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Juniper shade enables terricolous lichens and mosses to maintain high photochemical efficiency in a semiarid temperate sand grassland

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Abstract

On a semiarid sand grassland (*Festucetum vaginatae*) colonised by juniper (*Juniperus communis* L.) shrubs terricolous lichens and mosses segregate strongly between microhabitats: certain species grow in the open grassland, others almost exclusively in the shade of junipers. The contrasting irradiances of these microhabitats influence much the metabolism of these organisms, and thus affect their small-scale distribution. This was confirmed by determining the efficiency of photochemical energy conversion by measuring chlorophyll *a* fluorescence parameters. In the open grassland maximum photochemical efficiency of photosystem 2 (PS2, F_v/F_m) declined from the humid spring to the hot and dry summer in all species, and this was caused by an increase in base fluorescence (F_0), but not by the decrease in fluorescence maximum (F_m). In summer, mosses and lichens growing in the open grassland generally possessed lower F_v/F_m than cryptogams growing in the shade cast by juniper shrubs. Thus mosses and lichens in the open grassland suffer lasting reduction in photochemical efficiency in summer, which is avoided in the shade of junipers. Juniper shrubs indeed influence the composition and small-scale spatial pattern of sympatric terricolous lichen and moss communities by—among others—providing a shelter against high light in summer.

Additional key words: bryophytes; chlorophyll *a* fluorescence; *Cladonia*; *Diplosichtes*; *Hypnum*; *Neofuscelia*; *Polytrichum*; *Tortula*.

Introduction

Due to their small size and location at the ground level, terricolous lichens and mosses experience different microenvironment than sympatric vascular plants. Biotic interactions may have a more profound influence through—among others—modifying abiotic factors either for the benefit (facilitation) or at the expense (inhibition) of cryptogams. Small-scale vegetation patterns produced by vascular plants often create a series of different microenvironments that enables the coexistence of lichens and mosses with different environmental needs. Such situation occurs in the open sand grassland (*Festucetum vaginatae*) colonised by juniper (*Juniperus communis* L.) shrubs on the plains in Central Hungary. The grassland is sparse, almost semidesert-like due to a two-to-three-month-long dry period in summer and to grazing. Scattered juniper shrubs of 2-5 m height live long here in the absence of fire. Terricolous lichens and mosses segregate strongly between the open grassland and juniper shade microhabitats, since species grow in only one of these almost exclusively: the local occurrence of the mosses *Hypnum cupressiforme* and *Polytrichum juniperinum* and of the lichen *Cladonia rangiformis* is restricted to the shade of juniper shrubs, while the rest of species in Table 1 grows in the open grassland (Simon and Szerényi 1975, Mázsa *et al.* 1998). Cryptogam assemblages follow vegetation dynamics (shifting mosaic) with certain delay, thus infrequent non-typical occurrences (*e.g.*, shade species exposed to sun after a juniper dieback) make possible the study of the same species in both microhabitats. The abiotic environment

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Abbreviations: Chl = chlorophyll; F_0 = fluorescence origin; F_m = fluorescence maximum; F_v = variable fluorescence; F_v/F_m = maximum photochemical efficiency of photosystem 2; LSD = least significant difference; PS = photosystem.

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between the two microhabitats mostly differs in irradiance and—as consequence—in temperature and water regimes as well. In the same vegetation type at another locality in Central Hungary, the soil pH was also 0.7 units lower under junipers than in the open grassland (7.3 and 8.0, respectively), but this was more an effect than a cause of high cryptogam cover in the shade (Mázsa *et al.* 1987). Similarly, Simon and Szerényi (1975) found slight difference at our site in soil pH between the shade mosses *H. cupressiforme* and *P. juniperinum* and the open grassland bryophyte *Tortula ruralis*.

The difference in microhabitat irradiance may be particularly important, since these cryptogams posses several shade-plant-like characteristics, such as a low CO_2 compensation concentration and low saturation irradiance for CO_2 gas exchange (Mázsa *et al.* 1998). Thus they conform the general pattern for desiccation tolerant mosses and lichens (see Green and Lange 1994 for review). Influence of habitat irradiance heterogeneity on lichen assimilation and growth has already been studied at forest edges for epiphytic lichens originating from the forest interior (Renhorn *et al.* 1997, Gauslaa and Solhaug 2000).

