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Changes in Photosynthetic Activity of the Lichen *Cladonia mitis* and the Moss *Pleurozium schreberi* under Artificial High-Energy Lighting in Laboratory Conditions

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Assessment of photosynthetic activity is one of the quick and simple methods of verification whether the studied environmental factors have a stressful effect on photosynthetically active organisms. High-intensity light can be a stress factor that could have a potential impact on the maximum productivity of photosystem II. The purpose of the conducted research was to observe changes in photosynthetic activity of the lichen *Cladonia mitis* and the bryophyte *Pleurozium schreberi* exposed to artificial high-energy lighting under laboratory culture conditions. The obtained results showed variability of photosynthetic activity over time, depending on the amount of light energy supplied. *C. mitis* and *P. schreberi* at full exposure (light energy: 52.03 W m^{-2} and photosynthetically active radiation 167.24 µmol m^{-2}) showed a slow downward trend in photosynthetic activity, while at half the light intensity periodic fluctuations were observed without changes in the controls. Long-term and high-light intensity exposure of photosynthetically active organisms may cause gradual degradation of the photosynthetic apparatus, which in turn leads to cell death. Low values of photosynthetic activity may indicate a situation in which, due to excess light, the rate of photosystem II damage exceeds the rate of its repair. This leads to irreversible damage to the photosynthetic apparatus.

Keywords: 'Bory Tucholskie' National Park, bryophytes, high intensity light, lichens, photosynthetic activity, stress factor

INTRODUCTION

Photosynthesis is the most important biological process that aims to produce necessary energy materials for a plant organism (Tikhonov, 2018). Photosynthetic organisms use the sun's rays in the absorption spectrum in the 400-700 nm wavelength range, called photosynthetically active radiation (PAR) (Wimalasekera, 2019). The use of solar energy takes place in the bright phase of photosynthesis, during which light energy converts into chemical energy (Abas et al., 2020; Wimalasekera, 2019), as a result of photochemical and redox reactions (Rochaix, 2011), which take place in chloroplast membranes that contain two pigment-protein complexes, photosystem II (PS II) and photosystem I (PS I). However, the absorbed energy is not entirely used to trigger photochemical reactions because it is partially lost as heat or chlorophyll fluorescence (Guidi et al., 2007; Wimalasekera, 2019).

The chlorophyll fluorescence phenomenon is used to assess the efficiency of photosynthesis by determining the rate of photosynthetic activity in selected groups of organisms capable of performing it. In other words, by measuring the fluores-

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cence of chlorophyll, the reaction of PS II to changes in the intensity of photosynthetically active radiation (PAR) is assessed (Demmig-Adams and Adams,1992; Wu et al., 2017). In order to measure the quantum efficiency of PS II, the following variables are determined: Fo (minimum fluorescence) – shows the emission of excited chlorophyll a molecules in the antenna structure of PS II; Fm (maximum fluorescence) – the maximum value of fluorescence obtained for a continuous light intensity; Fv (variable of fluorescence) – (Fm – Fo) – marked as photochemical fluorescence quenching; Fv/Fm (maximum photochemical efficiency of PS II) – ratio of variable fluorescence (Fv) to maximum fluorescence (Fm) (Baker and Rosenqvist, 2004; Hansatech, 2008; Kalaji and Guo, 2008; Tuba et al., 2010). The maximum photochemical efficiency of PS II ranges from 0 to 1, most often plants under stress-free conditions achieve a value of around 0.83 (Björkman and Demmig, 1987; Maxwell and Johnson, 2000), while for lichens the range is between 0.6 and 0.7 (Węgrzyn et al., 2021a). Lower values of Fv/Fm indicate the presence of biotic or abiotic stress in photosynthetically active organisms (Hansatech, 2008; Węgrzyn et al., 2021a). However, very low values, below 0.3, indicate the occurrence of irreversible damage to the photosynthetic apparatus (Węgrzyn et al., 2021a). Therefore, measurement of photosynthetic activity is one of the fastest and easiest methods for assessing the condition of photosynthetically active organisms, including lichens and bryophytes, which are often species sensitive to habitat disturbances.

