Seasonal Changes in the Photosynthetic Activity of Terrestrial Lichens and Mosses in the Lichen Scots Pine Forest Habitat

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Abstract: Photosynthetic activity is one of the most important metabolic processes that can be quickly and easily studied in the field. It can be used for identifying the environmental factors affecting ecosystem balance, as any stressor influencing metabolic and physiological processes will have a measurable effect on photosynthesis. The aim of this study was to measure the photosynthetic activity of selected lichens and mosses and investigate its changes resulted from diurnal and seasonal variability. We studied two lichens (*Cladonia mitis* Sandst and *Cladonia uncialis* (L.) Weber ex F.H. Wigg.) and two mosses (*Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Dicranum scoparium* (L.) Hedw.). Samples were collected in the area of lichen Scots pine forest of the "Bory Tucholskie" National Park. Our study revealed that the photosynthetic activity of cryptogams depended on species, season, time of the day, and water availability. *Cladonia* species, which are the main component of lichen Scots pine forests, have higher photosynthetic activity than *Pleurozium schreberi*, which represents species of fresh coniferous forests. Photosynthetic activity increased from spring through summer and reached the highest values in autumn. It was also higher in soaked samples collected in the morning and afternoon compared to noon. Despite the water access, noon samples still showed the lowest activity. This can result from natural changes in humidity during the day to which cryptogams are well-adapted.

Keywords: *Cladonio-Pinetum* community; chlorophyll *a*; Tuchola forest; 91T0; fluorescence; habitat conservation

1. Introduction

For many years, science has been searching for tools to assess the conservation status of habitats and identify the main environmental factors stabilizing or disturbing the balance of the ecosystems, so-called ecosystems' health, or ecosystems' function [1–3]. In relation to plants, the influence of various unfavorable environmental conditions (stressors) on their physiological condition and development in the forest habitat was previously investigated [4–8]. Plants possess many complex mechanisms that help them to adapt to environmental conditions and survive despite the impacts of various stressors [9–13]. Photosynthetic activity, as one of the most important metabolic processes, is a good indicator for the assessment of the influence of environmental factors, because it can be very quickly examined in the field [14]. Its measurements are based on recordings of chlorophyll *a* fluorescence, i.e., the re-emission of light energy absorbed by the energy antennas of the photosynthetic apparatus [15–18].

Solar radiation in the range of 400–700 nm is defined as photosynthetically active radiation (PAR) [19–22]. The photosynthetic pigments, chlorophylls, and carotenoids (localized in light-harvesting complexes (LHCs)) are responsible for the absorption of radiation. Only part of the energy captured by them is used up [23,24]. Some of it is lost

as heat or emitted as chlorophyll fluorescence [25]. The chlorophyll fluorescence induction is termed as the Kautsky kinetics [26]. The emission of fluorescence takes place in chloroplasts and is related to all other metabolic and physiological processes within the plant cell. Hence, any change in the environment that impacts these processes will also affect the photosynthesis [25, 26, 27].

As a result of the chlorophyll fluorescence signal measurement, the F_V/F_M value is obtained—the maximum photochemical efficiency of photosystem II [27]. This parameter is considered as a reliable measure of the photochemical activity of the photosynthetic apparatus.

Research on the mechanisms of chlorophyll fluorescence activation in lichens and mosses and the influence of factors causing stress on cryptogam photosynthesis have been previously carried out in laboratory conditions on various species belonging to different ecological groups [28]. They are theoretically based on the assumptions of photosynthetic activity of vascular plants [29]. However, the CO_2 exchange patterns of lichens and mosses differ from those of vascular plants [30]. Lichens and mosses have simple thallus structures and little control over water loss. This has a strong impact on the biochemical metabolic processes which are only active when cryptogams are wet [31].

Apart from access to water, seasonal variation of climate may also cause significant changes in photosynthetic functioning [32,33]. However, only a few studies were devoted to this issue and considered the variability of photosynthetic activity over a longer period. Regarding terrestrial lichens, only Veres et al. [33] indicated such changes. In the case of mosses, such studies are also scarce [34]. In majority, they focus on the phenomenon of high resistance of mosses to long periods of dehydration, which is related to the theory that mosses as first land plants faced extremely dry conditions when moving to the terrestrial habitat [34]. In many of these studies, samples of mosses and lichens have been collected and soaked before measurement photosynthetic activity e.g., [28].

