Effect of light stress on maximum photochemical efficiency of photosystem II and chloroplast structure in cryptogams *Cladonia mitis* and *Pleurozium schreberi*

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Abstract. Lichens and bryophytes are cosmopolitan organisms found in diverse environments with varying sunlight availability. However, excessive light can be a stress factor for both lichens and bryophytes, as it can damage their photosynthetic apparatus, particularly the chlorophyll a and b pigments located in the chloroplasts. The measurement of photosynthetic activity and the use of fluorescence microscopy allows the assessment of the influence of light as a stress factor on the preservation state of the thallus. The main goal of our research was to determine the changes that occur in the photosynthetic activity and structure of chloroplasts of selected species lichen *Cladonia mitis* (Sandst.) and moss *Pleurozium schreberi* (Willd. Ex Brid.) under the influence of different light intensity in laboratory conditions: FL - 100% light, RL - 30% maximum light, and NL - natural sunlight. The results of the two-factor analysis of variance (ANOVA) tests showed a variation in the activities of the selected species over time depending on the amount of light energy supplied. It was also demonstrated that soaking lichens increased their photosynthetic activity, whereas in bryophytes, it had the opposite effect, decreasing it. The microscopic results showed that *Cladonia mitis* showed the lowest level of chloroplast fluorescence in the strongest and reduced light, which coincides with its low level of photosynthetic activity. The mosses exhibited strong fluorescence activity of the chloroplasts, suggesting its significantly higher resistance to light radiation.

Keywords: Photosynthetic activity, light stress, fluorescence, chloroplast, lichens, bryophyte

1. Introduction

Lichens are two-component organisms composed of photoautotrophic algae, primarily prokaryotic cyanobacteria or eukaryotic green algae and heterotrophic fungi, especially

ascomycetes, basidiomycetes or anamorphic fungi. In the interaction within lichens, the fungal component is responsible for providing protection against external factors such as drying out but also respond supplying water along with mineral nutrients, and producing ascorbic acid to stimulate intense CO_2 assimilation. On the other hand, the photoautotrophic component performs photosynthesis, and its products, along with synthesized carbohydrates, are supplied to the mycobiont (De Carolis et al., 2022; Grimm et al.2021; Ranković, 2019). The above cooperation between the fungal components and the alga is called symbiosis, and it takes place in the company of the bacterial mycobiome associated with the lichen thallus. Classification of this symbiosis falls somewhere between mutualism and controlled parasitism (Lücking et al., 2021). Lichens are very common in microhabitats where they can be exposed to adverse environmental conditions, including extreme temperatures (both very low and high), desiccation, solar radiation or heavy metal pollution (Beckett et al., 2021; Kumari et al., 2024 Nguyen et al., 2013). These tiny poikilohydric organisms have evolved defence mechanisms to protect themselves against changing environmental conditions, including reducing metabolism when water availability decreases, tolerating the loss of virtually all free water without dying, and resuming growth after rehydration. In turn, photoprotection focusses on light scattering, radiation shielding, heat dissipation, activation of antioxidant and macromolecular defenses, and membrane repair (Beckett et al., 2021; Dziurowicz et al., 2022; Nguyen et al., 2013). Bryophyte, on the other hand, unlike lichens, cope much better in a humid environment, which allows them to be fully hydrated and metabolically active for extended periods of time (Dziurowicz et al., 2022; Green et al., 2011). However, due to their distinctive morphology and physiology, bryophyte rely heavily on their external environment and are vulnerable to the impacts of climate change, which can alter the availability of water and nutrients, as well as affect the temperature and humidity conditions in their habitat (He et al., 2016). Therefore, the bryophyte faces great challenges associated with the drying and rehydration cycle and often high temperatures, which causes them to be metabolically inactive (Liu et al., 2003). One way to reduce water loss is for mosses to form dense clusters that reduce water evaporation (Charron and Quatrano, 2009). Assessing the physiological state of plants and their activity, in addition to monitoring their physical condition and the intensity of environmental stress, can provide important information about ecosystems. Various experimental and analytical methods have been developed to monitor the physiological state of plants (Chen et al., 2019). One of the methods uses the phenomenon of chlorophyll fluorescence. It is a simple tool widely used to analyze the state and function of the photosystem II (PSII). The maximum photochemical efficiency of photosystem II (Fv/Fm), otherwise called photosynthetic activity, is easy to

measure as a representation of the photosynthetic performance of a studied organism. Changes in the functioning of photosynthetic systems can be detected without any damage to the studied samples by measuring chlorophyll fluorescence. This is because a fraction of the light is absorbed by chlorophyll molecules in PSII and used for energy conversion in photosynthesis, while excess energy can be either dissipated as heat or re-emitted as light (Maxwell and Johnson, 2000). Chlorophyll fluorescence variations reflect the response of photosystem II (PS II) to changes in photosynthetically active radiation (PAR) intensity (Demmig-Adams and Adams, 1992; Dziurowicz et al., 2022; Wu et al., 2017). Studies conducted over the years using such measurements have identified several relationships, including the level of hydration and photosynthetic activity. Among the results, we find information that dehydration damages the photosynthetic apparatus and therefore causes inactivation of the photosynthetic process (Liu et al., 2014). Other studies indicate that in the case of desiccated mosses and lichens, wetting the thallus leads to its reactivation (Orekhova et al., 2022; Schlensog and Schroeter, 2001). Those so-called desiccation-tolerant organisms (DT) can be subdivided into two groups. Homoiochlorophyllous (HDT) are those that maintain their chlorophyll content during periods of desiccation, while poikilochlorophyllous (PDT) lose most or all their chlorophyll during these periods (Bewley, 1979; Gaff, 1989; Tuba et al., 1996). Equally detrimental to complete desiccation is the influence of excessive much water content, one that prevents optimal CO_2 exchange and contributes to stopping the process (Dziurowicz et al., 2022; Lakatos, 2011; Lange et al., 1993). Apart from water availability, the efficiency of photosynthesis can be significantly impacted by light conditions. Although light is its integral element, necessary for it to be carried out, the relationship between the amount of absorbed light and the intensity of photosynthesis is not linear since the rate of photosynthesis reaches a saturating point at a certain level. Research over many years has shown that too much light becomes a stressor and can be harmful (Beckett et al., 2021; Rochaix, 2011). Damage occurs when the absorption of photons exceeds the capacity of the downstream reactions to consume the products of the light phase, causing saturation in the reaction centers (Allorent et al., 2013; Barber and Andersson, 1992; Wobbe et al., 2016).

To date, most studies employing photosynthetic activity to assess the state of plant viability has focused on interpreting photosynthetic activity alone. However, the evaluation of photosynthetic activity combined with chloroplast fluorescence imaging through fluorescence microscopy can more accurately show the changes that occur in photosynthetically active organisms under stress. It is very easy to observe chloroplasts by chlorophyll fluorescence using

fluorescence microscopy (Wada, 2013), and it offers a way to test the viability status of lichen thalli and moss tisues (Kauppi, 1980).

Our research consisted of collecting selected lichens and bryophyte in the natural environment and subsequently cultivating them under precisely defined light conditions, while maintaining constant temperatures and humidity levels. For this study, we selected *Cladonia mitis* (Sandst.) and *Pleurozium schreberi* (Willd. Ex Brid.) Mitt. as representatives of lichens and bryophyte, respectively, which occur in the same type of pine forest habitat. The main goal of our research was to determine the changes that occur in photosynthetic activity and presence and location of chloroplasts of selected species under the influence of different amounts of light in laboratory conditions. We made the following hypotheses: (1) the photosynthetic activity of the studied species varies over time despite being exposed to a constant level of light energy; (2) the photosynthetic activity of the lichen is higher than that of the moss in all light types tested, (3) soaking treatment causes photosynthetic activity to increase in the lichen *C.mitis* and decrease in the moss *P.schreberi,* and (4) the structure of chloroplasts in both study species degrades under the influence of the strongest light (full light).

2. Material and Methods

2.1. Establishment and maintenance of laboratory cultures of lichen and bryophytes

Species of lichen *C. mitis* and bryophyte *P. schreberi* were randomly collected in Bory Tucholskie National Park within the lichen Scots pine forest community (*Cladonio-Pinetum* Ass.) in February 2022 (Dziurowicz et al., 2022). In Poland, the bryophyte species *P. schreberi* is protected, and an appropriate permit was obtained for its collection. The collected samples were cleaned of plant debris and soil particles and divided into 3 study samples, which were later placed in 3 experimental glass containers (aquariums) with different light treatments. Within each container, we placed 6 subsamples of *C. mitis* and 6 subsamples of *P. schreberi* as pseudoreplications (6 chambers per container eq. study sample) on the 1 cm layer of sterile sand (Fig. 1, Table 1). As treatment within containers, we used two types of artificial light conditions: 1) full light (FL) – 100% of artificial light; 2) reduction light (RL) – 30% of artificial light. The amount of light energy in the FL sample was more than three times greater than in the RL sample and ten times greater than in the NL sample (Table 1).