Lichens belong to a taxonomically and physiologically diverse group, which is why they are a very interesting object of research. For years, lichens had been included in the plant kingdom; however, careful study of the anatomical structure allowed for a more precise definition of their affiliation (Hawksworth, 2015). Currently, lichens (lichenized fungi) are part of the kingdom of fungi, defined as symbiotic organisms composed of heterotrophic fungi and one or more photoautrophic organisms belonging to prokaryotic or eukaryotic algae (Honegger, 2012; Hawksworth, 2015). In lichens, the photosynthetic process is closely related to the photosynthetic abilities of the photobiont. In their chloroplasts, lichen algae have centrally located pyrene, which is rich in proteins and lipids and contains the RuBisCo photosynthetic enzyme (Barták, 2014; Palmqvist et al., 1997). In the case of *Trebouxia,* pyrenoid can concentrate carbon (Barták, 2014; Palmqvist et al., 1998). As a result of the photosynthesis process, polyols, that is sugar alcohols, are formed in lichens and are used both to supply the mycobiont with nutrients and as key osmolytes that protect both algae and fungal tissues against water loss during drying (Barták, 2014; Ten Veldhuis, 2020).

Bryophyte *Bryophyta* are among the most ancient spore plants found on land (Martínez-Abaigar and Núñez-Olivera, 2022). They belong to a diverse group of Bryophyte (bryophytes), which also includes liverworts *Marchantiophyta* and hornworts *Anthocerotophyta* (Crandall-Stotler and Bartholomew-Began, 2007; Glime, 2017a; Huttunen et al., 2018; Lakatos, 2011). The term "Bryophyte" defines an informal group, including the above-mentioned clusters, which are characterized by the alternation of generations with the dominance of the gametophyte (Crandall-Stotler and Bartholomew-Began, 2007; Glime, 2017a; Huttunen et al., 2018). Within bryophytes, four separate classes have been distinguished: sphagnum *Sphagnopsida,* andreaea *Andreaeopsida,* haircaps *Polytrichopsida,* and bryopsida *Bryopsida* (Glime, 2017b). Unlike lichens, bryophytes belong to the plant kingdom; however, they are not vascular organisms, which means that they have no roots or vascular tissue. Like lichens, they draw water from the air through their surface, whereas more specialized organisms use rhizoids from the substrate (Huttunen et al., 2018). In bryophytes, photosynthesis occurs in gametophytes, which feed sporophytes (Pokorny et al., 2012). In mosses, the binding of carbon dioxide is similar to that of higher plants, the so-called C3 plants, in which the inclusion of CO_2 in organic matter is preceded by the Calvin-Benson cycle (Aro et al., 1984).

Lichens and mosses are characterized by a wide ecological range. Due to their low habitat requirements and very good adaptation to drought periods, they can be found almost everywhere (Lakatos, 2011). However, the phylogenesis of these two groups of organisms is very different, since lichens belong to the Kingdom Fungi and mosses belong to the Kingdom Plantae. Despite the different morphology, both species are nonhydroorganisms, that is, they are characterized by variable hydration of the thallus, which largely depends on the environmental conditions (Proctor and Tuba, 2002). Such hydration requires these organisms to develop certain strategies to deal with unstable water levels (Lakatos, 2011). Both species have de-

veloped the same defense mechanism against evolving environmental conditions by reducing metabolism when water availability declines, tolerating the loss of virtually all free water without dying, and resuming growth upon rehydration by high humidity or liquid water (Lakatos, 2011).

For this study, we selected *Cladonia mitis* (Sandst.) and *Pleurozium schreberi* (Willd. Ex Brid.) Mitt. as representatives of lichens and bryophytes, respectively. *P. schreberi* is a species of moss that is common in undergrowth and favors habitats with moderate access to light (Lappalainen et al., 2008). In sunny, dry weather, mosses are generally dry and metabolically inactive, since photosynthesis is usually carried out in rainy or cloudy weather (Lappalainen et al., 2008; Marschall and Proctor, 2004). In turn, the lichen *C. mitis* belongs to heliotropic species and prefers exposed habitats, displayed to strong light. Due to such habitat conditions, this organism had to develop certain protective mechanisms against an excessive amount of the supplied light energy (Nguyen et al., 2013). Adaptations of lichens to light stress can be classified into five ways: light scattering, radiation shielding, heat dissipation, activation of antioxidant defense and macromolecules, and membrane repair (Nguyen et al., 2013). Excess light can be a stress factor for both lichens and bryophytes, resulting in inhibition of photosynthesis (Nguyen et al., 2013).