Such research never has not been carried out in the protected lichen Scots pine forests habitat, even though its favorable conservation status depends on habitat factors (such as temperature, humidity and solar energy which shapes the forest) [35].

The lichen Scots pine forests are semi-natural-type communities with a lichen-rich field layer. They occur in the places with extremely poor and dry conditions associated with a specific substrate formation in the last glacial age [36,37]. It is also believed that anthropogenic factors, such as cattle grazing, litter raking (pine needles, pinecones, and small branches), deforestation, and clear felling (removal of all wood from the forest), had a crucial influence on the development of these habitats. Unfortunately, a rapid disappearance of lichen Scots pine forests resulted from strong eutrophication processes of forest substrate has been observed for several years. Preventing the loss of these habitats is an important issue, as Scots pine forests are protected by EU legislation as the Natura 2000 habitat (No. 91T0) [38,39]. We conducted research in the area of Bory Tucholskie (N Poland), which is currently a large forest complex covering the post-glacial sandy areas of the sanders of the Brda and Wda rivers, where Scots pine forests are still present [40]. One of its aims, to which this paper is dedicated, was to determine the photosynthetic activity of selected species of lichens (*Cladonia mitis* Sandst and *Cladonia uncialis* (L.) Weber ex F.H. Wigg.) and mosses (*Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Dicranum scoparium* (L.) Hedw.) in the field condition, as well as to investigate impact of seasonal and diurnal variability on this parameter. *C. mitis, C. uncialis*, and *D. scoparium* are characteristic species for lichen Scots pine forest habitat [35]. They are heliophytes that prefer forest habitats with a low tree cover. This results in greater amounts of solar light and heat energy reaching the substrate, and, in turn, this lowers the humidity conditions of the air and substrate [40]. On the other hand, *P. schreberi* is characteristic for the fresh form of pine forest [35] and prefers more shaded and moister habitats [41]. These species have been very common in all 20 study plots.

As our study area in previous years was subjected to active protection activities in order to provide habitat conditions favorable for terricolous lichens' development, we

assumed that present conditions are not optimal for mosses [35,40]. Existing findings indicate that the photosynthetic activity of both groups depends on water availability, which changes during the day [40]. To test this, we divided our samples into two groups: soaked and non-soaked (measured directly in field conditions). Species might uptake water first from a morning dew [33,41]. During the day, air humidity gradually decreases; thus, we assume that the studied species present the highest photosynthetic activity in the morning [35,40]. Since the air temperatures differ from highest in summer, lower in autumn, and the lowest in spring [35,40], we expected them to affect the photosynthetic activity of lichens and mosses. We set the following hypotheses: (1) the soaked thalli of selected lichens and mosses show higher photosynthetic activity compared to non-soaked thalli, (2) the photosynthetic activity of species differs between the seasons and is the highest in autumn, (3) the photosynthetic activity of lichens is higher than it is for mosses in all of the studied seasons, and (4) photosynthetic activity of all species is higher in the morning and afternoon than at noon.

