slightly fewer terricolous lichen taxa were found in the present research (Bugacpusztaháza 20; Fülöpháza 18; overall 22 species) compared to other European countries (Estonia 28 (Jüriado *et al.* 2016); Italy 33 (Gheza *et al.* 2020)) in calcareous sandy grasslands and half of the species also recorded belong to the genus *Cladonia*. The most frequent *C. foliacea*, *C. furcata*, *C. magyarica / pyxidata* and *D. muscorum* were found on acidic and calcareous soils and in arid and humid microhabitats proving their broad ecological tolerance (e.g. Adamska 2010; Balogh *et al.* 2017). Five of the lichen species recorded in the study area are listed on the Red List of lichens as occurring in Hungary and lacking in other mentioned European areas (Farkas & Lökös 2006; [Hungarian] Ministry of Rural Development 2013).

The influence of seasonality and microhabitat conditions on chlorophyll *a* fluorescence kinetics

For each of the investigated species, both seasonality and aspect had an effect on Fv/Fm ($p < 0.001$), as well as on NPQ ('BU' season: $p < 0.001$, aspect: $p = 0.006$; 'FH' $p < 0.001$ for both season and aspect).

Higher Fv/Fm values were measured in humid than in arid microhabitats. As previously revealed for epiphytic lichen species (e.g. Atala *et al.* 2015), there is a more remarkable, long-term reduction in Fv/Fm in lichens living in sunny, open places compared to shade populations. Usually, the spring and autumn samples showed higher values than the summer and winter samples, indicating that lichen thalli had been exposed to stress (Maxwell & Johnson 2000), similar to previous studies on epiphytic species (MacKenzie *et al.* 2002; Vráblíková *et al.* 2006). The results also revealed that the aspect influenced the extension of seasonal fluctuation in Fv/Fm, reaching a greater extent on arid than on humid sides. In general, a significant ('BU': $p = 0.036$, 'FH': $p < 0.001$) difference was detected among species in Fv/Fm values. The thalli of *C. foliacea*, *C. furcata* (both containing *Asterochloris* algae) showed higher Fv/Fm than was measured in *D. muscorum* (with *Trebouxia* algae). Their different morphology could also explain the variability in Fv/Fm between growth forms due to water holding capacity (Lange & Green 2003).

Usually, higher NPQ values were detected in humid compared to arid microhabitats. Populations living on humid sides are exposed to wet conditions in the early morning hours, and light can reach their surface more intensely than those growing on the opposite side. The cortical layer of wet lichen thallus is more translucent; therefore, the photosynthetic apparatus needs more protection against the harmful excess light energy than in dried thalli (Heber *et al.* 2006), where most of the radiation is reflected from the surface of the thallus (Ertl 1951). The autumn samples showed the highest

NPQ values between the seasons. Under prolonged moistened metabolically active periods as well as solar radiation, wet lichen thalli needed more protection against harmful excess light energy, resulting in higher NPQ (Barták *et al.* 2000). The exposition of microhabitat also impacted the seasonality of NPQ.

Significantly higher ($p < 0.001$) NPQ was measured in *C. foliacea* than in other investigated species. *Cladonia foliacea* and *C. furcata* exhibited an extended seasonal fluctuation, especially in arid populations. The species were more sensitive to the humidity conditions due to the thin cortical layer following the environmental changes more rapidly than the other investigated species.

The influence of seasonality and microhabitat conditions on photoprotection and high-light acclimation

Lichen secondary metabolites

A seasonal change in fumarprotocetraric acid concentration was detected in *C. furcata* ($p < 0.0001$) (spring, summer $<$ autumn, winter) and *C. foliacea* ($p = 0.03$), unlike in *C. magyarica* ($p = 0.44$). 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 exposition did not affect the amount of fumarprotocetraric acid in *C. magyarica* ($p = 0.36$).

Atranorin showed significant seasonal ($p < 0.0001$) (spring, summer $<$ autumn, winter) and microhabitat ($p = 0.007$) variation only in *C. furcata*. In *C. magyarica* atranorin did not vary across microhabitats ($p = 0.58$) or seasons ($p = 0.32$).

A significant seasonal change in usnic acid concentration was found in *C. foliacea* ($p = 0.0004$) (spring, summer $<$ autumn, winter). Meanwhile, usnic acid did not differ between sun and shade thalli ($p = 0.98$). The con-

concentrations of usnic acid reached three times higher values (mean 12.16 mg g⁻¹) than the other UV-protectant cortical pigment, atranorin (mean 3.99 mg g⁻¹).

Compared to *C. furcata*, *C. magyarica* showed a higher concentration of atranorin. *Cladonia furcata* showed approximately two times higher fumarprotocetraric acid concentration than the other two *Cladonia* species ($p < 0.0001$). An important result was that *C. magyarica* showed a constant high value during the year compared to the seasonal fluctuation in *C. furcata*.