The aim of the research was to investigate changes in the photosynthetic activity of *C. mitis* and *P. schreberi* in artificial high-energy lighting. The following hypotheses were presented: 1) photosynthetic activity varies with time, depending on the amount of light energy supplied; 2) the high level of light energy supplied to the species stimulates photosynthetic activity of *C. mitis* while inhibiting photosynthetic activity of *P. schreberi*. We conducted research under laboratory conditions of an experimental culture with the same temperature and humidity conditions, in which the photosynthetic activity of both species was influenced by different light intensities.

MATERIAL AND METHODS

EXPERIMENTAL CULTURE

Specimens of the lichen *C. mitis* and bryophyte *P. schreberi* were randomly collected in the 'Bory Tucholskie' National Park within the lichen Scots pine forest community (*Cladonio-Pinetum* Ass.) in June 2021 (Węgrzyn et al., 2020; 2021a; 2021b). The collected samples were cleaned of plant debris and soil particles and divided into 3 study samples, which were then placed in 3 experimental containers with different light treatments. Within each container we placed 6 subsamples of *C. mitis* (C) and 6 subsamples of *P. schreberi* (P) as pseudo-replications (6 chambers per container eq. study sample) (Table 1). As treatment within containers, we used 2 types of artificial photosynthetic conditions: 1) FL, full light – 100%; 2) HL, half light - 50% of maximum light (both defined by the lighting generated by lamps with the following specifications: type Led Grow 354, light PAR – 224.3 µmol / m^2s and wavelength range 50% max. 450 nm and 50% max. 650 nm). For the control container (NL), we used natural sunlight (Table. 1).

When FL samples were compared with NL samples, the former were characterized by 4 times higher light energy. In the case of HL samples, the energy was twice as high as in NL samples (Table 1). Artificial lighting was active 24 hours a day, there was no blackout period. Both the lichen and the bryophyte were systematically watered so that

TABLE 1. Segregation of six study samples (experimental containers N=60) of *C. mitis* (C) and *P. schreberi* (P) in field work into light types: FL 100% light; HL 50% maximum light; NL natural sunlight (control sample), with the values: Light energy (LE) and photosynthetically active radiation (PAR).

Study sample	**Species**	**Type of Light**	**LE [W/m^2]**	**PAR [µmol/m^2]**
FL-C	*Cladonia mitis*	Full light	52.03	167.24
FL-P	*Pleurozium schreberi*	Full light	50.76	163.82
HL-C	*Cladonia mitis*	Half light	28.76	84.26
HL-P	*Pleurozium schreberi*	Half light	25.16	83.13
NL-C	*Cladonia mitis*	Natural light	13.9	20.79
NL-P	*Pleurozium schreberi*	Natural light	13.9	20.57

their thalli and tissues were constantly moist. The experimental cultivation was carried out for 180 days.

MEASUREMENTS OF THE PHOTOSYNTHETIC ACTIVITY

Photosynthetic activity measurements were made five 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 14, 30, 90 and 180 days from the beginning of the experiment.

During the measurement, a small sample was taken from each chamber and placed in an Eppendorf filled with distilled water for homogeneous hydration of the samples before measurement. After a two-hour soak, the material was transferred to HPEA/LC clips for 20-minute dark adaptation aimed at extinguishing the activity of PS II. Measurements were then made with 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 for recording the maximum photochemical efficiency of PS II (Fv/Fm) (Węgrzyn et al., 2021a; Chowaniec and Rola, 2020).

STATISTICAL ANALYSIS

Two-way analysis of variance (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: a) experiment duration (1, 14, 30, 90 and 180 days) and the types of light (FL, HL, NL) for *C. mitis* and *P. schreberi* separately; b) experiment duration (1, 14, 30, 90 and 180 days) and the species (*C. mitis* and *P. schreberi*) for FL, HL and NL cultivation separately. 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.

