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## The influence of solar radiation on selected physiological processes of mosses in karst conditions of the spring niches of the Ojców National Park (Southern Poland)

Solar radiation has various and multidirectional effects on the growth and development of plants. It affects, incl. on the anatomical and morphological structure of individual organism structures, photosynthetic apparatus, quantity and quality of plant pigments (Öpik, Rolfe, 2005; Pilarski et al., 2012; Możdżeń, 2019). Depending on the season and day, 15 to 30% of solar radiation reaches the forest layer. However, a significant part of this solar radiation is scattered or reflected at different angles by plants from different layers of the forest (Swanson, Flanagan, 2001). Mosses, as poikilohydric organisms, may remain metabolically inactive when the solar radiation intensity is high or the water level is too low. Due to their small size and tolerance to low light, mosses often colonise habitats that are characterised by low solar radiation intensity (Niinemets, Niinemets, 2009).

The photosynthesis process is highly sensitive to abiotic stress factors, including light (Rzepka, 2008; Możdżeń, 2019). The intensity of photosynthetically active solar radiation is a factor that directly or indirectly influences the photochemistry of photosynthesis (Marschall, Proctor, 2004). The first symptom of high intensity of solar radiation is the degradation of chlorophylls and the reduction of photosynthesis (Tallis, 1959; Rastorfer, 1970). Sensitivity to light is the result of phylo- and ontogenetic adaptation. For plants growing in extreme shaded conditions, light with an intensity of several thousand lux can inhibit photosynthesis, while in other plants this effect occurs only at intensities exceeding 100,000 lux.

Plants adapt to light through structural adaptations and plant pigments. Bryophytes, unlike Tracheophytes, do not have a protective epidermis layer, under which there is a layer of palisade crumb, which additionally absorbs light before it reaches the pho-

tosynthetic tissue of the spongy crumb. Duckett and Renzaglia (1988) and Nasrullah-Boyce and Duckett (1991) described a large variation in the number of chloroplasts per cell between mosses exposed to direct and diffuse radiation. Bryophytes need to “invest” more in protection at the cellular level to mitigate the harmful effects of high levels of light (Robinson, Waterman, 2014).

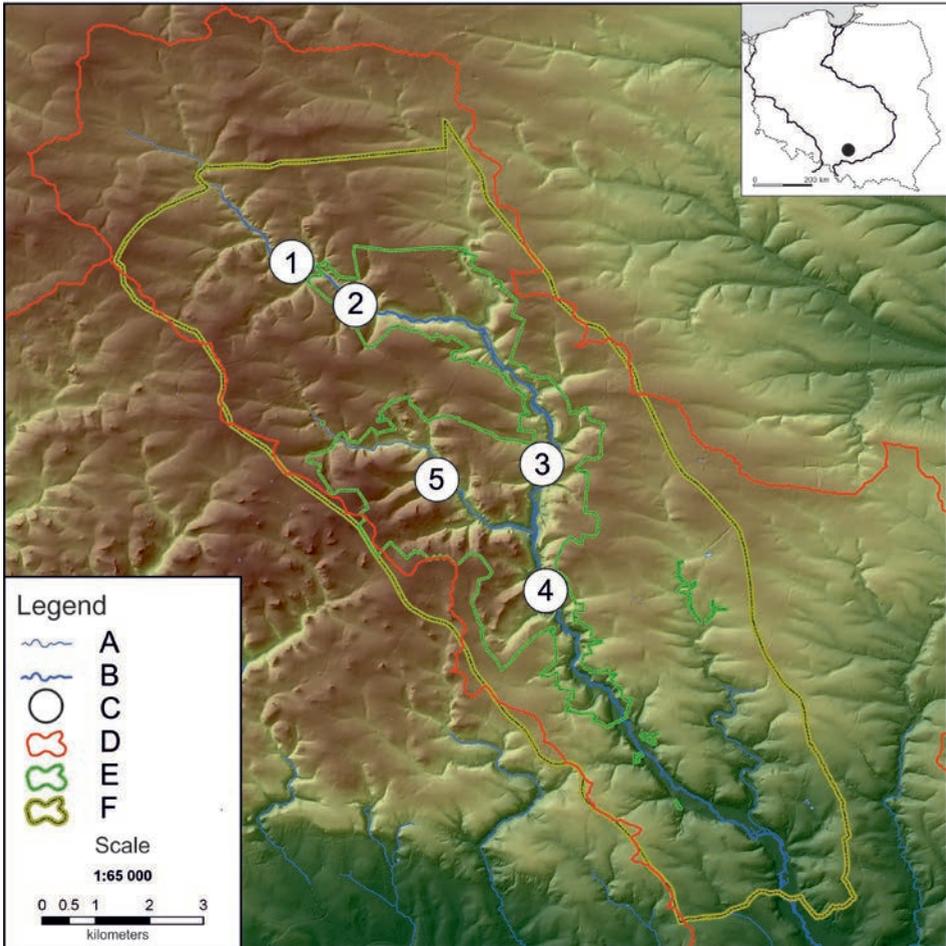
Mosses are found in many habitats around the world, but knowledge of their responses to various environmental factors is still largely unexplored. The aim of this study was to investigate the influence of solar radiation reaching the karst spring niches, on selected physiological parameters of the spring mosses: *Cratoneuron filicinum* (Hedw.) Spruce (obligatory krenophyte) and *Brachythecium rivulare* Schimp. (facultative krenophyte). The impact of habitat conditions on their photosynthetic activity was investigated by: (1) imaging the parameters of chlorophyll *a* fluorescence, (2) determining biomass and water content in gametophores and (3) analysing the degree of destabilisation of cell membranes.