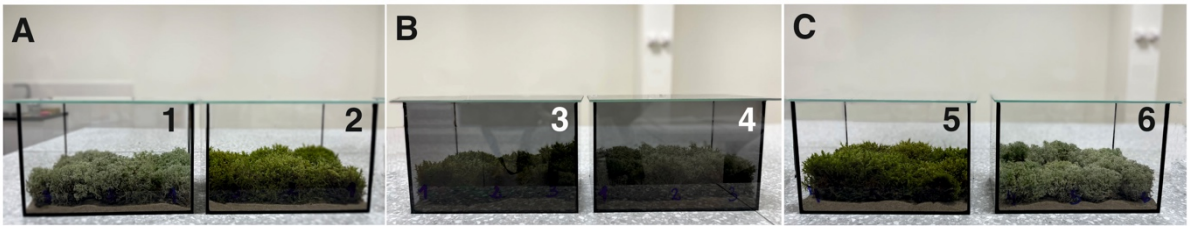

Fig. 1 Experiment consisting of three samples (A, B, C), each with two species: *Cladonia mitis* lichen and *Pleurozium schreberi* bryophyte. Each of the samples differed in the level of light: A (FL), B (RL) and C (NL) according to the parameters contained in Table 1.

Table 1. Division into six research samples (experimental containers) took into account the species: *Cladonia mitis* and *Pleurozium schreberi*, as well as three types of light: FL – 100% light; RL – 30% maximum light; NL – natural sunlight (control sample), with values for light energy (LE) and photosynthetically active radiation (PAR).

Experimental container number	**Species**	**Types of Light**	**LE [W/m^2]**	**PAR [µmol/m^2]**
1	*Cladonia mitis*	FL	122.7	506.9
2	*Pleurozium schreberi*	FL	125.2	495.1
3	*Pleurozium schreberi*	RL	42.0	165.3
4	*Cladonia mitis*	RL	40.6	151.4
5	*Pleurozium schreberi*	NL	11.5	178.5
6	*Cladonia mitis*	NL	11.5	178.6

The reduction of artificial light was achieved by covering the glass of the aquarium with a dark film. Both light conditions (FL and RL) were created by application of artificial lighting which was generated by lamps with the following specifications: type GROWY LED 354, light PAR - 224.3 µmol/m2s and wavelength range 50% max. 450 nm and 50% max. 650 nm. For the control container identified as natural light (NL), we used natural sunlight. Under these conditions, light energy (LE) and photosynthetically active radiation (PAR) measurements were taken once in each month of culture on a sunny day at noon so as to obtain the maximum values of the measured parameters. The measurements were averaged (Table 1). Artificial lighting was

active for 18 hours a day, it was automatically turned off for 6 hours from 9 pm to 3 am. Lichens and bryophyte were systematically watered so that their thallus and tissues were constantly moist. Watering was performed through sprinkling every other day of the week, with a total of 20 ml of distilled water administered per watering session. The experiment was carried out in a climatic chamber set at 21^{o}C and 50% humidity, spanning a duration of 150 days.

2.2.Measurements of photosynthetic activity

Photosynthetic activity measurements were performed six times, at different time intervals, to assess the viability of the examined samples. The first measurement was made on the day the culture was established; the next measurements took place after 30, 60, 90, 120 and 150 days from the beginning of the experiment. During each measurement, six samples of *C. mitis* and *P. schreberi* materials were collected for three types of light: FL, RL, and NL, resulting in a total of 36 samples. Each of these samples underwent measuring for photosynthetic activity in both non-soaked and soaked states, following the scheme: 1) non-soaked samples: *Cladonia mitis* (CM-NS) and *Pleurozium schreberi* (PS-NS) were measured directly after being transferred to the HPEA/LC clips without water treatment; 2) soaked samples: the same samples that were measured earlier, *Cladonia mitis* (CM-S) and *Pleurozium schreberi* (PS-S) were placed in Eppendorf filled with distilled water for a period of 2 h, and after this, the material was transferred to the HPEA/LC clips for a 15-minute dark adaptation aimed at extinguishing the activity of the photosystem II. Measurements were made using a Handy PEA + fluorometer (Handy PEA, Hansatech Instrument Ltd, King's Lynn, Norfolk, England). The fluorometer light probe emitted the dose of excitation light, which allowed recording the maximum photochemical efficiency of photosystem II (Fv/Fm) (Chowaniec and Rola, 2020; Dziurowicz et al., 2022; Węgrzyn et al., 2021).

2.3.Microscopic fluorescence imaging of chloroplasts

At the designated dates of photosynthetic activity measurements, small samples of lichen thalli and bryophyte gametophyte were also collected directly from the culture to make microscopic preparations showing the preservation status of the chloroplasts. In the case of lichens, the top fragments of the thallus were collected, where there are numerous cells of Asterochloris sp. algae of the lichen photobiont belonging to the Trebouxiaceae family within the Chlorophyta cluster. The thallus fragments were cut into thin flat sections, which were placed in a water solution of the microscopic preparation. In the case of bryophyte, gametophyte leaflets were collected, from which a water microscope preparation was made directly. In

visible and fluorescent light generate by NIKON Super High Pressure Mercury Lamp type C-SHG 1 with filter V-2A, EX 380-420, DM 430, BA450, the Nikon Eclipse Ni-U microscope with a Camera DS-Fi1c that transmits the image to a computer was used to observe the state of preservation of chloroplasts in the organisms tested. The resulting microscopic imaging was processed using NIS-Elements Advanced Research version 3.0 dedicated software.

2.4.Statistical analysis

A multivariate ANOVA followed by Tukey's HSD test (Honestly Significant Difference) for an equal sample size ($p < 0.05$) was performed to reveal significant differences in Fv/Fm between the duration of the experiment (1, 30, 60, 90 and 150 days) and light types (FL, RL, NL) separately for *C. mitis* (N = 648), and *P. schreberi* (N= 648) as well as for soaked or non-soaked samples. A graphical interpretation of the interaction between the duration of the experiment, the species, and the type of sample (soaked and non-soaked) for different types of light was presented. The paired-samples t-test was performed to test the differences between the Fv/Fm values and soaked and non-soaked samples of both species. Before analysis, the normality of the distribution was verified using the Kolmogorov-Smirnov test ($p > 0.05$) and the Levene test ($p > 0.05$) to assess the equality of variances. Box plots were presented to illustrate the differences in individual comparisons.

3. Results

3.1.Photosynthetic activity

The results of the statistical analysis indicated visible differences in the photosynthetic activity of *Cladonia mitis* and *Pleurozium schreberi* depending on the type of light used and the duration of the experiment (Table 2, Fig. 2).

Our results shown in Fig.2 include four graphs that illustrate the photosynthetic activity of CM-NS (Fig. 2A), CM-S (Fig. 2B), PS-NS (Fig. 2C) and PS-S (Fig. 2D) depending on light intensity (FL, RL, NL) and the duration of the experiment (1, 30, 90, 120, 150 days). CM-NS indicates the lowest values of photosynthetic activity under FL conditions, higher values in the RL sample, and the highest values in the control sample. The photosynthetic activity values range from 0.1 to 0.8 Fv/Fm for the FL sample (Fig. 2A). CM-S indicated the lowest values of photosynthetic activity under FL conditions, higher in RL and the highest in NL. As with the CM-S sample, CM- NS was characterized by the lowest decrease in photosynthetic activity for the NL sample, higher for the RL sample, and the highest decrease for FL sample. The values of photosynthetic activity range from 0.38 to 0.8 (Fig. 2B). For the PS-NS samples,

photosynthetic activity values range from 0.55 to 0.8. The highest values were observed in the NL samples (Fig. 2C). For PS-S, the average values of photosynthetic activity reach the range of 0.55 to 0.78 Fv/Fm. PS-S reaches the lowest activity level in FL conditions, then higher in the RL sample, and the highest in the NL conditions. Bryophyte (PS-NS, PS-S) and lichens (CM-NS, CM-S) showed the highest level of photosynthetic activity in NL and the lowest levels in FL, which are close to the values presented by the RL conditions.

Table 2. The results of the multivariate ANOVA analysis assess the influence of the experiment duration (1, 30, 90, 120, 150 days), type of lighting (FL, RL, NL), and the interaction of time and type of light on photosynthetic activity in the tested samples. Significant effects ($p < 0.05$) are marked in bold.

Samples	Variables	F	p
CM-NS	Measurement Day	**92.903**	**p < 0.001**
	Type of Light	**88.071**	**p < 0.001**
	Measurement Day x Type of Light	**8.185**	**p < 0.001**
CM-S	Measurement Day	**58.420**	**p < 0.001**
	Type of Light	**57.105**	**p < 0.001**
	Measurement Day x Type of Light	**5.224**	**p < 0.001**
PS-NS	Measurement Day	**9.32**	**p < 0.001**
	Type of Light	**6.23**	**p = 0.002**
	Measurement Day x Type of Light	**5.13**	**p = 0.003**
PS-S	Measurement Day	**13.39**	**p < 0.001**
	Type of Light	**21.22**	**p < 0.001**
	Measurement Day x Type of Light	**2.82**	**p = 0.002**