RESULTS

The results of the experimental culture of *C. mitis* and *P. schreberi* showed that Fv/Fm varied significantly with experiment duration and the type of lighting for both species (Table 2 and 3). *C. mitis* kept in FL showed a significant decrease in already low Fv/Fm after the 14th day of the experiment and showed a continuous downward trend. Throughout the last measurement, the photosynthetic activity of *C. mitis* ranged from 0.0 to 0.2.

During the experiment, the lichens that were kept in HL showed a completely different Fv/Fm than that in FL. A visible decrease could be observed 14 days after the start of the experiment.

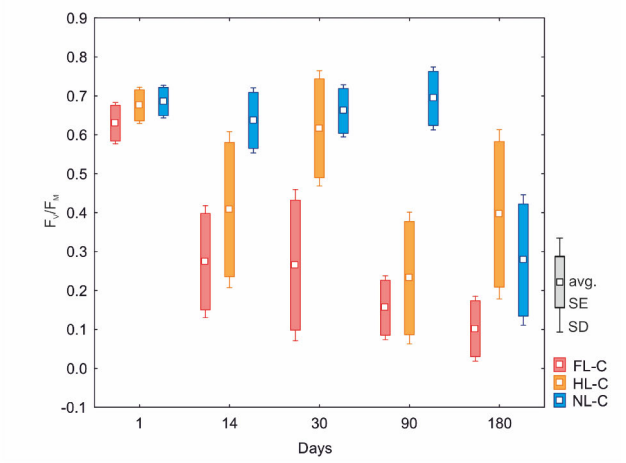

Fig. 1. Mean, ± SE and SD of *C. mitis* Fv/Fm under all types of photosynthetic conditions. The results of ANOVA ($p < 0.05$) are presented graphically (N=180).

TABLE 2. Results of the multivariate ANOVA for the effects of the following variables on the Fv/Fm of *C. mitis* species: a) experiment duration (1, 14, 30, 90 and 180 days) and b) type of lighting (FL, HL, NL). Significant effects ($p < 0.05$) are shown in bold.

Variable	F	p
Experiment duration	41.7731	**p < 0.001**
Type of lighting	44.9939	**p < 0.001**

TABLE 3. Results of the multivariate ANOVA for the effects of the following variables on the Fv/Fm of *P. schreberi* species: a) experiment duration (1, 14, 30, 90 and 180 days) and b) type of lighting (FL, HL, NL). Significant effects ($p < 0.05$) are shown in bold.

Variable	F	p
Experiment duration	6.1144	**p = 0.0153**
Type of lighting	43.9821	**p < 0.001**

However, after 30 days, *C. mitis* had an increase in Fv/Fm, ranging from greater than 0.45 to 0.8. After 90 days, Fv/Fm decreased again. During the last measurement, which took place after the 180th day from the beginning of the experiment, a slight increase in the Fv/Fm value was observed, ranging from 0.15 to 0.6. NL showed similar Fv/Fm values throughout the experiment, but with a decrease occurring only once, 180 days after the start of the culture (Fig. 2).

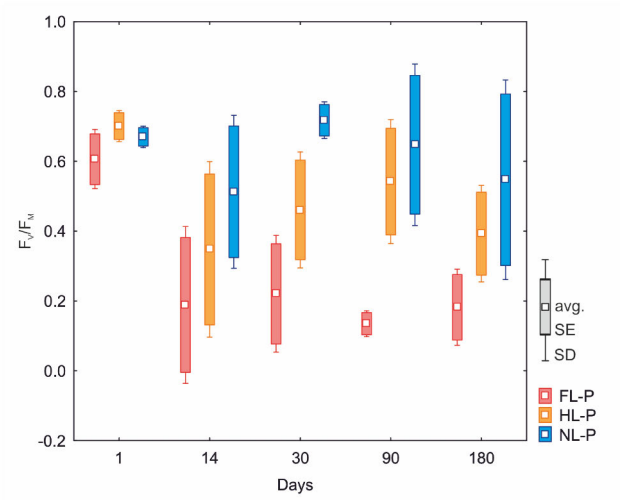

Fig. 2. Mean, ± SE and SD of *P. schreberi* Fv/Fm under all types of photosynthetic conditions. The results of ANOVA ($p < 0.05$) are presented graphically (N=180).