## Material and methods

### Study area

In the Ojców National Park (ONP) (southern Poland – 50°12'24"N 19°49'45"E ) the geological substrate consists of limestones and Upper Jurassic marls, with a thickness of over 250 m. The network of vertical and horizontal fractures in them enables easy migration of water (Aleksandrowicz, Wilk, 1962). The Prądnik and Sąspowska Valleys have the character of a deep ravine with asymmetrical slopes. The eastern slopes are steeper and the rock formations on them are more numerous. Only two permanent watercourses flow along the Valley bottoms – Prądnik and Sąspówka. All side valleys, connecting with the Prądnik and Sąspówka Valleys, are dry, without any permanent watercourses. There are numerous springs in this area – karst spring (Gradziński et al., 2008). Most of the springs are located in the Sąspówka and Prądnik alluvia, and the water flows directly from the rock-mantle Jurassic limestones (Rózkowski, Pawlik, 2001). The morphological diversity of the Park's terrain influences different solar and microclimatic conditions (Caputa, 2009; Caputa, Wojkowski, 2015; Wojkowski, Caputa, 2015). The region is characterised by a warm plateau region, a region of thermally diverse slopes and a region of cold valley bottoms (Brzeźniak, 1974; Kliein, 1972). The study area located at the valley floors is characterised by frequent thermal inversions, fogs and cold air (Brzeźnik, Partyka, 2008).

The five karst spring niches (4 in the Prądnik Valley, 1 in the Sąspowska Valley) were selected for the plant material collection, in which two of the moss species tested occurred simultaneously (Fig. 1–2).



**Fig. 1.** Distribution of study stands: A – rivers, B – Prądnik river, C – study stands, D – second-order catchment, E – park ONP border, F – boundary of the park’s buffer zone; 1–4 spring niches in Prądnik Valley: 1 – spring of “Orczyk” in Sułoszowa, 2 – spring of a car park in Pieskowa Skała, 3 – spring near the chapel “Na Wodzie” in Ojców, 4 – spring opposite the Wapiennik Rock in Ojców, 5 – spring in the Sąspowska Valley

#### *Spring of “Orczyk” in Sułoszowa*

A fissure spring, located on the right side of the Prądnik stream, 390 m a.s.l. Exposition NE. It is made up of two rivers flowing from under a limestone slope. One of them has a concrete housing that distorts its natural character. It is a high capacity spring of 14.5 L/s (main flow), 5.6 L/s (secondary flow). Its waters are bicarbonate-calcium, sweet, slightly alkaline, hard (Pawlik, 1998). The spring is surrounded by a forest, a meadow and a roadside.



**Fig. 2.** Selected study stands: A – spring the Sąspowska Valley, B – spring of “Orczyk”, C – spring opposite the Wapiennik Rock, D – spring near the chapel “Na Wodzie” (Photo. A. Sołtys-Lelek)

#### *Spring of a car park in Pieskowa Skala*

A fissure-karst spring, near the riverbed, located on the left side of the Prądnik stream, 390 m a.s.l., with an SSW exposure. It is made up of three outflows. The largest of them, being a spring niche, has a concrete lining; the other two flow naturally, almost in the very channel of the stream. This spring has a low capacity of 0.5 L/s. Its waters are bicarbonate-calcium, sweet, slightly alkaline, medium hard (Dynowska, 1983; Pawlik, 1998). The spring is surrounded by a forest and a parking lot.

#### *Spring near the chapel “Na Wodzie” in Ojców*

A fissure-karst spring, terraced, by the riverbed, located on the right side of the Prądnik stream, 325 m a.s.l., with ENE exposure. It is enclosed in an unworked limestone casing. The spring niche is an artificially directed outflow of water, which flows into Prądnik along a natural slope of limestone rubble. This spring has a low capacity of 1.2–0.5 L/s. Its waters are bicarbonate-calcium, sweet, slightly alkaline, medium hard (Aleksandrowicz, Wilk, 1962; Sadowski, Rózkowski, 1989; Pawlik, 1998). The spring is surrounded by meadows and a small tourist infrastructure.

*Spring opposite the Wapiennik Rock in Ojców*

Fissure-karst spring, near-channel, located on the right side of the Prądnik stream, 310 m a.s.l., with ENE exposure. It is enclosed in a concrete housing, and part of its water supplies the farm. Part of the spring also flows down to Prądnik in a small stream. This spring has a low capacity of 1.4 L/s. Its waters are bicarbonate-calcium, sweet, slightly alkaline, medium hard (Aleksandrowicz, Wilk, 1962; Pawlik, 1998). The spring is surrounded by meadows.