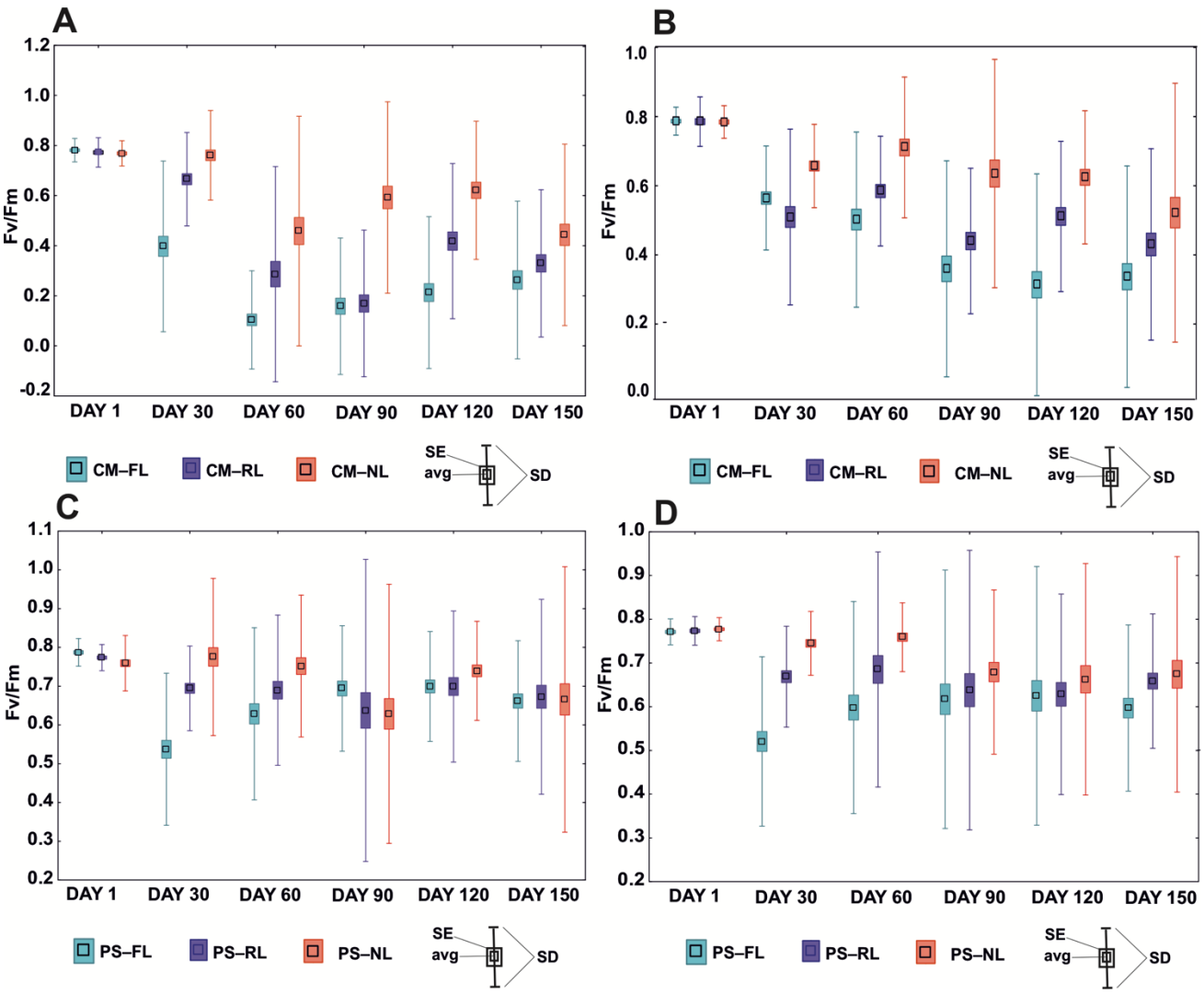

Fig. 2. Mean ± SE and SD of Fv/Fm, including days (1, 30, 60, 90, 120, 150) and type of light (FL, RL, NL) for A) CM-NS (N = 324), B) CM-S (N = 324), C) PS-NS (N = 324), D) PS-S (N = 324). The results of ANOVA ($p < 0.05$) are presented graphically.

Table 3. The results of the paired-samples t-test used to compare Fv/Fm values between soaked and non-soaked samples: lichens (A) and bryophytes (B). Significant effects ($p < 0.05$) are indicated in bold.

	Sample	Mean	SD	*t*-value	df	p
A)	CM-NS	0.4486	0.2757	-8.2405	323	**p<0.001**
	CM-S	0.5562	0.1905			
B)	PS-NS	0.6932	0.1231	2.8755	323	**p=0.004**
	PS-S	0.6698	0.1259			

The graphical interpretation of the interaction for three different types of light (respectively: Fig. 3 - FL, Fig. 4 - RL, Fig. 5 - NL) and the selected subsamples CM-S, CM-NS, PS-S and PS-NS were shown in Figs. 3-5.

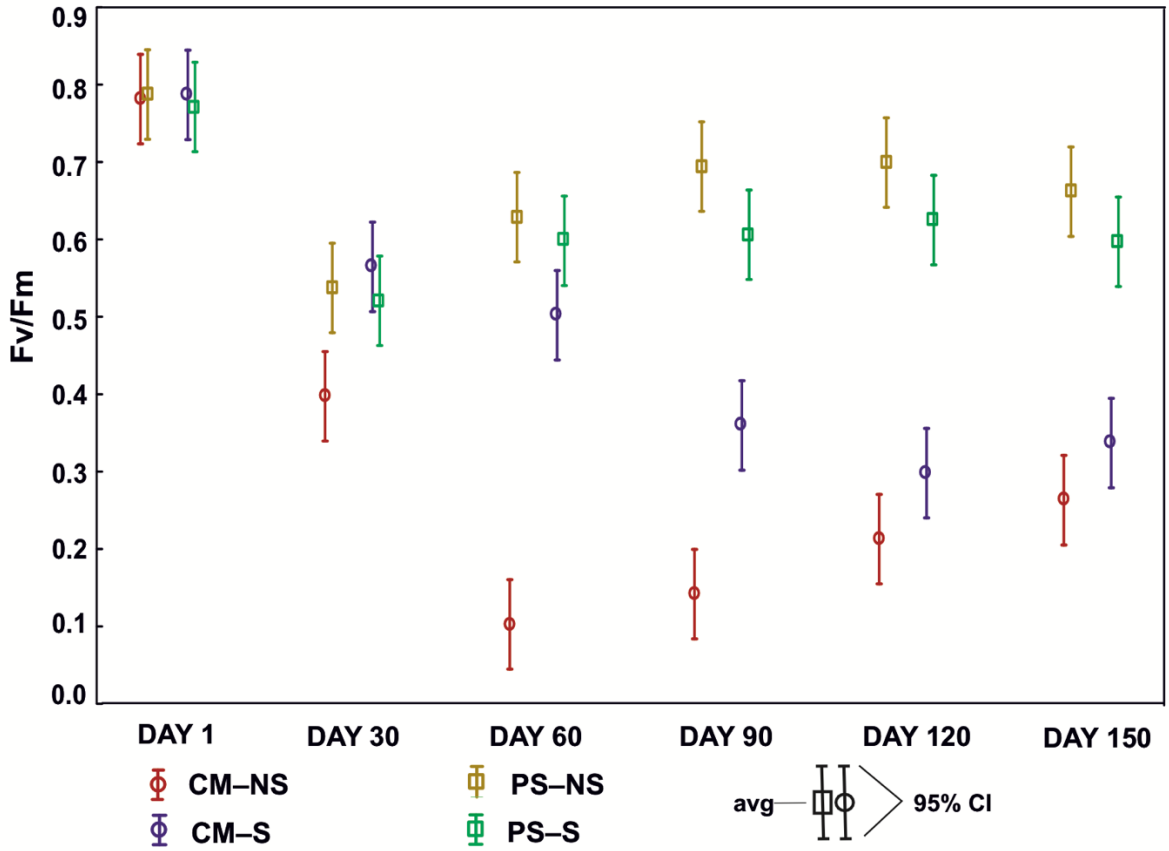

Fig. 3. Graphical interpretation for the ANOVA test (p = 0.026) including days (1, 30, 60, 90, 120, 150), selected subsamples: CM-NS, PS-NS, CM-S, and PS-S for the FL conditions (N = 436).

For FL conditions on each measurement day, CM-NS showed the lowest photosynthetic activity values among all selected subsamples and PS-NS species showed the highest values (Fig. 3). CM-NS noted decreasing values from the beginning of the experiment, with the lowest value occurring on day 60, which then increased until the end of the experiment. For CM-S a progressive decrease in photosynthetic activity in day 1 – day 120 period and slight increase in day 150 of measurement were noted. In turn, for PS-NS, the lowest activity values were observed on day 30, followed by an increase until day 150. Subsample PS-S showed activity slightly lower than that of its non-hydrated form, while maintaining an increase and decrease trend analogous to that of the PS-NS subsample. In turn, CM-S showed higher values of photosynthetic activity than its non-hydrated form (CM-NS) (Fig. 3, Table 3).