P. schreberi that was kept in FL showed a significant decrease in Fv/Fm after the 14th day of the experiment and showed a continuously decreasing trend. During the last measurement, the photosynthetic activity of this bryophyte ranged from 0.1 to 0.3 (Fig. 3). During the experiment, *P. schreberi*, which was kept in HL, showed completely different Fv/Fm from that of FL, like *C. mitis*. After the 14th day, there was a decrease in the tested Fv/Fm; however, after 30 and 90 days, slight increases in the Fv/Fm values were observed. The results of the last measurement day showed yet another decrease with photosynthetic activity values ranging from 0.2 to 0.5 (Fig. 3). For NL, the Fv/Fm values were at a high level; however, for measurements performed after the 14th, 90th and 180th day, the range of values had a broad spectrum from 0.3 to 0.85.

With reference to the Fv/Fm values for various species (*C. mitis* and *P. schreberi*) cultured under FL conditions, the differences between

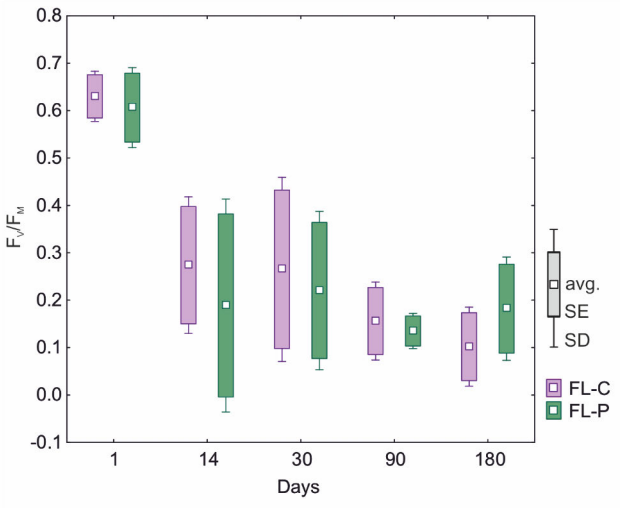

Fig. 3. Mean, ± SE and SD of the studied lichen and bryophyte species Fv/Fm cultured in FL. The results of ANOVA ($p < 0.05$) are presented graphically (N=120).

them were not statistically significant on designated measurement days (Table 4, Fig. 3). Significant effects were observed only for different experiment duration variable (Table 4).

TABLE 4. Results of the multivariate ANOVA for the effects of the following variables on Fv/Fm of the lichen and bryophyte species cultured in FL: a) experiment duration (1, 14, 30, 90 and 180 days) and b) species (*C. mitis* and *P. schreberi*). Significant effects ($p < 0.05$) are shown in bold.

Variable	F	p
Experiment duration	20.555	**p = 0.00003**
Species	0.1443	p = 0.70542

When comparing both species, there were no significant differences in Fv/Fm for the samples kept in HL. Significant effects only occurred for the experiment duration variable (Table 5, Fig. 4).

However, there were some differences, as mentioned above, in that *C. mitis* showed a significant increase in Fv/Fm after 30 days, while after 90 days there was decrease. In the case of *P. schreberi*, there was a slight increase in the value after 30 and 90 days. However, after 180 days, a decrease in the value of Fv/Fm could be observed (Fig. 4).

TABLE 5. Results of the multivariate ANOVA for the effects of the following variables on Fv/Fm of the lichen and bryophyte species cultured in HL: a) experiment duration (1, 14, 30, 90 and 180 days) and b) species (*C. mitis* and *P. schreberi*). Significant effects ($p < 0.05$) are shown in bold.

Variable	F	p
Experiment duration	6.2020	**p = 0.0156**
Species	0.1807	p = 0.6722

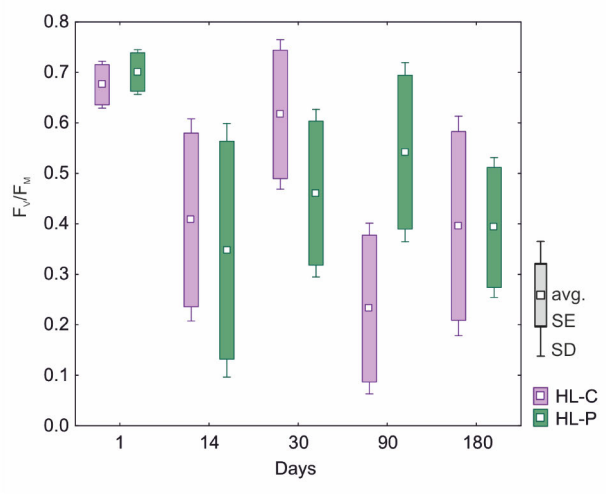

Fig. 4. Mean, ± SE and SD of the studied lichen and bryophyte species Fv/Fm cultured in HL. The results of ANOVA ($p < 0.05$) are presented graphically (N=120).