*Spring in the Sąspowska Valley*

A fissure-karst spring, near-channel, located on the right side of the Sąspówka stream, 350 m a.s.l., with NE exposure. They are two outflows of a natural character that merge and flow into the Sąspówka stream. This spring has a low capacity of 3.9 L/s. Its waters are bicarbonate-calcium, sweet, slightly alkaline, medium hard (Pawlik, 1998). The spring is surrounded by a forest. This spring is the only one of the surveyed, characterised by a completely natural spring niche, devoid of anthropogenic factors.

**Measurements of solar radiation and temperature**

Global solar radiation ( $K_c$ ) and reflected solar radiation were measured with the SP Lite pyranometer (Weiz, Austria). NR Lite Kipp & Zonen radiometer was used to measure net all-wave radiation (NR) for individual springs. Based on the quotient of reflected to total radiation ( $K_{odb}/K_{cal}$ ), the reflectance coefficient – Albedo was determined, which indirectly determines the ability of the surface to reflect radiation. Air temperature (2 m above the surface) –  $T_p$ , water –  $T_w$ , on the spring surface –  $T_{po}$  and inside moss turf –  $T_w$  was measured by thermometer LB401 with a Pt100 sensor with an accuracy of 0.1°C (Lab-El, Krakow, Poland). Solar radiation and temperature measurements were made on a sunny day from 11:00 to 16:00.

**Plant material – short botanical characteristic**

*Brachythecium rivulare* Schimp. in Bruch, Schimp. & W. Gümbel – (Canal moss) is green or yellow-green plagiotropic moss. It occurs all over Poland, in the mountains up to 1,800 m a.s.l. The upward stems are usually pinnate, 3 to 6 cm long. The leaves are ovoid-triangular, sudent at the top, sharpened briefly, narrowed at the base, concave, irregularly longitudinally folded, and finely, sharply serrated on the edge. The leaf rib is single, tapering towards the top. The leaf cells are elongated, prozenchymatic, with a small amount of chloroplasts, with thickened cell walls, orange in colour (Jusik, 2012).

*Cratoneuron filicinum* (Hedw.) Spruce – (Triangle moss) it is a plagiotropic moss that forms a pale green turf. This species is common throughout Poland. It occurs mainly in the Carpathians, Sudetes, Lakeland belt, Jura Krakowsko-Częstochowska and Roztocze. Its gametophores are creeping at the bottom, singly branched at the top, reaching 2 to 5

cm in length. The leaves are wide, heart-triangular and ovate-lanceolate. The rib is single, massive, biconvex, made of undifferentiated cells. The leaf cells are short-rectangular or 6-sided, and a few elongated, thick-walled, more elongated at the tip (Jusik, 2012).

### Chlorophyll *a* fluorescence

Chlorophyll *a* fluorescence measurements were performed on 5 different gametophores of mosses. During the study, the gametophores of mosses were put on filter paper wet of distilled water and adopted for darkness for 20 min in a closed chamber FluorCam FC 800C (Photon Systems Instruments, Czech Republic) according to the method used by Możdżeń (2019). Among the results obtained, the following parameters were analysed: the zero fluorescence ( $F_0$ ), the maximum fluorescence ( $F_m$ ), the maximum efficiency of the photochemical PSII ( $F_v/F_m$ ), the non-photochemical quenching (NPQ) and the vitality of PSII (Rfd).

### Fresh and dry mass, water content

Fresh and dry masses (FM and DM, respectively) were determined on a laboratory balance (Ohaus Adventurer Pro, USA) with an accuracy of 0.0001 g. Single moss gametophytes were dried for 48 h at 105°C temperature (dryer – Wamed SUP-100, Poland). On the basis of the masses obtained, the ratio of dry mass to fresh mass and the percentage of water content were determined according to the following formula (1):

$$WC [\%] = 100 - [(DM \times 100) / FM] \quad (1)$$

where: WC – water content, DM – dry mass, FM – fresh mass

### Electrolyte leakage

Separately gametophytes of two mosses were placed in vials containing 10 mL of deionised water with a specific conductivity of 0.05  $\mu$ S. Plant material was incubated on a shaker (Labnet, Rocker, USA) for 3 h at 25°C to determine the electrolytes leakage (E1). Then vials with mosses were frozen for 24 h at –80°C (Platilab 500Next, Angelantoni Industrie, Italy). Next day, samples were thawed and subjected to the shaking procedure described above. After this time, the flow of electrolytes (E2) were measured. The percentage of electrolyte leakage (EL) was calculated according to the formula:  $EL = (E1 / E2) 100\%$ . The electrolyte leakage measurements were made using a CX-701 conductometer (Elmetron, Poland) with an electrode with a constant  $K = 1.02$  (Elmetron, Poland).

### Data analysis

The mean results from 5 replicates were analysed in Microsoft Excel and StatSoft, Inc.

2018. STATISTICA (data analysis software system), version 13.1. The significance of differences between means ( $\pm$  SD) were analysed by Duncan's test at  $p \leq 0.05$ .

## Results

### The inflow of solar radiation and temperature

Total shortwave (Kc) and reflected (Ko) radiation were the highest on stand 3, and the lowest on stands 1 and 5 (Tab. 1). Albedo achieved the highest values on stand 2, and the lowest on stands 3, 4, 5. Air temperature (Tp) was the highest on stand 4, and the lowest on stand 1.