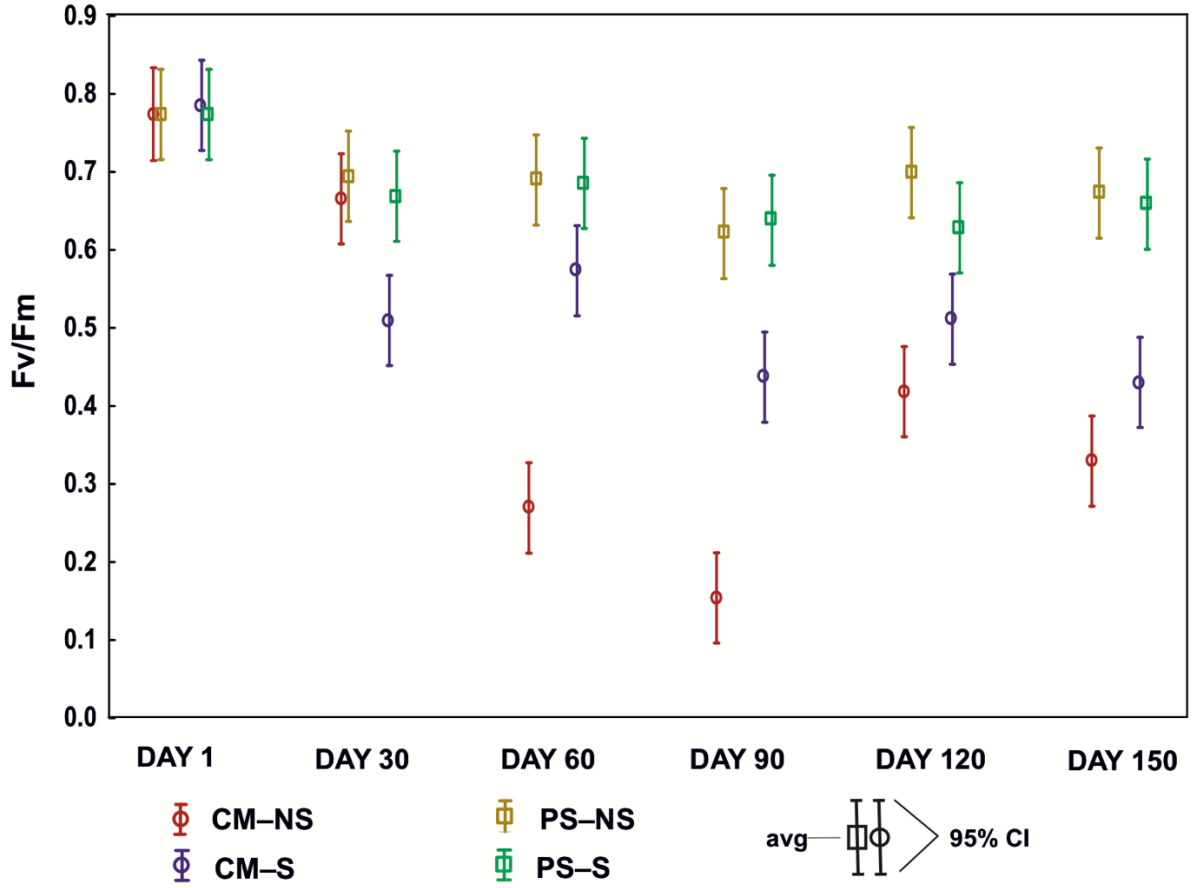

Fig. 4. Graphical interpretation for the ANOVA test (p = 0.026) including days (1, 30, 60, 90, 120, 150), selected subsamples: CM-NS, PS-NS, CM-S and PS-S for RL conditions (N = 436).

In the RL sample the highest values of the photosynthetic activity were recorded for the PS-NS subsample and slightly lower or similar for PS-S species (Fig. 4). Species *P. schreberi*, both in soaked and non-soaked samples, showed photosynthetic activity in the range of 0.6–0.7. The lowest values of the photosynthetic activity are shown by CM-NS, which reaches a critical level on day 90 and then increases until day 120. The Fv/Fm values of the CM-S thallus were higher than those of CM-NS, but still lower than those of both samples of *P. schreberi* (soaked and non-soaked). As for bryophyte, Fv/Fm values were higher for non-soaked samples than for soaked ones, except for day 120, when PS-S showed higher values than PS-NS (Fig. 4, Table 3).

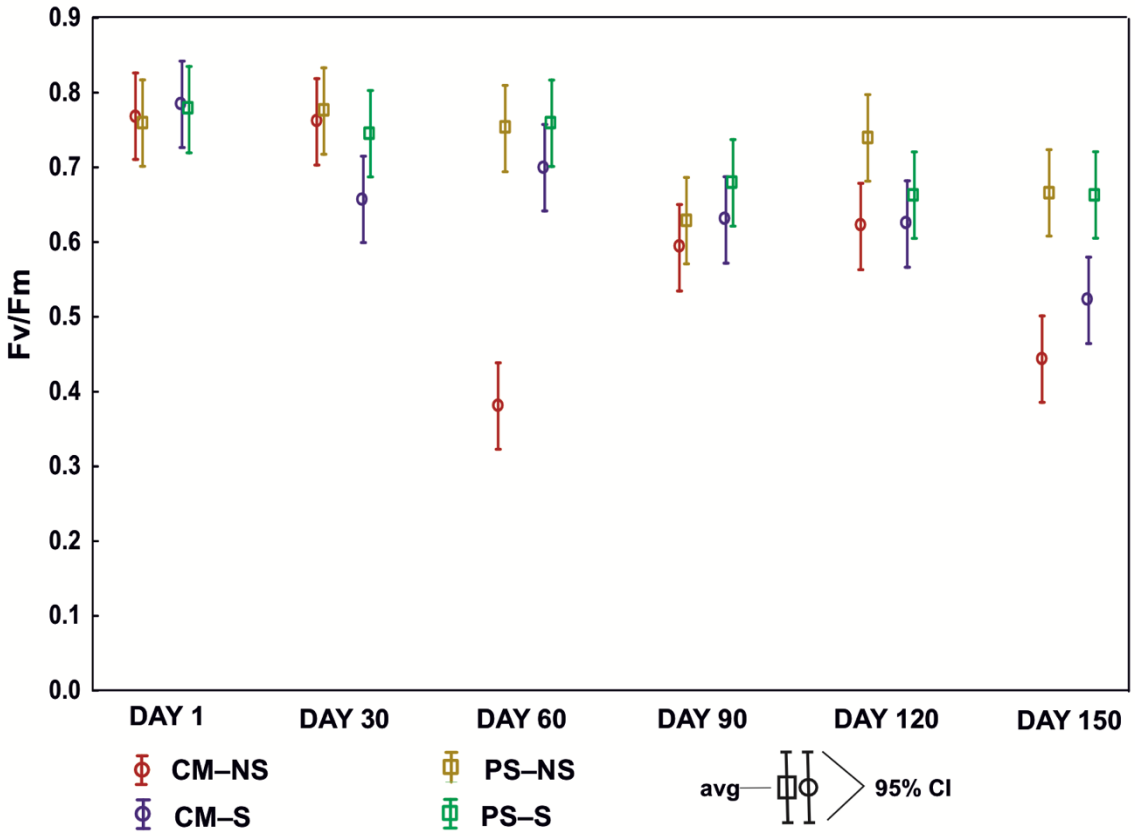

Fig. 5. Graphical interpretation for the ANOVA test (p = 0.026) including days (1, 30, 60, 90, 120, 150), selected subsamples: CM-NS, PS-NS, CM-S and PS-S for NL conditions (N = 436).

3.2. Microscopic fluorescence imaging of chloroplasts

The fluorescence of the chloroplasts in the cells of the photobiont in *Cladonia mitis* varied depending on the type of light and the length of the experiment. Initially, in all types of light, the fluorescence of chloroplasts was at a the similiar level. For the FL sample, the lowest fluorescence was on day 60 and day 90, which increased significantly during the following days. For the RL sample, a decrease in fluorescence was observed, with the lowest fluorescence occurring on day 90. On subsequent days, an increase in fluorescence could be observed. The control sample was characterized by similar chloroplast fluorescence for all days. The FL sample had the lowest chloroplast activity, while the control sample had the highest chloroplast activity relative to the rest of the tested groups (Fig. 6).

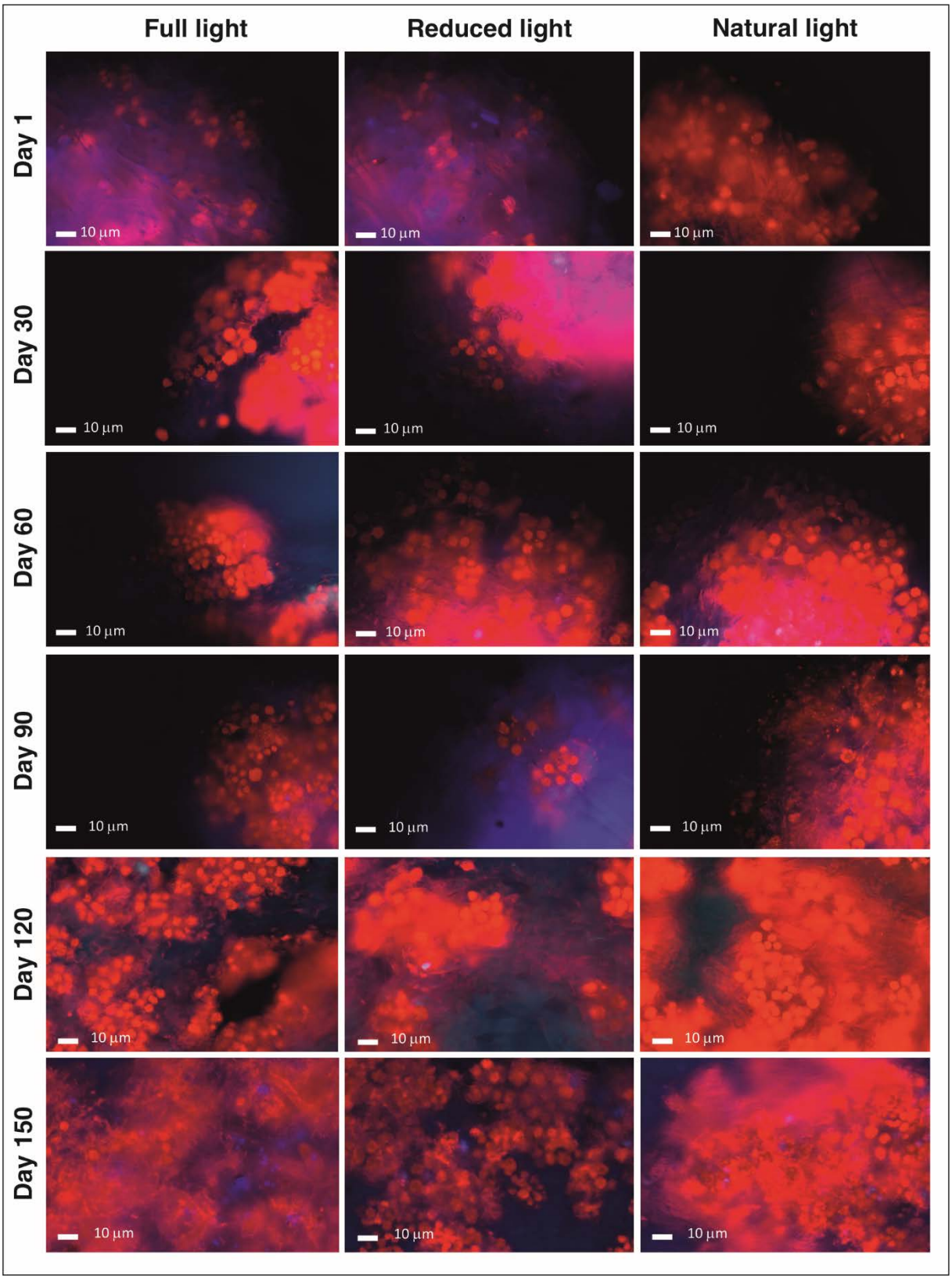

Fig. 6. Fluorescence microscope images of the lichen species *Cladonia mitis* for different lights (FL, RL, NL) and duration of the experiment (1, 30, 60, 90, 120, 150). Red colour refers to the fluorescence of the chloroplasts and the blue-violet colour refers to the fluorescence of the fungi hyphae.