The production of LSMs was consistent with the microclimatic conditions and length of hypothetical metabolically active periods (during day and night). Because the lichen can only produce solar radiation protectant substances in the hydrated state (Solhaug *et al.* 2003), the decreased level of the metabolites in the drier seasons may result from short active periods insufficient to provide the required amounts of photosynthates for LSM synthesis (Solhaug & Gauslaa 2004).

The concentration of photosynthetic pigments

The seasonal change of photosynthetic pigment concentrations differed among the species. *Cladonia furcata* showed the most apparent response to the seasonally changing environment in each parameter. In species where seasonality existed, 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) in the season. *Gyalolechia fulgens* and *X. pokornyi* occurred only in arid microhabitats (both containing *Trebouxia* photobiont). Therefore, the comparison was only possible between sun and shade populations of *Cladonia* species and *D. muscorum*. The concentration of chlorophylls was significantly higher in sun than in shade populations in

most species, and it was lower in *G. fulgens* and *D. muscorum* than in other species.

There was a species-specific seasonal trend in the mean chlorophyll a / b ratio; however, no significant difference was shown between arid and humid dune sides in any species. The chlorophyll a / b was higher in *G. fulgens* and lowered in *C. foliacea* than in the other species.

Usually, a significant seasonality of the carotenoid concentration occurred in the species. In general, the highest mean carotenoid concentration was detected in summer (43–145 $\mu\text{g g}^{-1}$), whereas the lowest values occurred in winter (71–105 $\mu\text{g g}^{-1}$) for *Cladonia* species and in autumn for the other three species (36–44 $\mu\text{g g}^{-1}$ in *D. muscorum*; 106 $\mu\text{g g}^{-1}$ in *X. pokornyi*; 222 $\mu\text{g g}^{-1}$ in *G. fulgens*). The sun populations contained significantly more carotenoids than shade populations in most of the species. 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.

Significant seasonal differences were detectable in the chlorophylls / carotenoids ratio in most of the species. The mean chlorophylls / carotenoids ratio usually peaked in autumn (2.12–4.74) and was the lowest in spring (0.59–4.01). Usually, the parameter was significantly higher in shade than in sun populations. The ratio of chlorophylls to carotenoids was the lowest in *G. fulgens* and the highest in *D. muscorum* among the species.

The short hydrated periods during drier seasons and on arid microhabitats can increase the need for more efficient use of light due to the higher amount of chlorophylls and carotenoids (Demmig-Adams & Adams 1992; Pintado *et al.* 1997). During humid seasons, high and more stable air humidity and lower irradiation frequently occurred, creating a more extended favourable environment for lichen photosynthesis. It may require a smaller chlorophyll antenna size for effective light-harvesting (Jin *et al.* 2001) but a

higher need for photoprotection (Barták *et al.* 2000). In the hydrated state, the transmittance of the cortical layer (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). Vrábliková *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 results suit the measured values of Tuba *et al.* (2008) in *C. foliacea* and *C. furcata*.

Partition of absorbed light energy between photochemical quenching, regulated non-photochemical quenching and non-regulated excitation dissipation

The ϕ_{PSII} was significantly lower in summer than in autumn or winter in each species, except for *G. fulgens*. However, the response of photochemical quenching to seasonal environmental changes seemed to be species-specific. Still, it differed significantly between the sun and shade populations in only a few cases.

A significantly lower ϕ_{NPQ} was measured in summer than in other seasons in *C. foliacea*, *C. furcata* and *X. pokornyi*, whereas *G. fulgens* exhibited the opposite seasonal pattern. *Cladonia magyarica* and *D. muscorum* did not show remarkable differences among the seasons. Generally, the ϕ_{NPQ} was higher in the humid (mean 28–52%) compared to the arid (mean 17–49%) microhabitats. This difference was always significant during winter in each species, whereas a species-specific response was characteristic for the other seasons.

The ϕ_{NO} was significantly higher in summer than in other seasons in each species except for *G. fulgens*, where winter samples showed the highest values. The ϕ_{NO} was usually higher in the arid (mean 20–70%) than in the humid (mean 18–52%) microhabitats.

Our results indicated that in summer, the ϕ_{NPQ} was less involved in dissipating excess light energy ($\phi_{\text{NO}} > \phi_{\text{NPQ}}$), especially on arid dune sides. 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).

The ϕ_{NPQ} was higher than ϕ_{NO} , 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 utilised by photochemical processes leading to the most productive period of the year in semi-arid sandy grasslands, as also found by former studies (Raggio *et al.* 2014; Versegny 1976).

A more contrasting environmental difference may be required, for example, different forest stands (Gauslaa *et al.* 2006), to induce a clear difference in distribution between photochemical and non-photochemical quenching mechanisms 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 characterising arid and humid seasons.