**Tab. 1.** Characteristics of environmental factors on the researched springs in Ojców National Park (Wojkowski, Caputa, 2009)

No. of spring	Radiation coefficients							Spring temperature [°C]				Annual sum of total radiation [MJ × m <sup>-2</sup> ]	The annual amount of potential insolation [h]
	Measurement data [mV]			Radiation [W × m <sup>-2</sup> ]				Tp	Tpo	Tm	Tw		
	Kc	Ko	NR	Kc	Ko	NR	Albedo						
1	65	9	56	77	155	36	0.15	14.35	11.65	8.15	8.65	3484	3235
2	103	12	91	102	122	51	0.19	15.85	16.85	16.1	8.35	2871	2570
3	603	80	523	68	150	354	0.13	17.2	22.93	13.7	8.75	3566	3156
4	392	50	342	86	117	292	0.13	18.1	15.7	10.4	9.30	3302	2746
5	71	9	62	82	126	46	0.13	17.5	16.0	11.4	8.50	3200	< 2700

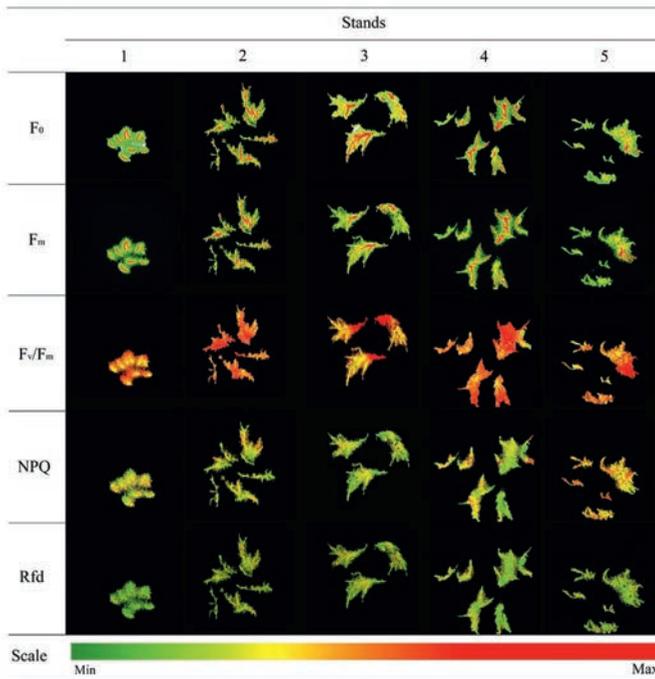
1 – spring of “Orczyk” in Sułoszowa, 2 – spring of a car park in Pieskowa Skała, 3 – spring near the chapel “Na Wodzie” in Ojców, 4 – spring opposite the Wapiennik Rock in Ojców, 5 – spring in the Sąspowska Valley; Kc – total short-wave radiation, Ko – reflected short-wave radiation, NR – balance of short- and long-wave radiation, Albedo – determines the ability of a surface to reflect short-wave radiation: albedo = Kodb/Kcal, Tp – air temperature, Tpo – surface temperature above the spring, Tm – temperature in the moss, Tw – water temperature

The surface temperature above the spring was the highest at stand 3, and the lowest at stand 1. The temperature in the moss turf (Tm) was the highest on stand 2, and the lowest on stand 1. The water temperature (Tw) was the highest at stand 4, and the lowest at stand 2. The annual sum of total radiation reached the highest values at stand 3, and the lowest at stand 2. The annual sum of potential insolation showed the highest values at stand 1, and the lowest at stand 2.

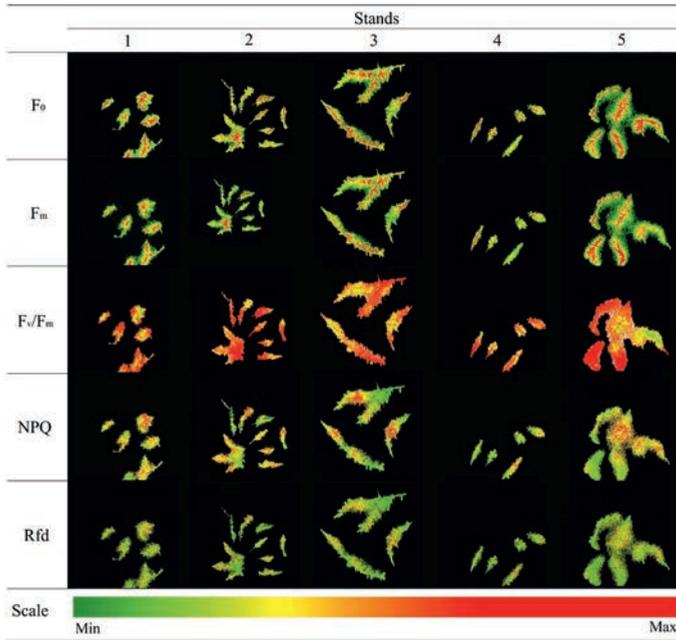
### Chlorophyll *a* fluorescence

The zero fluorescence ( $F_0$ ) *Brachythecium rivulare* was the highest in plants growing on stand 3 (the most yellow and red colour), compared to the gametophores from stands 1 and 5 (Fig. 3). Intermediate values of  $F_0$  were reached by mosses from stands 2 and