The fluorescence of chloroplasts of the moss *Pleurozium schreberi* varied over time depending on the type of light. Referring to the FL sample, a decrease in the fluorescence of the chloroplasts was evident from day 30 to day 90. On subsequent days, an increase in the fluorescence of chloroplasts was observed. For the RL sample, slight decreases in fluorescence could be observed on day 30 and day 90, however, there was a resurgence later. For the control sample, there were no major differences in the change in chloroplast fluorescence (Fig. 7).

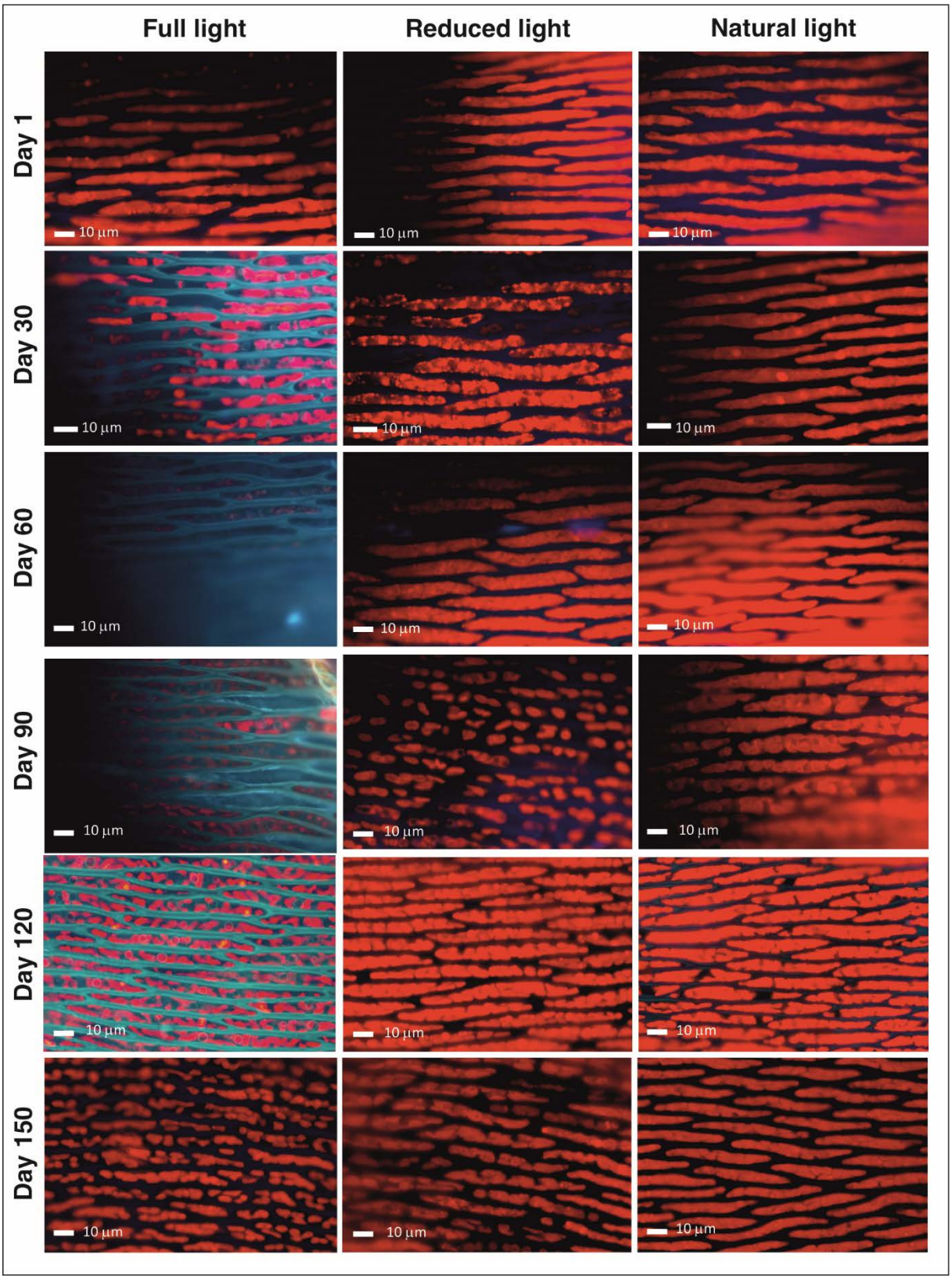

Fig. 7 Fluorescence microscope images of the lichen species *Pleurozium schreberi* for different lights (FL, RL, NL) and duration of the experiment (1, 30, 60, 90, 120, 150). Red colour represents the fluorescence of the chloroplasts and the blue-violet colour refers to the fluorescence of the bryophyte cell walls.

4. Discussion

4.1 Photosynthetic activity

Mosses and lichens are two distinct groups of organisms, often co-occurring in the same habitats that share certain ecological and morphological characteristics. It is well-known that both hydration and access to light are crucial for the photosynthesis and growth of the organisms mentioned. Both groups tolerate full desiccation without suffering photooxidative damage under strong light. The results of two-factor analysis of variance (ANOVA) tests showed a variation in photosynthetic activity in *C. mitis* and *P. schreberi* over time depending on the amount of light energy supplied. The results obtained in the present work refer to earlier research (Dziurowicz et al., 2022) in which the authors also supported the influence of light intensity on photosynthetic activity. Current research is another step in understanding the mechanisms, which confirmed that changes in photosynthetic activity occur in mosses and lichens depending on the amount of PAR energy supplied (Beckett et al., 2021; Dziurowicz et al., 2022; Wu et al., 2017). Evaluation of the methods and findings resulted in updated methodology and data collection, this time using both non-soaked and soaked samples, as well as fluorescence imaging.

Under non-stressful conditions, Fv/Fm levels usually remain at the same level, but this balance can be disturbed by the influence of stress factors, which include water, high temperature, and excessive radiation (PAR) (Lan et al., 2012). Absorption of more light that can be used for photosynthesis can lead to oxidative reactions that cause damage. This is especially dangerous for poikilohydric photoautotrophs that retain their chlorophyll during periods of dehydration (Heber and Lüttge, 2011). In the present study, the photosynthetic activity of *P. schreberi* and *C. mitis* was lowest at the highest light intensity, which consequently coincides with the adaptation of lichens and mosses to perform photosynthesis under reduced sunlight and even shade (Tobias and Niinemets, 2010; Wegrzyn et al., 2021). Species that are adapted to photosynthesise in the areas with access to light limited by natural factors (e.g., tree cover), show maximum photochemical potential and the highest solar energy conversion efficiency in PS II when the reaction centres are completely open (Krause, 1988; Franklin et al., 1992). Too much light intensity leads to oxidative stress during which free radicals or reactive oxygen species (ROS) are released. This reaction induces a partial or complete shutdown of the photosystem II reaction centre resulting in reduced photosynthetic activity (Lan et al., 2012; Telfer, 2005). In extreme cases, excess energy can trigger the formation of reactive oxygen species (ROS), which in turn can damage the photosynthetic apparatus and other cellular components leading to photoinhibition and photooxidative stress

(Mkhize et al., 2022). The first line of defense against oxidative stress in lichens involves the inactivation of reactive oxygen species (ROS) by enzymatic systems and the accumulation of lipophilic and hydrophilic compounds within cells (Beckett et al., 2021). However, under moderate light conditions, ROS is also produced, and a small amount of it is a signaling element responsible for acclimation and programmed cell death (Pospíšil, 2016). Results from the early 2000s (de la Torre et al., 2004; de Vera et al., 2004; de la Torre Noetzel et al., 2007) have shown that the ability to withstand high UV radiation can be credited to the fungus (mycobiont) that protects the more-sensitive photosynthetic active algae (photobiont) of the lichen with a dense cortex it develops (Vera et al., 2010). Furthermore, the concentration of specific secondary metabolites, such as depsidones, and dibenzofurans, often increases in lichens under stress conditions (Holger, 2014). Responsible for the radiation shielding effects is the production of metabolites that absorb radiation, such as parietin (Solhaug et al., 2003; Solhaug and Gauslaa, 2004; Wynn-Williams et al., 2002) and usnic acid (e.g. Quilhot et al., 1994; Rikkinen, 1995; Solhaug and Gauslaa, 1996).