In this study we used Chl fluorescence measurements (cf. Schreiber *et al.* 1994, Maxwell and Johnson 2000) to study the photochemical quantum conversion of mosses and lichens in the open grassland and under the juniper canopy. Our aim was to explore the effect of microhabitats and seasons (humid spring *versus* hot and dry summer) on the photosynthetic light reactions of terricolous cryptogams showing a strong microhabitat preference.

Materials and methods

Study site and species investigated: The area studied lies on the floodplain of the Danube river, 50 km SE of Budapest, near the village Csévharaszt. The climate is semiarid temperate with a slight submediterranean influence (yearly mean temperature 10.3 °C, annual precipitation 515 mm), it has two precipitation maxima (spring and autumn), and 1-3 months of summer drought (Kakas 1967). Winds had turned the alluvial deposit—coarse calcareous sand—into a duneland with 5-10 m differences in relief. The soil has low humus content, dries up easily near the surface, but stores available water below *ca.* 0.5 m, although soil water table is usually deeper than 2 m (Kovács-Láng 1974). This arid duneland is recently covered with a forest-steppe vegetation mosaic. In valleys between dunes poplar (*Populus alba*, *P. canescens*) forms small forest stands, while on the dunes semidesert-like perennial grasslands (*Festucetum vaginatae*) with scattered juniper (*Juniperus communis*) shrubs appear (Simon and Mészáros-Draskovits 1972). Desiccation tolerant lichen and moss species are common in the sparse grassland on bare surfaces between vascular plants and under the shade cast by juniper shrubs, and even contribute considerably to phytomass production (Verseghy and Kovács-Láng 1971). In this vegetation both water and nitrogen limit plant growth and phytomass production (Kovács-Láng 1974, 1975), where ecological opportunist terricolous cryptogams are able to utilise even ephemerous water supplies (*e.g.*, dew, small rainfalls). Lichen and moss species involved in our study are listed in Table 1. *Diplosichtes muscorum* (*Thelotremaceae*) contains filamentous green algal photobiont, while the rest of the lichen species belong to *Lecanoraceae* and host unicellular green algal photobiont (Hawksworth *et al.* 1995, Tehler 1996).

Sampling and measurements: Lichen and moss samples were collected in their natural habitat with 5 replicates per species and microhabitat in early April and late August 1999. Since most species grow almost exclusively in one of the two studied microhabitats (open grassland and juniper shade, respectively), it was possible to collect thalli from both microenvironments only for one lichen (*Cladonia convoluta*) and one moss (*Hypnum cupressiforme*) species (in late summer only). Samples were transferred to laboratory on the day of collection and were kept wet for at least one day prior to measurements by frequent spraying with tap water and by storage in humid air under moderate natural irradiance [<300 μmol(photon) m^{-2} s^{-1}]. Chl fluorescence induction measurements with dark-incubated parameters (F_0, F_m, F_v, F_v/F_m) were completed by using a pulse-modulated Chl fluorometer (Hansatech Fluorescence Monitoring System *FMS2*, *Hansatech Instruments*, King's Lynn, UK). To avoid changes in thallus water content during dark incubation and subsequent measurement, that influences Chl fluorescence parameters considerably (*e.g.*, Lange *et al.* 1996, Calatayud *et al.* 1998, Gauslaa and Solhaug 1998, Csintalan *et al.* 1999), samples were kept in contact with wet filter paper throughout the incubation period and the measurement. Special care was taken that cryptogam samples would cover completely the wet filter paper. After about 20 min dark incubation F_0 was measured, then F_m was determined by using a saturation pulse [4 500 μmol(photon) m^{-2} s^{-1}, 0.7 s duration]. F_v/F_m was calculated as $(F_m - F_0)/F_m$. The influence of season (for grassland samples only) or microhabitat (for summer sampling only) was analysed by one way analysis of variance. Differences between means were tested by a subsequent least significant difference (LSD) test (Sokal and Rohlf 1981). Differences were considered significant at $p<0.05$ probability level. The *Statistica 4.5* package (StatSoft 1993) was used for these analyses.