4. The maximum fluorescence ( $F_m$ ) was similar between specimens of *B. rivulare* from stands 2 and 3 (the most yellow and red). Slightly lower values of this parameter were found for mosses collected from stands 1 and 4. The lowest values of  $F_m$  were found for plants from stand 5 (green colour is dominant). The maximum efficiency of the photochemical PSII ( $F_v/F_m$ ) was clearly the highest for the gametophores collected from stands 2 and 4 (intense red colour dominated). Intermediate values of this parameter were observed in plants from the remaining 3 stands (1, 3 and 5 – half yellow and red, respectively). The non-photochemical quenching (NPQ) reached the highest values in *B. rivulare* taken from stand 5 (yellow and red predominance). The lowest NPQ values were observed for gametophores from stand 3 (green and yellow colours dominate). Intermediate values of this parameter were found for plants from stands 1, 2 and 4 (mostly yellow and green, a small proportion of red). The vitality of PSII (Rfd) reached the lowest values in *B. rivulare* from stand 1 (green was the dominant colour). The Rfd values were similar in plants from the remaining 4 stands (Fig. 3). The zero fluorescence ( $F_0$ ) *Cratoneuron filicinum* was similar in the 5 tested stands (red and green colours). Maximum fluorescence values were similar in plants collected from stands 1, 3 and 5. Clearly lower values were observed for plants from stands 2 and 4 (a small proportion



**Fig. 3.** Imaging of fluorescence parameters of *Brachythecium rivulare* Schimp. from the five karst spring niches (1–4 in the Prądnik Valley, 5 in the Sąspowska Valley);  $F_0$  – the zero fluorescence,  $F_m$  – the maximum fluorescence,  $F_v/F_m$  – the maximum efficiency of the photochemical PSII, NPQ – the non-photochemical quenching, Rfd – the vitality of PSII



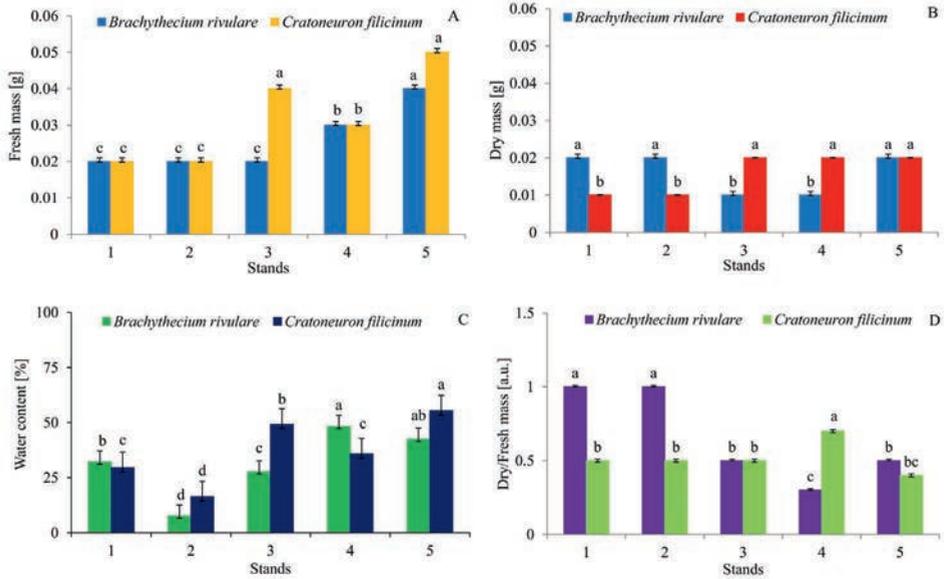
**Fig. 4.** Imaging of fluorescence parameters of *Cratoneuron filicinum* (Hedw.) Spruce from the five karst spring niches (1–4 in the Prądnik Valley, 5 in the Sąpowska Valley);  $F_0$  – the zero fluorescence,  $F_m$  – the maximum fluorescence,  $F_v/F_m$  – the maximum efficiency of the photochemical PSII, NPQ – the non-photochemical quenching, Rfd – the vitality of PSII

of red, the dominant colour is green). The maximum efficiency of the photochemical PSII for gametophores from stands 2, 3 and 4 were similar (red and yellow colours were dominant).

The lowest  $F_v/F_m$  values were recorded for mosses from the stand 5 (a large share of red colour; however, a green colour also appeared). The non-photochemical quenching values were similar in plants from stands 1, 2 and 5. *C. filicinum* gametophores from stands 3 and 4 achieved similar NPQ values (small proportion of red colour; green was the dominant colour). The vitality of PSII (Rfd) was similar in plants harvested from all 5 stands (Fig. 4).

### Fresh and dry mass, water content

The fresh mass of *Brachythecium rivulare* gametophytes was significantly the highest in plants growing on stand 5, compared to the other 4 stands. Intermediate values were observed for plants from stand 4, in relation to the other results. The smallest increase in fresh mass was recorded in mosses collected from stands 1, 2 and 3. In the case of *Cratoneuron filicinum* gametophytes, fresh mass was the largest for plants harvested from stands 3 and 5. On stand 4, the fresh mass was smaller than the mass of gametophytes from stands 3 and 5, but larger than that of plants growing on stands 1 and 2.