2. Materials and Methods

2.1. Fieldwork with Measurement of the Maximum Quantum Efficiency of PSII Photochemistry in Lichens and Mosses

In 2020, during spring, summer, and autumn, measurements of photosynthetic activity in selected two lichens (*Cladonia mitis* Sandst. and *Cladonia uncialis* (L.) Weber ex F.H. Wigg.) and two mosses (*Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Dicranum scoparium* (L.) Hedw.) were conducted in the field. The winter period was not included in the research, due to the snow cover. The research was carried out in the experimental area of lichen Scots pine forest of "Bory Tucholskie" National Park (stand No. 18 and 19) established in 2017 (Figure 1). In this area, 25 plots were randomly marked in the field by a benchmark. From among 25 plots, 20 plots containing all 4 selected species of lichens and mosses were randomly chosen (Figure 1). In the designated periods (spring = June, summer = July, and autumn = September) and time (at 9:00 a.m., 12:00 a.m., and 3:00 p.m.), two samples of each lichen and moss species were randomly taken from each plot: (A) The first sample (ca. 2 g) was placed in conical tubes (5 mL) filled with rainwater for a period of 2 h, and after this, time measurements were taken. Thallus watering aimed to uniformly hydrate samples for measurements. This provided a similar level of thallus hydration. (B) The second sample was measured directly after harvesting without treatment. All measurements were carried out on samples collected after 2 days without rain to ensure a similar dryness of the non-soaked samples. Altogether, 40 samples of each selected species were collected once on a given day and at a given time (20 of them were soaked and 20 non-soaked). The measurements were performed with the use of Handy PEA+ fluorometer of (Handy PEA, Hansatech Instrument Ltd., King's Lynn, Norfolk, England). We used the prompt fluorescence (PF) method [42]. The measurements were performed after adapting the sample in the dark for approximately 15 min [43]. This was performed to extinguish the reaction of the light phase of photosynthesis. After adaptation, each sample was irradiated with continuous light with a wavelength shorter than 670 nm. During the irradiation, the photodetector registered the chlorophyll fluorescence in the range of 680–760 nm. After the measurement, the F_V/F_M ratio was recorded, namely the maximum photochemical efficiency of photosystem II, which is considered as the most reliable measure of the photochemical activity of the photosynthetic apparatus [29].
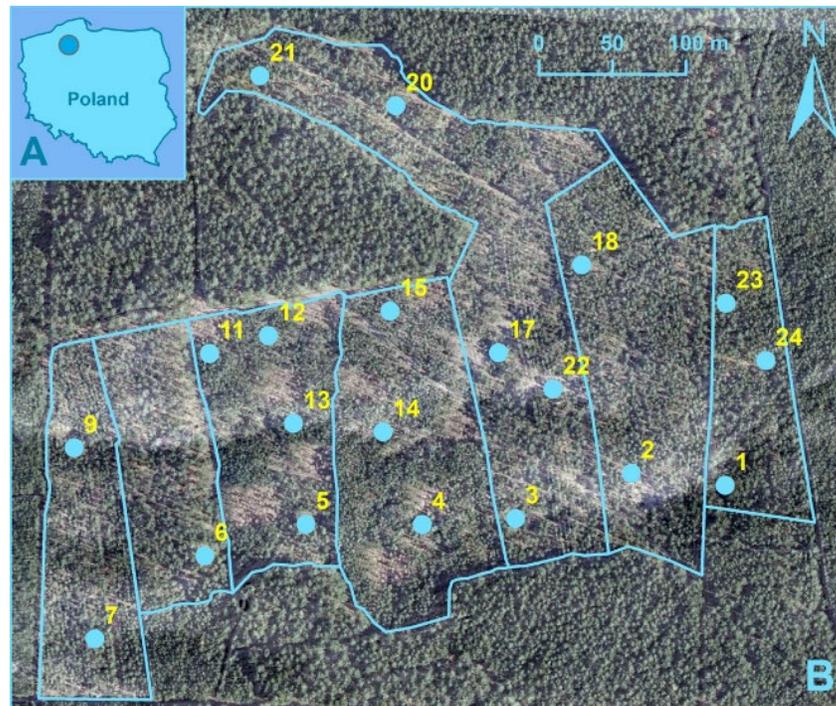
Figure 1. Study area: (**A**) locality of the "Bory Tucholskie" National Park in Poland; (**B**) twenty sampling plots in experimental area of the lichen Scots pine forest habitat in "Bory Tucholskie" National Park. Blue line indicates forest stands (© The Head Office of Geodesy and Cartography, www.geoportal.gov.pl).

2.2. Statistical Analysis

Two-way analysis of variance (ANOVA), followed by Tukey's HSD (Honestly Significant Difference) test for equal sample size ($p < 0.05$), was performed to reveal significant differences in F_V/F_M between the following pairs of variables: (a) species (*C. mitis*, *C. uncialis*, *D. scoparium*, and *P. schreberi*) and sample type (soaked or non-soaked) (including soaked and non-soaked samples, N = 4320); (b) species and season (spring, summer, and autumn) (including only soaked samples N = 2160); and (c) species and daytime (9:00 a.m., 12:00 a.m., 3:00 p.m.) (including only soaked samples, N = 2160). Prior to the analysis, the normality of the distribution was verified by using the Kolmogorov–Smirnov test ($p > 0.05$), and Levene's test ($p > 0.05$) was performed to assess the equality of variances.

3. Results

Species and sample type, as well as the interaction between these factors, significantly affected F_V/F_M (Table 1 and Figure 2). All soaked samples showed higher values of F_V/F_M compared to non-soaked samples; however, these differences were not always significant (Figure 2). The F_V/F_M of soaked *C. mitis*, *C. uncialis*, *D. scoparium*, and *P. schreberi* reached a significantly higher value than the F_V/F_M of non-soaked *P. schreberi*. Within same species, soaked and non-soaked samples significantly differed only in the case of *C. mitis* and *P. schreberi* (Figure 2).