Results

Spring-to-summer changes: For the comparison of early spring and late summer values we have values for four lichen and one moss species, all from the open grassland habitat. Maximum photochemical efficiency of photosystem 2 (PS2, F_v/F_m) declined significantly from spring to summer for all species (Fig. 1*A*). The mean F_v/F_m was 0.794 in April but only 0.685 in August. The change was the greatest for the moss *T. ruralis* (29 %) and the smallest for the lichen *D. muscorum* (7 %). The seasonal decline in F_v/F_m was caused by a 1.4 to 3.0-fold increase in F_0, while a significant change in F_m did not occur (Fig. 1*B,C*).

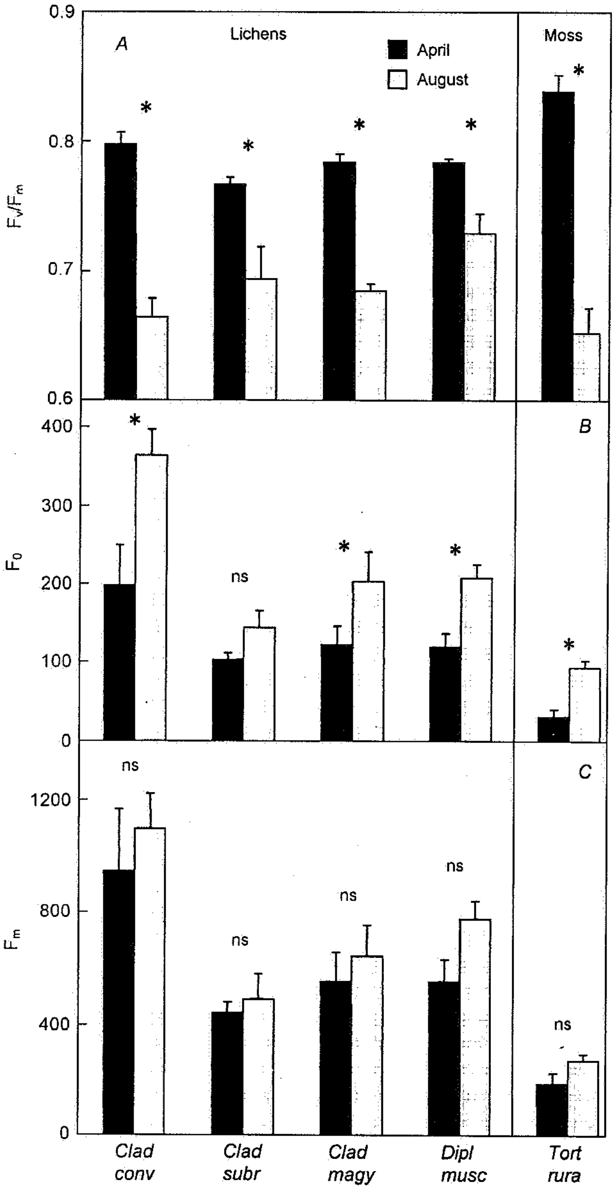

Fig. 1. Spring-to-summer changes in dark-incubated chlorophyll fluorescence parameters for four terricolous lichen and one moss species from the open grassland habitat. *A*: Maximum photochemical efficiency of photosystem 2 (F_v/F_m). *B*: Fluorescence origin (F_0). *C*: Fluorescence maximum (F_m). Mean values ± 1 SE ($n = 5$). Species names are abbreviated, for full names consult Table 1. For species marked with an asterisk the seasonal difference is significant (ANOVA with subsequent LSD test, $p < 0.05$).

Differences between microhabitats: Comparison between the open grassland and the juniper shade microhabitats was performed in summer, since spatial heterogeneity in abiotic factors (irradiance, water, temperature) is usually greatest in that time. F_v/F_m was significantly higher in the shade than in the open field, in both intra- and inter-specific comparisons, and for mosses and lichens similarly (Fig. 2). The mean values for F_v/F_m were 0.789 and 0.681 for shade and sun, respectively.