Lichens are specialized to live in environments with limited access to water and can quickly recover from dehydration when water becomes available again. On the contrary, bryophytes are better suited for occupying moist habitats, often those that are only available seasonally, but have slower recovery times after experiencing dehydration (Green and Proctor, 2016). The higher the PAR energy, the faster the drying of the thallus (Tobias and Niinemets, 2010; Veres et al., 2022b), which in turn leads to photoinhibition and confirms the first research hypothesis that photosynthetic activity varies over time depending on the amount of PAR energy supplied. The response to high PAR is observed in both *C. mitis* and *P. schreberi,* and is more pronounced in lichens (Kappen et al., 1996). Lichens under conditions of water scarcity become dehydrated very quickly and go into a state of anabiosis, limiting or completely stopping photosynthesis (Kappen et al., 1996; Lange et al., 1993). An example is the CM-NS sample for which very low and sometimes critical Fv/Fm values were observed in full and reduced light. The completely opposite situation was observed for the PS-NS sample in which very high levels of photosynthetic activity were recorded throughout the experiment. The indicated differences are due to the different physiology of the studied species, and thus the degree of hydration of their forms. Single bryophyte shoots have low resistance to water loss, while packed shoots forming turf have an increased capacity to store and transport water, which significantly prolongs their physiological activity (Tobias and Niinemets, 2010).

As a part of our investigation, we have not only measured the photosynthetic activity of the lichens in their non-soaked state, but also after irrigating them for a period of two hours.

This approach was adopted based on importance of hydrating the samples under investigation before measuring their physiological parameters, that has already been shown in the previous study (Węgrzyn et al., 2021). Exposure to the sunlight of the dry lichen thallus can cause the accumulation of severe damage in PS II, and water is the endogenous factor for the regeneration of the damaged apparatus (Veres et al., 2022a). In the study, the hydrated form of *C. mitis* showed significantly higher levels of photosynthetic activity than the non-soaked thallus, which is a natural process that occurs in lichens (Grimm et al., 2021; Wegrzyn et al., 2021). The process of desiccation is responsible for reducing the amount of light that can pass through the upper cortex of a lichen thallus (Büdel and Lange, 1994; Ertl, 1951). Additionally, it is believed to create a functional disconnection of components of the photochemical apparatus (Sigfridsson, 1980; Bilger et al., 1989) On the other hand, soaked *P. schreberi* sample showed lower Fv/Fm values in each light, which may be the result of the supersaturation phenomenon (Green et al., 2011) and limited CO_2 diffusion (Green et al., 2011; Möller et al., 2022). The results presented here did not confirm the second research hypothesis that lichens in any type of light show higher values of photosynthetic activity than mosses. However, they did confirm the third hypothesis, as we noted that soaked lichen samples showed a significant increase in photosynthetic activity, compared to non-soaked samples. In turn the Fv/Fm values for non-soaked mosses were higher than soaked ones. These studies suggest that soaking specimens is not always recommended, as there are environmental conditions in which cryptogamous organisms maintain higher photosynthetic activity. It can be explained by the fact that both lichens and bryophytes are classified as homoiochlorophyllous, which means that they can rapidly resume photosynthesis after rewetting. However, a disadvantage of this trait is that chlorophyll continues to absorb photons even after desiccation, and the energy from the excess light cannot be used for photochemical work (Gasulla et al., 2021; Heber et al., 2006; Kranner et al., 2003). To prevent photooxidative damage in the desiccated state, homoiochlorophyllous poikilohydric cryptogams have evolved a highly efficient mechanism of photoprotection intended to prevent photodamage through controlled dissipation of thermal energy that is assessed by measuring non-photochemical quenching (NPQ) (Hájek et al., 2009; Heber and Lüttge, 2011; Mkhize et al., 2022). NPQ is induced rapidly on a time scale of seconds to a few minutes, making it ideal for dealing with sudden fluctuations in light intensity (Goss and Lepetit, 2015). In the case of lichens, NPQ is induced only after algae have been acclimated to prolonged light, so it would be a mistake to calculate NPQ values while measuring photosynthetic activity (Goss and Lepetit, 2015; Maxwell and Johnson, 2000).

4.2. Chloroplast structure

Fluorescence microscopy is used to study the viability of photosynthesizing cells based on the autofluorescence phenomenon of chloroplasts (Boluda and Hawksworth, 2014; Kauppi, 1980; Takahashi, 2019). Assessing chloroplast cell viability based on fluorescence microscope images alone is not precise enough (Bolhàr-Nordenkampf and Öquist, 1993). However, in combination with the measurement of photosynthetic activity, it provides a reliable picture of the changes that occur in the studied species caused by excessive light exposure (Dutta et al., 2015). Chloroplasts can move depending on the amount of light energy provided to them, and their movement is directly proportional to the amount of PAR energy demand (Davis et al., 2011; Wada, 2013). In conditions of low illumination, chloroplasts engage in an accumulation process, exposing themselves to light. Conversely, under conditions of excessive light, chloroplasts undergo an avoidance process, concealing themselves by positioning behind one another (Dutta et al., 2015; Suetsugu and Wada, 2012). The combination of accumulation and avoidance responses presumably allows plant cells to strike a balance between maximising light uptake and minimizing photodamage (Davis and Hangarter, 2012). The microscope images are an illustration of the trends of photosynthetic changes that occur in *C. mitis* and *P. schreberi* along with their chloroplast structure. At low fluorescence of chloroplasts, the preparation exhibited diminished color intensity, with the dominance of the cell wall color (blue). Conversely, under conditions of full chloroplast fluorescence, a prevalence of red color was observed. Notably, *C. mitis* demonstrated the lowest chloroplast fluorescence levels under the strongest and reduced light, aligning with its correspondingly reduced photosynthetic activity. This observation may indicate that chloroplast degradation or its avoidance reaction is occurring. As noted by other authors (Beckett et al., 2021; Derks et al., 2015; Veres et al., 2022b), high light intensity leads to progressive changes in the cell, which in most cases are irreversible. However, lichens in the sample of natural light showed very high photosynthetic activity and thus were accompanied by intense fluorescence, which informed about the normal state of chloroplast behavior. In *P. schreberi*, the identification of chloroplasts was much simpler, as they are arranged in a single layer. This stands in contrast to lichens, where chloroplasts are grouped within algal cells, presenting a more complex identification challenge. The moss species suffered the greatest loss of chloroplast fluorescence in the sample of intense light. As photosynthetic activity decreased, fluorescence decreased, but at the final stages of the experiment, activity increased significantly, translating into intense fluorescence of chloroplasts. In bryophytes, the movement of chloroplasts is more likely to occur than their complete degradation. In a situation where the structure of chloroplasts was destroyed, they

would not show any fluorescence activity, as the chlorophyll in them is degraded (Otegui, 2018). The activity of the repair apparatus depends on the regeneration time and the rate of progressive photodamage. This condition is known as photoinhibition of photosynthesis and occurs when the rate of photodamage exceeds the repair capacity (Derks et al., 2015; Melis, 1999). Under reduced and natural light conditions, the mosses showed both high photosynthetic activity and intense fluorescence of the chloroplasts. Thus, the results presented partially confirm the fourth hypothesis, which assumes that chloroplasts are degraded under the influence of the strongest light. In lichens, this phenomenon is already noticeable in the first days of measurement, and the damage caused by PAR energy leads to the degradation of chloroplast cells. However, the degradation is small, or at least imperceptible, at a given stage of analysis. More research is needed to assess the viability of chloroplasts along with their photosynthetic activity.

5. **Conclusion**

Our comprehensive study delved into several key hypotheses, shedding light on the mutual interaction between photosynthetic activity and chloroplast dynamics under the influence of light energy on lichens and bryophytes. Firstly, our findings strongly confirm that photosynthetic activity changes over time in both species *C. mitis* and *P. schreberi* and depends on the supplied PAR energy. Higher PAR energy leads to faster thallus drying, subsequently resulting in the degradation of the photosynthetic apparatus and the photoinhibition process. On the other hand, consistent measurements of photosynthetic activity combined with chloroplast imaging using fluorescence microscopy allowed us to observe the behavior and viability of chloroplasts in both lichens and bryophytes more precisely. Consequently, we were able to observe the phenomena of displacement, relocation, and degradation of chloroplasts in response to specific PAR energy. Currently, we can say that by taking microscope images of chloroplasts, we can estimate the predictive amount of light to which a given species was exposed. In our research, we also validated the intriguing hypothesis that bryophytes, regardless of the light type, consistently exhibit higher photosynthetic activity than lichens. This fact is interesting due to the generally accepted opinion that lichens are highly adapted to extreme conditions and they should show a higher level of photosynthetic activity. This unexpected dynamic emphasizes the complex responses of these organisms to light conditions. Additionally, our studies reveal that the hydration state has a significant impact on the photosynthetic activity of the studied species. Soaked lichens showed a substantial increase in photosynthetic activity compared to their non-soaked counterparts, while the trend was reversed for bryophytes. This phenomenon can be

explained by unique defense mechanisms specific to each species: lichens entering a state of anabiosis under water-deficient conditions and bryophytes exhibiting superstorage properties under conditions of excessive hydration and slowing down photosynthesis. In summary, our work provides valuable insights into the diverse reactions of lichens and bryophytes to changing light conditions and hydration states. The delicate balance between photosynthetic activity and chloroplast dynamics underscores the adaptive capabilities and resilience of these organisms in the face of environmental challenges. This study serves as a solid foundation for further research into the intricate ecological adaptations of lichens and bryophytes.