Table 1. Results of the two-way ANOVA for the effects of the following variables on cryptogam F_V/F_M: (a) species (*C. mitis*, *C. uncialis*, *D. scoparium*, and *P. schreberi*) and sample type (soaked or non-soaked); (b) species and season (spring, summer, and autumn); and (c) species and daytime (8:00 a.m., 12:00 a.m., and 3:00 p.m.). Significant effects ($p < 0.05$) are shown in bold.

|	Variables	F	*p*
	Species	**16.238**	**<0.001**
(a)	Sample type	**37.091**	**<0.001**
	Species × sample type	**2.729**	**0.043**
	Species	**55.393**	**<0.001**
(b)	Season	**543.092**	**<0.001**
	Species × season	**5.626**	**<0.001**
	Species	**28.891**	**<0.001**
(c)	Daytime	**7.416**	**<0.001**
	Species × daytime	1.247	0.281
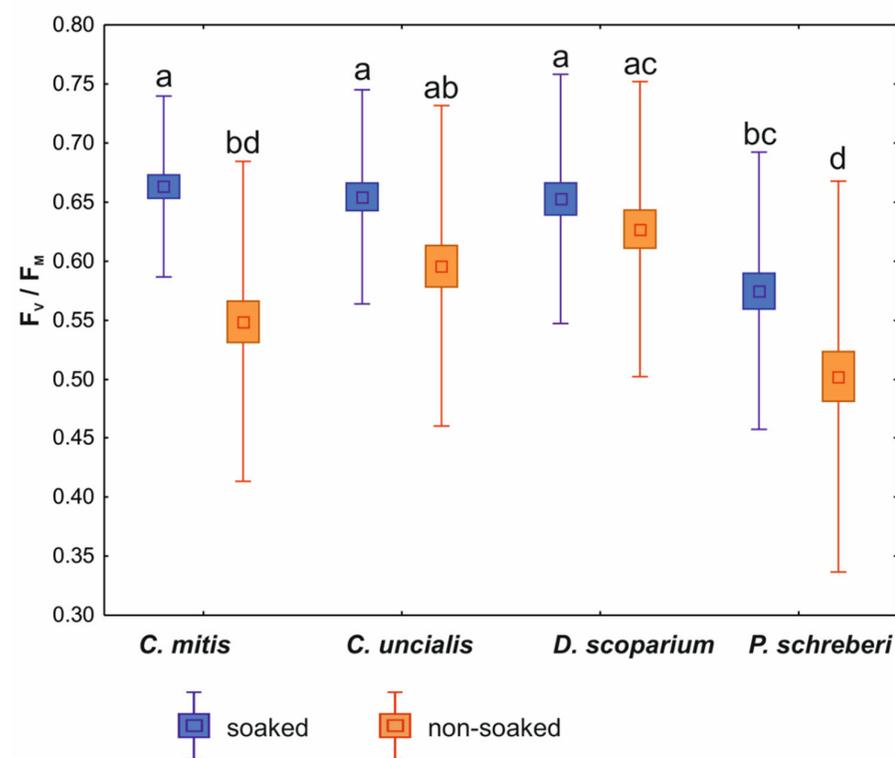
Figure 2. Mean ± SE and SD of FV/FM, including division into species (*C. mitis*, *C. uncialis*, *D. scoparium*, and *P. schreberi*) and sample type (soaked or non-soaked). The results of ANOVA ($p < 0.05$) are presented graphically (N = 4320). The lowercase letters indicate the statistically significant interaction between habitat type and location (see Table 1 for details on the main effects and interactions).