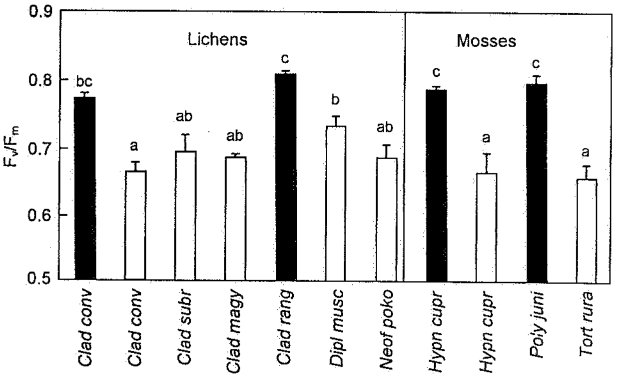

Fig. 2. Variation in maximum photochemical efficiency of photosystem 2 (F_v/F_m) within species and/or microhabitat in late summer. Dark columns indicate samples from the juniper shade, light columns are from samples of the open grassland microhabitat. Species names as in Fig. 1. Means ± 1 SE ($n = 5$). Columns marked with the same letter are not significantly different (*ANOVA* with subsequent LSD test, $p < 0.05$).

The comparison of absolute Chl fluorescence parameters F_0 and F_m is valid only within species, since between species the Chl content may differ substantially, which greatly influences these variables (Lichtentaler 1988). For such intra-specific comparison we have values only for two species. For both, F_0 was significantly lower in the shade than in the open (183 and 363 for *C. convoluta*, and 96 and 187 for *H. cupressiforme*, respectively), while F_m was not significantly different between microhabitats (values not shown). For *C. convoluta* in summer the shade F_0 was almost equal to F_0 in spring in the open grassland (183 and 198, respectively).

Discussion

Differences between spring and summer: Terricolous lichens experience contrasting seasonal environment in semiarid grasslands. From autumn to spring thalli can spend extended periods (days or weeks) in the hydrated state and are able to continue assimilation and growth under moderate irradiance and temperature, except for the time of below-freezing temperatures and snow cover in winter. The hot and dry summer is less conducive for these organisms: they remain mostly inactive in the desiccated state, become hydrated for short periods only after rains or on dew deposition, and may occasionally experience high irradiance in the hydrated state (Verseghy and Kovács-Láng 1971, Mázsa 1994, Leisner *et al.* 1996). Although the short episodes of physiological activity in summer may not contribute significantly to growth, yet may keep plant carbon balance positive and prevent lengthy desiccation, which is harmful for poikilochlorophyllous desiccation tolerant plants (Tuba *et al.* 1996).

Table 1. Cryptogam species studied and their short ecological characterisation. All lichen species listed contain green-algal photobionts. For future reference, herbarium specimens of each species were deposited in the Herbarium of the Hungarian Natural History Museum, Budapest. The specimen identification number is given in squared brackets after the species' name.

Species	Ecological character
Lichens	
Cladonia convoluta (Lam.) Anders [BP 90546]	fruticose, common on the Great Hungarian Plain in extremely dry habitats on calcareous sand
Cladonia subrangiformis Sandst. [BP 90547]	fruticose, xerothermic species widespread in lowland and colline dry grasslands
Cladonia magyarica Vainio [BP 90544]	fruticose, xeric Great Hungarian Plain endemism
Cladonia rangiformis Hoffm. [BP 90545]	a rather variable fruticose species, most widespread in hilly regions; in the sand vegetation of the plains it appears under juniper shade
Diplosichtes muscorum (Scop.) R. Sant. [BP 90548]	crustose, frequent in sand grasslands
Neofuscelia pokornyi (Zahlbr.) Essl. [BP 90555]	fruticose, typical xerothermic lichen in the sand areas of the Great Hungarian Plain and on the south-facing slopes of the hills
Mosses	
Hypnum cupressiforme Hedw.	highly variable xero-mesophyte prevalent in forests, grasslands and in rock grasslands; at our site it forms thick mats under juniper shade
Polytrichum juniperinum Willd.	grows from plains to mountains on nutrient-poor acidic soils in dry open forests; at our site it forms cushions under junipers
Tortula ruralis (Hedw.) Gaertn. *et al.*	a calcicole ecological generalist xerophyte; at our site typical in the dry open grassland