In the case of lichens and bryophytes grown in NL, both species showed similar Fv/Fm. However, the Fv/Fm values for *P. schreberi* after 14 and 90 days from the beginning of the experiment showed large fluctuations. On the last day of measurement, that is, 180 from the beginning of the experiment, a decrease in the Fv/Fm value for *C. mitis* was visible, while the values for *P. schreberi* showed a large distribution of values ranging from 0.25 to even 0.85 (Fig. 5). As a result of the analysis of variance, only differences in experiment duration variable were shown and no significant differences between the species were found (Table 6).

DISCUSSION

Evaluation of photosynthetic activity by measuring chlorophyll fluorescence is one of the methods that allows for determining whether a given photosynthetic organism is affected by stress factors (Orekhova et al., 2022). Many scientists have focused their research on determination of the tolerance to high levels of light in photosynthetic organisms (Beckett et al., 2021). However, despite numerous studies, research is still being conducted to expand our understanding of this phenomenon, especially with respect to lichen and bryophyte species.

The photosynthetic activity of lichens is strongly related to the hydration level of their thalli. However, the amount of water in their thalli depends on climatic conditions (Chowaniec and Rola, 2022; Lange et al., 1993; ten Veldhuis, 2020). Thallus dehydration leads to a gradual loss of photosynthetic activity of the photobiont, causing changes in PS II, characterized by a decrease in the efficiency of absorbed energy transmission (Chowaniec and Rola, 2022).

Reduction of the maximum efficiency of PS II may cause its irreversible damage to PS II, which

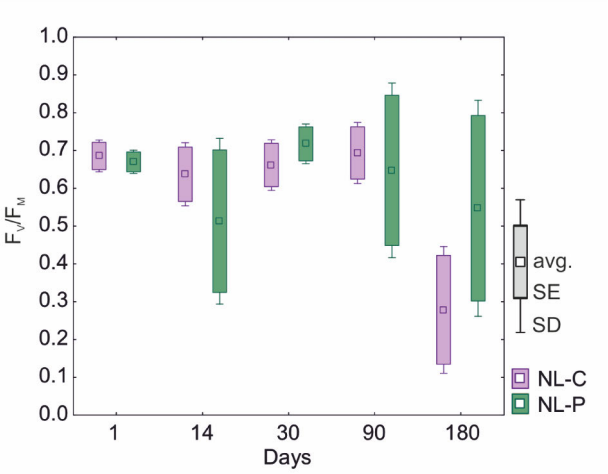

Fig. 5. Mean, ± SE and SD of the studied lichen and bryophyte species Fv/Fm cultured in NL. The results of ANOVA ($p < 0.05$) are presented graphically (N=120).

TABLE 6. Results of the multivariate ANOVA for the effects of the following variables on Fv/Fm of the lichen and bryophyte species cultured in NL: a) experiment duration (1, 14, 30, 90 and 180 days) and b) species (*C. mitis* and *P. schreberi*). Significant effects ($p < 0.05$) are shown in bold.

Variable	F	p
Experiment duration	12.089	**p = 0.0009**
Species	0.3620	p = 0.5497

will decrease the viability of the entire thallus (Chowaniec and Rola, 2022). As mentioned above, lichens do not have stomata and therefore cannot control the water level in their mold, which means that they have to adapt to periodic drought conditions (Ten Veldhuis, 2020). Complete dehydration of the thallus results in inactivation of the photosynthetic process, gas exchange, and loss of chlorophyll a fluorescence (Oukarroum et al., 2012). However, when the thallus is moistened with water, it can restore its photosynthetic activity in a few minutes (Lange et al., 1993; Oukarroum et al., 2012). Interestingly, not only can dehydration of the thallus inactivate the photosynthesis process, but also long-term excess water content in the thallus, which limits optimal CO_2 exchange, stops this process (Lange et al., 1993; Lakatos, 2011).