Species and season as well as interaction between these factors significantly affected F_V/F_M (Table 1; Figure 3). In case of all analysed species, F_V/F_M was lowest in spring, increased in summer and reached higher values in autumn (Figure 3). F_V/F_M of *C. mitis* and *P. schreberi* significantly differed between spring, summer, and autumn (Figure 3). For *C. uncialis* and *D. scoparium*, there was no significant difference between summer and autumn F_V/F_M values, however the spring F_V/F_M values significantly differed from summer and autumn (Figure 3). F_V/F_M of *P. schreberi* collected in spring showed the lowest F_V/F_M, which significantly differed from F_V/F_M of other species collected in all seasons (Figure 3).
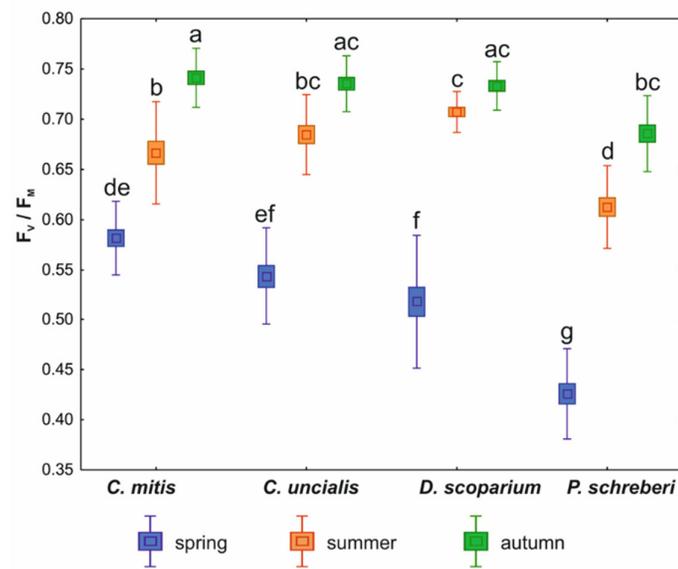
Figure 3. Mean ± SE and SD of F_V/F_M, including division into species (*C. mitis*, *C. uncialis*, and *D. scoparium*, *P. schreberi*) and season (spring, summer, and autumn). The results of ANOVA ($p < 0.05$) are presented graphically (N = 2160). The lowercase letters indicate the statistically significant interaction between species and season (see Table 1 for details on the main effects and interactions).

Concerning the effect of species and daytime, both of these variables influenced F_V/F_M; however, the interaction between them was not significant (Table 1 and Figure 4). Only F_V/F_M of *P. schreberi* was significantly lower compared to the F_V/F_M of *C. mitis*, *C. uncialis*, and *D. scoparium* (Figure 4). In the case of daytime, the F_V/F_M significantly differed between 12:00 a.m. and 3:00 p.m. (Figure 4). For all species F_V/F_M decreased from 9:00 a.m. to 12:00 a.m. and then increased at 3:00 p.m. (Figure 4).
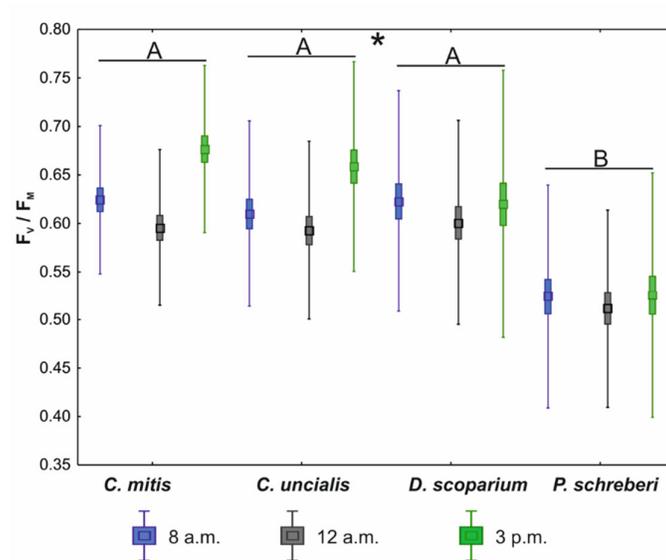
Figure 4. Mean ± SE and SD of F_V/F_M, including division into species (*C. mitis*, *C. uncialis*, *D. scoparium*, and *P. schreberi*) and daytime (8:00 a.m., 12:00 a.m., and 3:00 p.m.). The results of ANOVA ($p < 0.05$) are presented graphically (N = 2160). The capital letters show the significant main effect of the species; the asterisk (*) indicates the significant main effect of daytime (see Table 1 for details on the main effects and interactions).