**Fig. 5.** Fresh and dry mass, and water content in gametophytes of *Brachythecium rivulare* Schimp. – A and *Cratoneuron filicinum* (Hedw.) Spruce – B. The five karst spring niches (1–4 in the Prądnik Valley, 5 in the Sąpowska Valley); mean values ( $n = 5$ ,  $\pm$  SD) marked with different letters differ significantly according to Duncan's test at  $p \leq 0.05$

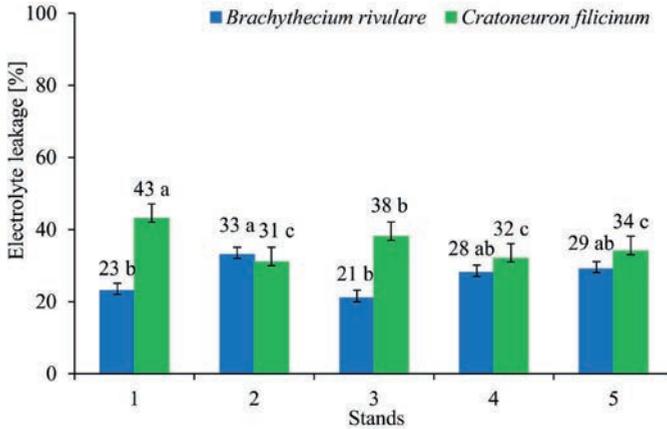
Mosses from stands 1 and 2 showed the lowest values of this parameter in relation to the remaining stands (Fig. 5A).

The dry mass of *B. rivulare* gametophytes was similar and was the largest in plants from stands 1, 2 and 5. On the other two stands (3 and 4), the dry mass values were significantly lower. For *C. filicinum*, the significantly largest dry mass increase was obtained for plants collected from stands 3, 4 and 5, compared to other stands (Fig. 5B).

The percentage of water content in *B. rivulare* cells was significantly the highest in plants from stand 4, compared to the other stands. The lowest values of this parameter were found for mosses from stand 2. For *C. filicinum*, the highest water content was found in plants from stand 5. Intermediate values are shown in stand 3. The lowest water concentration in the tissues of this moss was observed in plants growing on stand 2 (Fig. 5C).

The ratio of dry mass to fresh mass in *B. rivulare* was the highest for plants collected from stands 1 and 2, compared to the other 3 stands. Intermediate values of this coefficient were shown for mosses from stands 3 and 5. The smallest ratio was calculated for the gametophytes from stand 4. For *C. filicinum*, the value of this parameter was clearly the highest in the plants from stand 4, compared to the other stands (Fig. 5D).

The percentage of electrolyte leakage from *B. rivulare* gametophores was the highest in plants from stand 2. Intermediate values were observed for the gametophores from



**Fig. 6.** Electrolyte leakage of *Brachythecium rivulare* Schimp. and *Cratoneuron filicinum* (Hedw.) Spruce. The five karst spring niches (1–4 in the Prądnik Valley, 5 in the Sąspowska Valley); mean values ( $n = 5$ ,  $\pm$  SD) marked with different letters differ significantly according to Duncan's test at  $p \leq 0.05$

stands 4 and 5. Significantly, the lowest destabilisation of cell membranes was demonstrated for plants from stands 1 and 3. For *C. filicinum*, the significantly highest electrolyte leakage was found for plants from stand 1, in relation to the remaining 4 stands. The lowest degree of destabilisation of cell membranes was observed for gametophores from stands 4 and 5 (Fig. 6).

## Discussion

The analysed stands in the Ojców National Park are located in the bottoms of deep karst valleys (Fig. 1–2). The concave terrain forms such as the bottoms of valleys and canyons are characterised by much lower incoming solar radiation values compared to plateaus (Caputa, Wojkowski, 2009, 2013, 2015). According to Bárányi-Kevei (2011), microclimatic differences are responsible for the diversity of vegetation in the karst ecosystem. In such ecological conditions, pioneering plants, such as bryophytes, find their refuge. These are the conditions of the variable ratio of short-wave and long-wave radiation and direct radiation that appear systematically in the same place during the day such as “sun flakes” (Sołtys-Lelek, 2009; Pilarski et al., 2012).

In the conducted research, the solar radiation flux at individual measurement stands was strongly differentiated due to the topography and vegetation growing there (Fig. 1–2; Tab. 1). High values of solar radiation above the sunlit surface proved that mosses strongly absorbed light. Lower values obtained in the immediate vicinity of shaded trees indicated limitations in absorption of diffuse radiation (Caputa, Wojkowski, 2015). These types of changing conditions affect the formation of specific morphological and physiological features of mosses and allow them to occur in a variety of ecosystems.

Bryophytes have developed filters that help protect them from high levels of solar radiation. For example, some species of the genus *Polytrichum* have lamellae, surrounded by a curled leaf blade, so that their structure does not differ much from that of a tree leaf. Others have leaves with filaments – *Crossidium*, hyaline tips (*Hedwigia ciliata*, *Bryum argenteum*), and awns (*Tortula* sp., *Syntrichia* sp.), that overlap the next leaf and help to deflect light before it reaches the cell interior. Other mosses have warts that become more transparent when wet, doubling their ability to absorb solar radiation (Glime, 2017). The anatomical and morphological differences of mosses are treated as an expression of the adaptation arising in the phylogenetic development, allowing them to operate the photosynthetic apparatus in the most favourable conditions in the given habitat (Krupa, 1974).