Unlike lichens, most bryophytes prefer moist habitats, which allows them to be active and fully hydrated over a long period of time (Green et al., 2011). In the absence of water, the mosses become dry and, like the lichens, inactive. As in the case of lichens, the photosynthetic activity of mosses is strongly related to the hydration status of their thallus (Green et al., 2011). The water content of the thallus changes as the thallus seeks balance with the environment. Changes in water content affect the rate of photosynthesis and respiration (Green et al., 2011). Complete dehydration of the thallus inactivates the photosynthetic process, but rehydration of the thallus results in recovery of metabolism (Csintalan et al., 1999; Huttunen et al., 2018). Bryophytes usually form dense clusters to increase water storage for longer photosynthetic activity. As a result, they have to tolerate very high levels of light when active, often in full sun (Green et al., 2011). Bryophytes appear to have an excellent ability to tolerate strong light and UV radiation when wet (Green et al., 2011).

Our results of the two-way analysis of variance (ANOVA) showed the variability of photosynthetic activity over time, depending on the amount of light energy supplied, thus confirming our first hypothesis. Long-term light stress and changes in seasonality affect the photosynthetic activity of lichens and mosses (Węgrzyn et al., 2021a). The decrease in the photochemical activity of PS II caused by light is called photoinhibition (Pospíšil, 2016). Moderate lighting causes energy and electron transfer in PS II, leading to production of various reactive oxygen species (ROS) (Beckett et al., 2021; Pospíšil, 2016). However, the amount of ROS produced in moderate light is small and serves primarily as signaling molecules that activate the acclimatization response and programmed cell death (Pospíšil, 2016). The amount of produced ROS increases significantly when the absorbed light exceeds that which can be used for carbon binding (Beckett et al., 2021). ROS produced by lichens and bryophytes, mainly hydrogen peroxide (H_2O_2), superoxide (O^{2-}), and hydroxyl radicals (HO), pose a threat to the survival of their cells under various environmental stresses (Hu et al., 2016). Risks caused by ROS include damage or even destruction of dye protein complexes in the photosynthetic apparatus and, as mentioned earlier, inhibition of photochemical processes (Barták, 2014). Photosynthetically active organisms must have photoprotective mechanisms that will limit the negative effects of emerging reactive oxygen species (Barták, 2014). In our study we observed that long and too high exposure to lighting causes gradual degradation of the photosynthetic apparatus leading to cell death, which was also proven in studies of other authors (Derks et al., 2015). Initially, sunlight triggers PS II activation, which is associated with high Fv/Fm values. Continued exposure to light produces ROS, which, in turn, leads to photoinhibition. In a situation where the rate of photosynthetic damage to PSII exceeds the rate of PS II repair, irreversible damage to the photosynthetic apparatus occurs and thus leads to low values of photosynthetic activity (Fig. 6) (Derks et al., 2015).

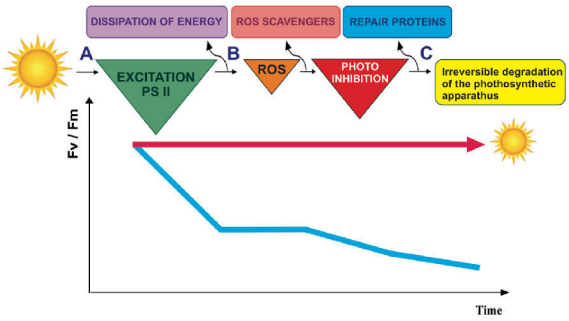

Fig. 6. Graphical interpretation of the changes in photosynthetic activity observed in the lichen study samples. Reduction of Fv/Fm in *C. mitis* during the culture process - blue line. Physiological changes that occured in the photosynthetic apparatus: A) activation of photosystem II (PSII), B) formation of reactive oxygen species (ROS), C) irreversible destruction of the photosynthetic apparatus (based on Derks et al., 2015).