This environmental contrast is reflected in the photochemical quantum conversion of these organisms. A uniform significant decline of maximum PS2 efficiency (F_v/F_m) from April to August indicates that the photochemistry of these lichens and particularly the moss species is under stress. This decline can be due either to photoinhibition or to an increased non-photochemical quenching, but the dark-incubated Chl fluorescence parameters alone—that our measurements were restricted to—are insufficient to distinguish between these components. In lichens (Demmig-Adams *et al.* 1990), mosses (Tuba 1987, Seel *et al.* 1992a,b), or both (Heber *et al.* 2000) photoinhibition (or reduction in photosynthetic capacity, Tuba 1987) was detected when cryptogams were exposed to high irradiance in the hydrated state, but not when they were treated so in the desiccated state. However, in these experiments the decline in F_v/F_m was more substantial and slowly recovering than in our study. Additionally, even if the decrease of quantum efficiency observed from spring to summer in our study is a sign of some sort of damage, it can be caused by factors other than high irradiance. These factors are, *e.g.*, frequent dehydration-rehydration cycles, or lengthy periods spent in the desiccated state in summer. Further experimental work is needed to elucidate the mechanism of seasonal decline in F_v/F_m in this ecological situation.

Differences between microhabitats: The shade cast by juniper shrubs provides protection against high irradiance. Summer F_v/F_m values were significantly and consistently higher for cryptogams growing under juniper canopy than for those thriving in the open grassland, and this was true in both intra- and inter-specific comparisons (Fig. 2). Within a species a greater F_0 in the open field than in the shade caused the decreased F_v/F_m. The protection ability of juniper shade is indicated; under it F_0 in summer is not higher than in spring in the grassland for *C. convoluta*. Again, a decreased F_v/F_m and a higher F_0 may be an indication of both photoinhibition and photoprotection, but our dark incubated Chl fluorescence values are insufficient to make the distinction. For lichens and mosses, PS2 maximum photochemical efficiency in high irradiance compared to shaded microenvironments was lower (Leisner *et al.* 1996), similar (Renhorn *et al.* 1997), or after an initial decline slowly equalised due to acclimation changes after transplantation from shade to sun (Gauslaa and Solhaug 2000). Decreased F_v/F_m in high irradiance relative to shaded microhabitats was observed among vascular plants as well (*e.g.*, Roden *et al.* 1997, Láposi *et al.* 2000). For the perennial herbs *Ammophila breviligulata* and *Solidago sempervirens* growing on coastal sand dunes in a small scale vegetation mosaic (very similar to that in this study), F_v/F_m was significantly greater under the protective canopy of the nitrogen fixing shrub *Myrica pensylvanica* than outside of that. The influence of shade—in addition to the improved soil N status—was then experimentally proven (Shumway 2000).

This work merely detected the decline of PS2 photochemical efficiency for terricolous lichens and mosses in the high-irradiance dry grassland habitat. In this vegetation certain cryptogams (xero-mesophytes, Simon and Szerényi 1975) survive in the shelter of juniper shrub canopies only. More tolerant species (xerophytes) inhabit the open grassland and certainly posses traits that decrease the impact of high irradiance and associated heat load on assimilation. In a mediterranean xeric environment, Deltoro *et al.* (1998) found *H. cupressiforme* (typical xero-mesophyte at our site) to posses lower tolerance of desiccation (indicated by less complete regeneration of PS2 photochemistry on rehydration) than *Tortula ruralis* (xerophyte in our study). However, the shade cast by single juniper shrubs or of groups not greater than a few metres in diameter has limited potential to ameliorate the extreme abiotic environment of the open grassland. Changes in Chl fluorescence induced by thallus desiccation were also studied in *Hypogymnia physodes*, *Lobaria pulmonaria*, and *Peltigera aphthosa* (Jensen *et al.* 1999). Thus, mosses and lichens capable of inhabiting the juniper shade microhabitat are xero-mesophytes, since the establishment of true mesophytes (Simon and Szerényi 1975) needs larger forest patches and better site hydrology. To understand the mechanism of the decline of F_v/F_m and its components recorded in this study, further work is needed including measurements of light-incubated Chl fluorescence parameters and relaxation kinetics. Also, additional studies—including cross-transplant experiments between microhabitats—are necessary to explain what exactly determines the microhabitat preference of terricolous lichens and mosses in this vegetation mosaic.

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