In many studies, the response of bryophytes – e.g. *Bryum argenteum* (Rastorfer, 1970), *Racomitrium lanuginosum* (Kallio, Heinonen, 1975), *Grimmia pulvinata* and *Tortula ruralis* (Alpert, Oechel, 1987) – to solar radiation showed saturation of photosynthesis even at low, 20% light intensity. Murray et al. (1993) showed that mosses from shady areas, exposed to high intensity of light, lost their ability to photosynthesize. On the other hand, mosses that had been transferred from full sun to shade grew at a rate of 2–3 times higher. The photosynthesis in bryophytes is limited at very low light levels, yet these plants can survive in low light conditions, as previously mentioned. According to Smith et al. (2009) and Niinemets and Niinemets, (2014) the total leaf area can absorb much more light and increase photosynthetic activity. The leaf structure of bryophytes, with lower plant density, seems to provide the plant with an increased efficiency of light uptake (Niinemets, Niinemets, 2009; Rice et al., 2008).

The phenomena accompanying the disintegration of the photosynthetic apparatus are reflected in changes in the values of chlorophyll *a* fluorescence parameters (Lichtenthaler et al., 1986; Bolhár-Nordenkampf, Öquist, 1993; Thach et al., 2007; Demmig-Adams et al., 2014; Ruban, 2016). In this study, the variability of chlorophyll fluorescence may suggest that it was the result of photoinhibition (Murray et al., 1993). The photoinhibition was indicated by lower  $F_v/F_m$  values and activated photoprotection mechanisms, as evidenced by higher NPQ values, depending on the habitat conditions in the analysed stands (Marschall, Proctor, 2004). According to Proctor et al. (2007) the increase in NPQ can be explained by the degree of cell hydration, which decreased in *Brachythecium rivulare* and *Cratoneuron filicinum* specimens from stands 1 and 2 (Fig. 3–5). The ability of the protective mechanisms that make up NPQ is specific and characteristic of a given moss species. Most often it is related to the PSII antenna system, i.e. performance of two essential light-harvesting complex (LHC)-like proteins, photosystem II subunit S (PSBS) in plants and light-harvesting complex stress-related (LHCSR) (Rintamaki et al., 1994; Pinnola et al., 2015; Dikaios et al., 2019). Mosses, depending on the species, are able to quickly regenerate physiological activity disturbed

by a stress factor (Proctor, Tuba, 2002; Ciu et al., 2008; Mozdzeń, 2019). They share many photoprotective mechanisms with vascular plants. However, there are some key differences in the photoprotection available (Robinson, Waterman, 2014).

The state of hydration of the cells affects the moss ability to absorb or reflect light (Lappalainen et al., 2008). This suggests that the mosses have developed mechanisms that allow them to scatter light internally and/or externally. In dried mosses, increased reflection (albedo) and reduced solar radiation absorption (low NR values) should provide them with some protection against the harmful effects of light. In fully hydrated mosses (low albedo and high NR), the surface and interior are more homogeneous and absorb solar radiation more effectively (Lovelock, Robinson, 2002). In the analyses carried out here, the differences in the fresh and dry mass influenced the water content in the gametophores of the studied species (Fig. 5). The water content was significantly the lowest in both mosses collected from stands 1 and 2, compared to the 3 remaining stands. This was most likely due to the fact that mosses are highly flexible in relation to environmental conditions. At these two stands, the measurements show a high temperature and strong absorption of solar radiation by the surface of the mosses (Tab. 1). This is probably why the tested mosses were characterised by the lowest masses and water content values (Fig. 5). This result could also depend on other environmental factors (Tab. 1). It can be assumed that the substrate, species composition of other plants, temperature and humidity of the environment played an important role here. At stands 1 and 2, the spring niche is created by a semi-circular concrete lining, which makes the substrate highly exposed to drying out. In the remaining stands, mosses grew on soil or calcareous rock-mantle mixed with soil (Fig. 1–2). Mosses are characterised by different hydration depending on, among others light, the availability of surface water, the action of capillary forces, supported by the setting of gametophore leaves (Proctor et al., 2007; Romańska, 2020). This directly affects the rate of their elongation growth, masses gain and changes in the chemical composition of plant pigments and other metabolites. Such interactions are also perceived at the cellular and molecular level (Ueneka, 2005).

The effects of stress caused by different spectral composition and light intensity destabilise the proper functioning of mosses, causing changes in the permeability of cell membranes (Mozdzeń, 2019). Cell membranes react the fastest to the influence of a stress factor. They are highly selective permeation barriers but do not completely isolate because they contain specific channels, conveyors and pumps. Undamaged cell membrane allows water molecules to enter the cell interior and is a barrier for molecules of substances dissolved in the cell. The higher the degree of damage to membranes by stress factors, the higher part of the cell contents flows out (Kocheva et al., 2014). The stress-induced electrolyte leakage is accompanied by changes in the structure of proteins and lipids, the concentration of ions in the vacuole and cytoplasm, and the generation and accumulation of reactive oxygen species, which in extreme cases leads to cell death

(Demidchik et al., 2014; Scotti-Campos, Pham-Thi, 2016). The studies of electrolyte leakage carried out here in *B. rivulare* and *C. filicinum* showed the highest membrane destabilisation in plants from stands 1 and 2, respectively, compared to other stands (Tab. 1; Fig. 6). The obtained results prove the most unfavourable environmental conditions for the existence of mosses in these stands. Within them, mosses do not occur on natural ground, because the spring niches have been quite strongly transformed by human – the surrounding of the outflow with a concrete lining (Fig. 2).