Our hypothesis about the positive influence of a high level of light energy on lichens and negative on bryophytes was only partially confirmed by the obtained results. The lack of the stimulating effect of light on the growth of *C. mitis* indicates that although this species belongs to the group of light-requiring organisms found in an environment with high sunlight, too much light energy supplied causes stress and stops the photosynthetic process. Like any photosynthetically active organisms, it has a certain maximum photosynthesis rate, beyond which photosynthesis will not be able to proceed properly and efficiently (Beckett et al., 2021). Regarding the tested samples grown under full irradiation, the downward trend was maintained throughout the experiment. The decrease in photosynthetic activity is related to the amount of photosynthetically active light (PAR) delivered, which causes photoinhibition in both *C. mitis* and *P. schreberi*. The obtained Fv/Fm values below 0.3 indicate irreversible changes in the structure of PS II (Węgrzyn et al., 2021a). The likelihood of constantly keeping the thallus moist can also reduce the photosynthetic activity of organisms exposed to too much light radiation. Other studies show that lichens and bryophytes withstand light stress better when they are dry and metabolically inactive (Grimm et al., 2021; Heber et al., 2006). Due to the high intensity of light, bryophytes dry up quickly and remain metabolically inactive (Tobias and Niinemets, 2010).

Bryophytes in the dried state prevent photooxidation by increasing the thermal scattering of the absorbed light energy, which enables the survival of photosynthetically active organisms under the most extreme environmental conditions (Heber et al., 2006). In turn, in lichens, after drying, the changes which occur in the morphology of their thalli increase light scattering and reduce light transmission to the photobiont (Veerman et al., 2007). Hydrated lichen thalli reduce light reflection in the upper bark of lichens, increasing light transmittance and their susceptibility to photoinhibition (Barták et al., 2004; Beckett et al., 2021). However, sunlight, despite drying of the thallus, is still absorbed by the pigments of the photosynthetic apparatus (Heber et al., 2006). The energy of absorbed light is efficiently dissipated as heat; therefore, it does not generate potentially harmful reactions (Hu et al., 2016). On the other hand, some studies indicate that for lichens, the presence of water is necessary to repair a damaged photosynthetic apparatus, and exposure to high solar radiation for a long period of dried thallus can cause accumulation of serious damage to PS II (Veres et al., 2022). In the case of bryophytes, some studies also suggest that they withstand light stress better when the thallus is fully hydrated (Green et al., 2011). The concept of high light stress is closely related to acclimatization or induced tolerance and the ability of lichens to cope with adverse light environments (Beckett et al., 2021).

In the case of lichens, decreasing values of Fv/Fm indicate degradation of algal cells, while increasing values of maximum photochemical yield, in PS II, suggest acclimation and regeneration of the photosynthetic apparatus in surviving algal cells located in the part of the thallus exposed to less light (Gauslaa and Solhaug, 2000). It has been suggested that after a certain period, damaged algae are gradually degraded which causes their consequent death (Gauslaa and Solhaug, 2000). Like in lichens, bryophytes' shoots are believed to acclimate to environmental conditions, and thus to different light intensities (Tobias and Niinemets, 2010). Further studies are needed to understand defense and adaptation mechanisms against light stress in lichens and bryophytes.

CONCLUSION

The conducted research indicates that although the lichen *C. mitis*, unlike the studied *P. schreberi*, belongs to organisms found in wide open areas, when exposed to high intensity of solar radiation, it was subjected to photoinhibition. Despite many defense mechanisms, exceeding the maximum rate of photosynthesis makes the photosynthetic apparatus of lichens unable to use light. Exposition to too long exposure to high doses of radiation had a negative impact on both studied species, as their photosynthetic apparatus was destroyed, and their cells were gradually degraded. However, further research is needed for detailed investigation of the long-term effect of light on poikilohydric organisms in terms of their defense mechanisms and their adaptive capabilities in terms of light stress.

AUTHORS' CONTRIBUTIONS

M.H.W. conceptualization, methodology, and project management. P.D., P.F, K.W. and M.H.W. carried out field material collection. P.D., P.F. and

M.H.W. supervised the findings of this work. P.D. and M.H.W. wrote the manuscript with support from P.F, K.W. and P.W.-P., P.D. performed statistical analysis of the data. All authors discussed the results and contributed to the final manuscript.

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