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Declarations

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References

Allorent G., Tokutsu R., Roach T., Peers G., Cardol P., Girard-Bascou J., Seigneurin-Berny D., Petroutsos D., Kuntz M., Breyton C., Franck F., Wollman F. A., Niyogi K., Krieger-Liszkay A., Minagawa J., Finazzi G., 2013, A dual strategy to cope with high light in Chlamydomonas reinhardtii, TPJ 25(2):545–557, https://doi.org/10.1105/tpc.112.108274

Barber J., Andersson B., 1992, Too much of a good thing: light can be bad for photosynthesis, TIBS 17(2): 61–66, https://doi.org/10.1016/0968-0004(92)90503-2

Beckett R., Minibayeva F., Solhaug K., Roach T., 2021, Photoprotection in lichens: Adaptations of photobions to high light, Lichenologist 53(1): 21–33, https://doi.org/10.1017/S0024282920000535

Bewley J.D., 1979, Physiological aspects of desiccation tolerance, Annu Rev Plant Physiol 30(1) 195–238, https://doi.org/10.1146/annurev.pp.30.060179.001211

Bilger W., Rimke S., Schreiber U., Lange O. L., 1989, Inhibition of energy-transfer to photosystem II in lichens by dehydration: different properties of reversibility with green and blue-green phycobionts, J Plant Physiol 134(3):261–268, https://doi.org/10.1016/S0176-1617(89)80240-8

Bolhàr-Nordenkampf H. R., Öquist G., 1993, Chlorophyll fluorescence as a tool in photosynthesis research. In: Hall DO, Scurlock JMO, Bolhàr-Nordenkampf HR, Leegood RC, Long SP (eds.) Photosynthesis and Production in a Changing Environment. Springer, Dordrecht, https://doi.org/10.1007/978-94-011-1566-7_12

Boluda C. G., Rico V., Hawkswort D. L., 2014, Fluorescence microscopy as a tool for the visualization of lichen substances within Bryoria thalli, Lichenologist 46(5):723–726, https://doi.org/10.1017/S0024282914000292

Büdel B., Lange O. L., 1994, The role of cortical and epinecral layers in the lichen genus Peltula, Cryptogamic Botany 4:262–269

Charron A. J., Quatrano R. S., 2009, Between a rock and a dry place: the water-stressed moss, Mol Plant 2(3):478–486, https://doi.org/10.1093/mp/ssp018

Chen Y. E., Wu N., Zhang Z. W., Yuan M., Yuan S., 2019, Perspective of monitoring heavy metals by moss visible chlorophyll fluorescence parameters, Front Plant Sci 10(35), https://doi.org/10.3389/fpls.2019.00035

Chowaniec K., Rola K., 2022, Evaluation of the importance of ionic and osmotic components of salt stress on the photosynthetic efficiency of epiphytic lichens, Physiol Mol Biol Plants:1–15, https://doi.org/10.1007/s12298-022-01134-2

Davis P. A., Caylor S., Whippo C. W., Hangarter R. P., 2011, Changes in leaf optical properties associated with light-dependent chloroplast movements, Plant Cell Environ 34:2047–2059, https://doi.org/10.1111/j.1365-3040.2011.02402.x

Davis P. A., Hangarter R. P., 2012, Chloroplast movement provides photoprotection to plants by redistributing PSII damage within leaves, Photosynth Res 112:153–161, https://doi.org/10.1007/s11120-012-9755-4

De Carolis, R., Cometto, A., Moya, P., Barreno, E., Grube, M., Tretiach, M., D.leavitt, S., Muggia, L. (2022). Photobiont diversity in lichen symbioses from extreme environments. Frontiers in microbiology, 13, 809804, https://doi.org/10.3389/fmicb.2022.809804

de la Torre Noetzel R., Sancho L. G., Pintado A., Rettberg P., Rabbow E., Panitz C., Deutschmann U., Reina M., Horneck G., 2007, BIOPAN experiment LICHENS on the Foton M2 mission: pre-flight verification tests of the Rhizocarpon geographicum-granite ecosystem, ASR 40(11):1665–1671, https://doi.org/10.1016/j.asr.2007.02.022

de la Torre R., Horneck G., Sancho L. G., Pintado A., Scherer K., Facius R., Deutschmann U., Reina M., Baglioni P., Demets R., 2004, Studies of lichens from high mountain regions in outer space: the BIOPAN experiment, In: Harris RA, Ouwehand L (eds.) ESA Publications Division, Noordwijk, The Netherlands:193–194

De Vera J. P., Horneck G., Rettberg P., Ott S., 2004a, The potential of lichen symbiosis to cope with the extreme conditions of outer space II: Germination capacity of lichen ascospores in response to simulated space conditions. Adv Space Res 33:1236–1243 https://doi.org/10.1016/j.asr.2003.10.035

Demmig-Adams B., Adams W. W., 1992, Photoprotection and Other Responses of Plants to High Light Stress, Annu Rev Plant Physiol Plant Mol Biol 43:599–626, https://doi.org/10.1146/annurev.pp.43.060192.003123

Derks A., Schaven K., Bruce D., 2015, Diverse mechanisms for photoprotection in photosynthesis, Dynamic regulation of photosystem II excitation in response to rapid environmental change, BBA-Bioenergetics 1847(4-5):468–485, https://doi.org/10.1016/j.bbabio.2015.02.008

Dutta S., Cruz J. A., Jiao Y., Chen J., Kramer D. M., Osteryoung K. W., 2015, Non-invasive, whole-plant imaging of chloroplast movement and chlorophyll fluorescence reveals photosynthetic phenotypes independent of chloroplast photorelocation defects in chloroplast division mutants, TPJ 84(2):428–442, https://doi.org/10.1111/tpj.13009

Dziurowicz P., Fałowska P., Waszkiewicz K., Wietrzyk-Pełka P., Węgrzyn M. H., 2022, Changes in photosynthetic activity of the lichen Cladonia mitis and the Pleurozium schreberi under artificial high-energy lighting in laboratory, ABCbot 64/2 accepted article, https://doi.org/10.24425/abcsb.2022.143381

Ertl L., 1951, Über die Lichtverhältnisse in Laubflechten, Planta 39:245–270, https://doi.org/10.1007/BF01909397

Franklin L. A., Levavasseur G., Osmond C. B., Henley W. J., Ramus J., 1992, Two components of onset and recovery during photoinhibition of *Ulva rotundata*, Planta 187:399–408, https://doi.org/10.1007/BF00195321

Gaff D. F., 1989, Responses of desiccation tolerant 'resurrection' plants to water stress, In: Kreeb K. H., Richter H., Hinckley T. M. (eds) Structural and Functional Responses to Environmental Stresses SPB Academic Publishing:264–311

Gasulla F., del Campo E. M., Casano L. M., Guéra A., 2021, Advances in Understanding of Desiccation Tolerance of Lichens and Lichen-Forming Algae, Plants 10(4):807, https://doi.org/10.3390/plants10040807

Goss R., Lepetit B., 2015, Biodiversity of NPQ, J Plant Physiol 172:13–32, https://doi.org/10.1016/j.jplph.2014.03.004

Green T. A., Proctor M. C., 2016, Physiology of photosynthetic organisms within biological soil crusts: their adaptation, flexibility, and plasticity, Biocrusts: an organizing principle in drylands:347–381, https://doi.org/10.1007/978-3-319-30214-0_18

Green T. G. A., Sancho L. G., Pintado A., 2011, Ecophysiology of Desiccation/Rehydration Cycles in Mosses and Lichens, In: Lüttge U, Beck E, Bartels D (eds.) Plant Desiccation Tolerance, Ecol stud 215, Springer, Berlin, Heidelberg, https://doi.org/10.1007/978-3-642-19106-0_6

Grimm M., Grube M., Schiefelbein U., Zühlke D., Bernhardt J., Riedel K., 2021, The lichens' microbiota, still a mystery?, Front Microbiol 12:714, https://doi.org/10.3389/fmicb.2021.623839

Hájek T., Tuittila E. S., Ilomets M., Laiho R., 2009, Light responses of mire mosses–a key to survival after water-level drawdown?, Oikos 118(2):240–250, https://doi.org/10.1111/j.1600-0706.2008.16528.x

He X., He K. S., Hyvönen J., 2016, Will bryophytes survive in a warming world?, PPEES *19*:49–60, https://doi.org/10.1016/j.ppees.2016.02.005

Heber U., Lange O. L., Shuvalov V. A., 2006, Conservation and dissipation of light energy as complementary processes: homoiohydric and poikilohydric autotrophs, J Exp Bot 57(6):1211–1223, https://doi.org/10.1093/jxb/erj104

Heber U., Lüttge U., 2011, Lichens and Bryophytes: Light Stress and Photoinhibition in Desiccation/Rehydration Cycles – Mechanisms of Photoprotection, In: Lüttge U, Beck E, Bartels D (eds.) Plant Desiccation Tolerance ECOLSTUD 215, Springer, Berlin, Heidelberg, https://doi.org/10.1007/978-3-642-19106-0_7

Holger T., Marie-Laurence A., David D., Joël B., 2014, Oxidative stress regulation in lichens and its relevance for survival in coastal habitats, Advances in Botanical Research 71:467–503, https://doi.org/10.1016/B978-0-12-408062-1.00016-0

Kappen L., Schroeter B., Scheidegger C., Sommerkorn M., Hestmark G., 1996, Cold resistance and metabolic activity of lichens below 0 C, ASR 18(12):119–128, https://doi.org/10.1016/0273-1177(96)00007-5