The seasonal variations of investigated parameters showed species-specific differences. Lichens are poikilohydric organisms that cannot actively regulate their water content but can extend or shorten their metabolically active period and protect themselves from the damaging effect of high irradiation due to different long term adaptation strategies (e.g. morphological traits, anatomical differences, LSMs production, choice of microhabitats).

NEW SCIENTIFIC RESULTS

The following new scientific results have been achieved:

1. The T_{air} , PAR (corrected with slope and orientation), T_{soil} and VPD values were significantly higher on the SW than on the NE oriented dune side, where the RH and WC_{soil} proved to be significantly higher.
2. The daily fluctuation of differences for every micrometeorological parameter was changing during the seasons. The daily fluctuation was higher in summer and lowered in winter.
3. The quality and quantity of incoming irradiation on dune sides varied among the seasons. In winter and autumn, the direct illumination lasted 3–4 h longer on the exposed than on the opposite side because of the later sunset. During the summer months, the direct illumination reached the shaded side 1–2 hours longer because of the significantly earlier sunrise.
4. The site (by the disturbance history), dune side (by the microclimate) and soil surface variables (as microenvironment) were found to be important factors determining terricolous lichen assemblages and species richness in calcareous semi-arid sandy grasslands.
5. The cover and the average height of vascular plants were lower, and the moss cover was higher on arid compared to humid dune sides.
6. The abundant species differed in their habitat and microhabitat preference, and almost all abundant species were negatively influenced by a high moss cover.
7. Lower photosynthetic activity, chlorophyll / carotenoid ratio, NPQ and ϕNPQ were characteristic during brighter and drier seasons and on arid dune sides. The chlorophyll and carotenoid concentration and the ϕNO were higher in arid than humid seasons and dunes sides.

8. The proportion of absorbed light between photosynthesis and the different photoprotection quenching mechanisms is species-specific and changes seasonally in lichens.
9. A significant seasonal change in atranorin, fumarprotocetraric acid and usnic acid concentration was found in *C. foliacea* and *C. furcata* (spring, summer < autumn, winter). The level of LSMs constantly remained high in *C. magyarica* during the year.
10. Higher levels of LSMs were found in the shade compared to sun populations in *C. foliacea* and *C. furcata*. It did not differ between arid and humid dune sides in *C. magyarica*.
11. Since the synthesis of light screening LSMs requires more time than is necessary to activate non-photochemical quenching mechanisms, the latter seems to be a more efficient process during the short metabolically active period in drier and brighter seasons in some species (e.g. *C. furcata*). 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.

CONCLUSIONS, RECOMMENDATIONS AND PERSPECTIVES

Based on the received information on microclimate, we concluded that it strongly influenced lichen functioning and abundance at a large and a fine scale. It was established that lichens could significantly contribute to the biodiversity of dry calcareous grasslands due to their heterogeneous community structure, having high conservation importance. Some lichen species were to be found only on arid dune sides or more open sites (e.g. the protected steppe species or the key species of the *Fulgensietum fulgentis* association), while others only on humid dune sides or on the site hosting more closed vegetation and trees (e.g. the wood-correlated species). Therefore, it is important to protect and maintain a diverse topography and landscape structure hosting various lichen communities when considering habitat-specific conservation and monitoring in inland dunelands. It is worth considering that the different species forming duneland communities have various microenvironmental needs and are very sensitive to different environmental factors. We can postulate that as a result of climate change (drier and warmer conditions are projected in this region), lichens can gain more space due to the shrinkage of vascular plant vegetation. However, lichens have to compete with mosses for these free surfaces. These changes will supposedly lead to higher cryptogamic biodiversity.

In our extensive study, we showed that the effect of microhabitat conditions and seasonal changes on photosynthetic functioning and photoprotection is species-specific and varies in space and time. We suggest future workers study more than one species to investigate the response of lichens to changing environmental conditions in space or in time. Additionally, because photosynthetic activity and a part of photoprotection derive from the photobiont, future work should focus on species-specific differences of

chlorophyll fluorescence in the different photobiont partners found in lichens (e.g. *Asterochloris*, *Trebouxia*).

The different species can acclimate to the changing environmental conditions by taking advantage of each season in various ways. The regulated non-photochemical quenching seemed the most species- and microhabitat-specific protection mechanism. Our results showed that only c. 25% of the absorbed light energy was utilised 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). The proportion of intensity in the protection of lichen thalli against the excessive radiation between algal and fungal partners is a promising field for further studies, for example, from antioxidant enzyme activity point of view or in species containing LSMs other than the investigated substances.

LIST OF PUBLICATIONS PROVIDING THE BASIS OF THE THESIS

Published papers in refereed journals

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