4. Discussion

Under optimal vascular plant-growth conditions, the F_V/F_M value is ca. 0.85 relative units [44], but for lichens, it always shows maximal values of ca. 0.6–0.7 F_V/F_M [45]. Recent studies have shown that environmental stress caused by, for example, increased content of heavy metals, can cause F_V/F_M values to reach even 0.77 [28]. Our study showed similar results for lichens species (0.79 in autumn season). A lower value of this parameter indicates the occurrence of stress, manifested in the form of photo-inhibition [44,46]. Very low values of this parameter (0.2–0.3) indicate irreversible changes in the PSII structure [44,46]. However, it was noticed that F_V/F_M is not proportional to the intensity of photosynthesis (expressed by CO_2 assimilation or O_2 release) [47]. It has also been proven that F_V/F_M is not sensitive to certain stresses, such as drought [27]. Lichens and mosses occur in all the plant zones of the Earth. They can live in habitats characterized by extreme conditions. Lichens are known to be extremely tolerant to drought stress and low and high temperatures [48–50]. Due to their features, they are considered pioneer species having important roles in the process of primary succession where habitat conditions are especially severe [51–53].

Cryptogams, especially lichens and mosses, are important organisms in the structure and function of the plant habitats because they are a form of ecotone that divides the aboveground and belowground as insulator and filter [31,35]. This is crucial for lichen Scots pine forests, where the appropriate development of the lichen-rich baseground together with healthy functioning of cryptogams allows for the maintenance of the ecosystem's balance and, thus, the proper state of habitat preservation. We found that species and sample type, as well as the interaction between these factors, significantly affected F_V/F_M. The rehydrated specimens had a higher F_V/F_M, but differences were statistically significant only between *Cl. mitis* and *P. schreberi*. Thus, our hypothesis on difference in photosynthetic activity between soaked and non-soaked samples was only partly confirmed. Nevertheless, our results showed the importance of the hydration of the tested samples before measurement of physiological parameters and drawing conclusions on condition and functioning.

In the case of lichens, thallus hydration is especially important, because the spaces between the hyphae in core layer are filled with water and the not-scattered light can reach the photobionts layer. The type of green algae photobiont clearly determines lichen reactions to air humidity; for example, lichens with *Trentepohlia*-type photobionts showed higher F_V/F_M in lower hydration condition than those with *Trebouxia*-type photobionts [54]. The effect of the relative humidity (RH) factors on the trebouxioid lichens varied among species, yet they generally attained the highest F_V/F_M when RH reaches 95% [54]. The coccomyxoid lichens (like those used in our study) had the weakest overall response to steam reactivation and may be better adapted to exploiting liquid water sources [54]. Previous research showed that, regardless of the photobiont type, the highest F_V/F_M values were reached at an RH above 95% [54].

Compared to lichens, mosses have been mainly studied in terms of desiccation tolerance [55–57]. Mosses showed varying levels of desiccation tolerance, allowing them to occur in more extreme and unstable habitats; however, there are also species that are moderately dry-tolerant and those which poorly tolerate dry periods [56]. It was previously shown that *P. schreberi* and *D. scoparium* are presenting the variability of drying tolerance with seasonal patterns of tolerance to desiccation, which decreases in spring and fall and increases in mid-summer and winter. Our results did not fully support these findings. They showed an increase in F_V/F_M activity in all species from low in spring to medium in summer and high in autumn. However, a decrease in this activity in the autumn may only take place after a drastic drop in temperature and first frosts, which appear in the study area only in November. Our high F_V/F_M values for the autumn also did not agree with the results of seasonal activity of *Syntrichia ruralis* Hedw. [58]. In the autumn, the F_V/F_M of this species was also slightly lower than the values for the summer period, but the measurements were made in October, while ours we made at the turn of

September/October, and this might be a reason for the differences. In general, the photosynthetic activity in the studied species of lichens and mosses changed with the seasons. However, we found the highest photosynthetic activity to be in the fall, at the end of September; and this was agreed with our assumptions and other studies, such as References [33,59].