Kauppi M., 1980, Fluorescence microscopy and microfluorometry for the examination of pollution damage in lichens, Ann Bot Fenn:163–173

Kranner I., Zorn M., Turk B., Wornik S., Beckett R. P., Batič F., 2003, Biochemical traits of lichens differing in relative desiccation tolerance, New Phytol 160:167–176, https://doi.org/10.1046/j.1469-8137.2003.00852.x

Krause G. H., 1988, Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms, Physiol Plant 74:566–574, https://doi.org/10.1111/j.1399-3054.1988.tb02020.x

Kumari, K., Kumar, V., Nayaka, S., Saxena, G., Sanyal, I. (2024). Physiological alterations and heavy metal accumulation in the transplanted lichen Pyxine cocoes (Sw.) Nyl. in Lucknow city, Uttar Pradesh. Environmental Monitoring and Assessment, 196(1), 1-16.https://doi.org/10.1007/s10661-023-12256-9

Lakatos M., 2011, Lichens and Bryophytes: habitats and species, In: Lüttge U, Beck E, Bartels D (eds.) Plant Desiccation Tolerance, Ecol stud 215:65–87, https://doi.org/10.1007/978-3-642-19106-0_5

Lan S., Wu L., Zhang D., Hu C., 2012, Composition of photosynthetic organisms and diurnal changes of photosynthetic efficiency in algae and moss crusts, Plant Soil 351(1):325–336, https://doi.org/10.1007/s11104-011-0966-9

Lange O. L., Büdel B., Heber U., Meyer A., Zellner H., Green T. G. A., 1993, Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO2 exchange, Oecologia 95(3):303–313, https://doi.org/10.1007/BF00320981

Liu, M., Zhang, Z., Gao, H., Yang, C., Fan, X., Cheng, D., 2014, Effect of leaf dehydration duration and dehydration degree on PSII photochemical activity of papaya leaves. Plant physiology and biochemistry, 82, 85-88, https://doi.org/10.1016/j.plaphy.2014.05.003

Liu Y., Cao T., Glime J., 2003, The Changes of Membrane Permeability of Mosses under High Temperature Stress, Bryologist 106(1):53–60, https://doi.org/10.1639/0007-2745(2003)106[0053:TCOMPO]2.0.CO;2

Lücking, R., Leavitt, S. D., Hawksworth, D. L., 2021, Species in lichen-forming fungi: balancing between conceptual and practical considerations, and between phenotype and phylogenomics. Fungal Diversity, 109(1), 99-154, https://doi.org/10.1007/s13225-021-00477-7

Maxwell K., Johnson G. N., 2000, Chlorophyll fluorescence—a practical guide, J Exp Bot 51(345):659–668, https://doi.org/10.1016/B978-0-12-408062-1.00016-0

Melis A., 1999, Photosystem-II damage and repair cycle in chloroplasts: what modulates the rate of photodamage in vivo?, Trends Plant Sci 4(4):130–135, https://doi.org/10.1016/S1360-1385(99)01387-4

Mkhize K. G. W., Minibayeva F., Beckett R. P., 2022, Lichen photobionts can be hardened to photoinhibition by pretreatment with light, Acta Physiol Plant 44(11):1–10, https://doi.org/10.1007/s11738-022-03458-8

Möller T., Porada P., Petersen I., 2022, The effect of water potential on the water balance of lichens and mosses – distribution patterns of internal and external water, PREPRINT Version 1 Res Sq https://doi.org/10.21203/rs.3.rs-1915047/v1

Nguyen K. H., Chollet-Krugler M., Gouault N., Tomasi S., 2013, UV-protectant metabolites from lichens and their symbiotic partners, Nat Prod Rep 30(12):1490–1508, https://doi.org/10.1039/C3NP70064J

Orekhova A., Barták M., Hájek J., Morkusová J., 2022, Species-specific responses of spectral reflectance and the photosynthetic characteristics in two selected Antarctic mosses to thallus desiccation, Acta Physiol Plant 44(1):1–19, https://doi.org/10.1007/s11738-021-03339-6

Otegui M. S., 2018, Vacuolar degradation of chloroplast components: autophagy and beyond, J Exp Bot 69(4):741–750, https://doi.org/10.1093/jxb/erx234

Pospíšil P., 2016, Production of reactive oxygen species by photosystem II as a response to light and temperature stress, Front Plant Sci 7:19–50, https://doi.org/10.3389/fpls.2016.01950

Quilhot W., Fernandez E., Hidalgo M. E., 1994, Photoprotection mechanisms against UV radiation, Brit Lichen Soc Bull 75:1–5

Ranković, B., Kosanić, M., 2019. Lichens as a potential source of bioactive secondary metabolites. Lichen secondary metabolites: bioactive properties and pharmaceutical potential, 1-29. https://doi.org/10.1007/978-3-030-16814-8_1

Rikkinen J., 1995, Whats behind the pretty colours. A study on the photobiology of lichens, Bryologist 4:1–239, https://doi.org/10.2307/3244316

Rochaix J. D., 2011, Regulation of photosynthetic electron transport, BBA-Bioenergetics 1807(3):375–383, https://doi.org/10.1016/j.bbabio.2010.11.010

Schlensog M., Schroeter B., 2001, A new method for the accurate in situ monitoring of chlorophyll a fluorescence in lichens and bryophytes, Lichenologist 33(5):443–452, https://doi.org/10.1006/lich.2001.0340

Sigfridsson B., 1980, Some effects of humidity on the light reaction of photosynthesis in the lichens Cladonia impexa and Collema flaccidum, Physiol Plant 49:320–6, https://doi.org/10.1111/j.1399-3054.1980.tb02671.x

Solhaug K. A., Gauslaa Y., 1996, Parietin, a photoprotective secondary product of the lichen Xanthoria parietina, Oecologia 108:412–418, https://doi.org/10.1007/BF00333715

Solhaug K. A., Gauslaa Y., 2004, Photosynthates stimulate the UV-B induced fungal anthraquinone synthesis in the foliose lichen Xanthoria parietina, Plant Cell Environ 27:167–176, https://doi.org/10.1111/j.1365-3040.2003.01129.x

Solhaug K. A., Gauslaa Y., Nybakken L., Bilger W., 2003, UV induction of sun-screening pigments in lichens, New Phytol 158:91–100, https://doi.org/10.1046/j.1469-8137.2003.00708.x

Suetsugu N., Wada M., 2012, Chloroplast photorelocation movement: a sophisticated strategy for chloroplasts to perform efficient photosynthesis, In Advances in Photosynthesis — Fundamental Aspects, InTech:215–234, ISBN 978-953-307-928-8

Takahashi T., 2019, Routine management of microalgae using autofluorescence from chlorophyll, Molecules 24(24):44–41, https://doi.org/10.3390/molecules24244441

Telfer A., 2005, Too much light? How β-carotene protects the photosystem II reaction centre, PPS 4(12), 950-956, https://doi.org/10.1039/B507888C

Tobias M., Niinemets Ü., 2010, Acclimation of photosynthetic characteristics of the moss Pleurozium schreberi to among-habitat and within-canopy light gradients, Plant Biol 12(5):743–754, https://doi.org/10.1111/j.1438-8677.2009.00285.x

Tuba Z., Csintalan Z., Proctor M. C., 1996, Photosynthetic responses of a moss, Tortula ruralis, ssp. ruralis, and the lichens Cladonia convoluta and C. furcata to water deficit and short periods of desiccation, and their ecophysiological significance: a baseline study at present-day CO2 concentration, NEPHAV 133(2):353–361, https://doi.org/10.1111/j.1469-8137.1996.tb01902.x

Vera J. P. D., Möhlmann D., Butina F., Lorek A., Wernecke R., Ott S., 2010, Survival potential and photosynthetic activity of lichens under Mars-like conditions: a laboratory study, Astrobiology 10(2):215–227, https://doi.org/10.1089/ast.2009.0362

Veres K., Csintalan Z., Laufer Z., Engel R., Szabó K., Farkas E., 2022a, Photoprotection and high-light acclimation in semi-arid grassland lichens–a cooperation between algal and fungal partners, Symbiosis 86(1):33–48, https://doi.org/10.1007/s13199-021-00823-y

Veres K., Sinigla M., Szabó K., Varga N., Farkas E., 2022b, The long-term effect of removing the UV-protectant usnic acid from the thalli of the lichen Cladonia foliacea, Mycol Prog 21(9):1–13, https://doi.org/10.1007/s11557-022-01831-y

Wada M., 2013, Chloroplast movement, Plant Science 210:177–182, https://doi.org/10.1016/j.plantsci.2013.05.016

Węgrzyn M. H., Fałowska P., Alzayany K., Waszkiewicz K., Dziurowicz P., Wietrzyk-Pełka P., 2021, Seasonal changes in the photosynthetic activity of terrestrial lichens and mosses in the lichen scots pine forest habitat, Diversity 13, https://doi.org/10.3390/d13120642

Wobbe L., Bassi R., Kruse O., 2016, Multi-level light capture control in plants and green algae, Trends Plant Sci 21(1):55–68, https://doi.org/10.1016/j.tplants.2015.10.004

Wu L., Lei Y., Lan S., Hu C., 2017, Photosynthetic recovery and acclimation to excess light intensity in the rehydrated lichen soil crusts, PLoS One 12(3), https://doi.org/10.1371/journal.pone.0172537

Wynn-Williams D. D., Edwards H. G. M., Newton E. M., Holder J. M., 2002, Pigmentation as a survival strategy for ancient and modern photosynthetic microbes under high ultraviolet stress on planetary surfaces, Int J Astrobiology 1:39–49, https://doi.org/10.1017/S1473550402001039