Kinetic activation is an important property of the photosynthetic apparatus and photosynthetic (PSII) activity response to environmental conditions, such as water availability [60]. Distinguishing between the reactions of lichens to rain and humidity revealed that their ability to utilize each of these water sources strongly influenced both their total wetting time and the activity performed [60]. In our opinion, kinetic activation is directly related to desiccation tolerance, as only those species with rapid activation can retain high photosynthetic activity in dry areas, where rain falls sporadically and for a very short time [61]. The lichen Scots pine forest belongs to a dry habitat, not because of rarely falling rains, but because of the type of well-drained sandy soils. Due to this type of substrate, water escapes very quickly, causing rapid drying of the surface. Both the lichens and mosses growing in this habitat must have fast kinetic activation. The lichen species taken for our study are the most characteristic species for lichen Scots pine forest habitat, in contrast to *P. schreberi*, which represents the species of the coniferous forests (*Vaccinio-Piceetea* Br.-Bl. 1939), where the substrate temperatures are lower, and the humidity is higher compared to lichen Scots pine forests. *D. scoparium* prefers drier habitats, e.g., dry heaths (*Pohlio-Callunion* Shimwell 1973 em. Brzeg 1981), and therefore it tolerates very well extreme temperature and humidity changes of lichen Scots pine forest. It is worth noting that studied species represent different growth forms; that is, lichens belong to fruticulose species, while *D. scoparium* and *P. schreberi* represent short turf and weft, respectively [30,62]. Probably, this factor might also influence kinetic activity of species; however, this issue requires further study.

Our results for soaked samples clearly showed that lichens had higher photosynthetic activity through all studied seasons than mosses. Only *D. scoparium* showed higher photosynthetic activity in the summer and autumn, as compared to lichens. Thus, our fourth hypothesis on higher photosynthetic activity of lichens than mosses through all seasons was partially confirmed. Nevertheless, our results confirmed the different habitat preferences of individual species.

Interestingly, all studied species showed the highest photosynthetic activity at 9:00 a.m. and 3:00 p.m. Photosynthetic activity at noon in relation to data from all three seasons showed the lowest values. This confirmed our last hypothesis on highest photosynthetic activity of all species in the mornings and afternoons. It should be emphasized that these results were obtained for soaked samples. This might indicate that cryptogams are coded for a decrease in photosynthetic activity at noon. Even in a situation where the availability of water appears at noon (simulated as a two-hour soaking period), they do not react anyway. In the morning and afternoon, the air humidity is the highest [35], while at noon, when the air temperature is the highest, the humidity drops rapidly. The scale of this phenomenon in the lichen Scots pine forest habitat changes over the seasons, from low differences in spring to high differences in summer and autumn [35]. Probably, this pattern is preserved in the photosynthetic activity of the studied species and showed. It is also worth to noting that lichens with green algae photobiont are dependent on air humidity/water vapour [49], and those with cyanobacteria needs liquid water [63]. Faster activation of photosynthesis in lichens with eukaryotic algae may result from easier penetration of water into the photosynthetic system. In the case of cyanobacteria, more water is necessary because of the rehydration period, which is required to imbibe polysaccharides sheaths of cyanobacterial cells with water [64]. Species selected for this study are the trebouxioid lichens, and they have *Asterochloris* sp. green algae photobiont [65].

We are aware that other factors that are not included in these studies may affect the variability of photosynthetic activity during the year. However, we conducted research directly in the field, and this allowed us to measure the response of species in their natural

environment. Our study revealed the existence of differences in photosynthetic activity of selected cryptogams of lichen Scots pine forest. We can conclude that, as a part of the active protection of this habitat, the availability of water expected by diagnostic species can be regulated by the alternation of basic factors, such as light and temperature. This, in turn, affects the photosynthetic activity and the viability of cryptogams that are dominant components of protected lichen Scots pine forests.

5. Conclusions

Our study provides insight into the photosynthetic activity (F_V/F_M) of selected cryptogam species. The obtained results showed that it is closely correlated and dependent on both the time of the day and the season. *Cladonia* species and *D. scoparium* (which are main component of lichen-rich Scots pine forests) tended to have higher photosynthetic activity values than *P. schreberi*. This moss represents species of coniferous forests, but at the same time, it successively displaces *Cladonia* species in the field layer of lichen Scots pine forests.

During the day, photosynthesis of all studied species was the lowest at noon, while its highest values were recorded in the afternoon. Throughout the year, F_V/F_M reached the lowest values in spring, intermediate values in summer, and the highest values in autumn.

For both moss and lichen species, higher F_V/F_M values were shown for soaked samples than non-soaked, and this outcome is directly linked with water availability. It is worth noticing that, despite the presence of water, samples collected at noon still exhibited the lowest $F_V/F_{M \text{ when}}$ compared to samples collected in the morning and afternoon. This is most likely connected with cryptogam adaptations to humidity fluctuations during the day; they are high in the morning and afternoons, but then they decrease at noon.

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