Comparing the photosynthetic activity of moss gametophores is not easy, because the response of plants is often the result of many different environmental factors. From an ecological point of view, an important role is played by the leaf area to volume ratio and the percentage of assimilation tissues in the total leaf mass (Miyata et al., 2015). The comparison of photosynthesis efficiency to mass is relative and it seems that there is no adequate relationship in terms of the total photosynthetic production (Krupa, 1974). The analysis of selected physiological parameters did not clearly indicate which of the studied stands is the most optimal for mosses. Therefore, further research in this area is necessary in order to distinguish both the most convenient stands of spring mosses in the ONP area and to verify which environmental factors play a key role in their physiology.

## Conclusion

- (1) The photosynthetic activity of mosses was specific and depended on the stand and species. Such reactions most likely resulted from the structure of mosses and their different adaptations to environmental conditions.
- (2) The fresh mass of gametophytes was significantly the largest in plants growing on stand 5, where there is the only completely natural spring niche among the studied. Mosses from stands 1 and 2 showed the lowest values of this parameter. The dry mass of mosses varied and also depended on the species and stand. The percentage of water content of both tested mosses was the lowest for plants growing in stand 2 with the most transformed spring niche; bryophytes appeared here only on the artificial substrate of concrete lining.
- (3) The degree of destabilisation of the cell membranes of *Brachythecium rivulare* and *Cratoneuron filicinum* gametophores was specific and, as in the previous parameters, depended on the species and location. In general, the highest percentage of electrolytes leakage was found in plants harvested from stands 1 and 2, which proves the highest environmental stress in these two examined positions.

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## Conflict of interest

The authors declare no conflict of interest related to this article.

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## Abstract

The availability of light is one of the most important environmental factors influencing the floristic diversity of spring niches, especially in the specific conditions of deep, karst valleys occurring in the Ojców National Park (southern Poland). The aim of this study was to investigate the influence of solar radiation reaching the karst spring niches, on selected physiological parameters of the spring mosses: *Cratoneuron filicinum* (Hedw.) Spruce (obligatory krenophyte) and *Brachythecium rivulare* Schimp. (facultative krenophyte). The five karst spring niches (4 in the Prądnik Valley, 1 in the Sąspowska Valley) were selected for the plant material collection, in which two of the moss species tested occurred simultaneously. On sunny days, measurements of total and reflected radiation, as well as the radiation balance in the full spectrum range over the vegetation were made. The temperature was measured for air, water, and on the surface and inside the plants. The collected biological material was subjected to laboratory analysis. Fresh mass of moss gametophytes was significantly the highest from plants growing on stand 5 (intermediate values of light and temperature parameters), and the lowest from mosses on stands 1 and 2 (including lowest air temperatures). Dry mass varied depending on the species and stand. The percentage of water in *B. rivulare* was highest in plants from stand 4 (highest air and water temperature), and in *C. filicinum* from stand 5. Significantly the lowest values of this parameter were found for plants growing in stand 2 (lowest temperature of water). The electrolytes leakage from moss cells was specific and depended on the species. The greatest destabilisation of cell membranes was demonstrated in plants harvested from stands 1 and 2, where it was the coldest. The fluorescence of chlorophyll *a* varied depending on the moss species and the habitat of spring niches. This paper, presenting of preliminary results, is a kind of introduction to wider research in this topic.

**Key words:** albedo, biomass, *Brachythecium rivulare*, *Cratoneuron filicinum*, chlorophyll *a* fluorescence, electrolyte leakage, net all-wave radiation

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## Wpływ promieniowania słonecznego na wybrane procesy fizjologiczne mchów w warunkach krasowych nisz źródłiskowych Ojcowskiego Parku Narodowego (Południowa Polska)

### Streszczenie

Dostępność światła jest jednym z najważniejszych czynników środowiskowych wpływających na różnorodność florystyczną nisz źródłiskowych, zwłaszcza w specyficznych warunkach głębokich, krasowych dolin, występujących w Ojcowskim Parku Narodowym (Południowa Polska). Celem niniejszej pracy było zbadanie wpływu promieniowania słonecznego, docierającego do nisz źródłiskowych, na wybrane parametry fizjologiczne mchów źródłiskowych: *Cratoneuron filicinum* (Hedw.) Spruce (krenofit obligatoryjny) i *Brachythecium rivulare* Schimp. (krenofit fakultatywny). Do zbioru materiału roślinnego wytypowano 5 krasowych nisz źródłiskowych (4 w dolinie Prądnika, 1 w dolinie Sąspowskiej), w których występowały jednocześnie obydwa gatunki mchów. W słoneczne dni dokonano pomiarów promieniowania całkowitego, odbitego oraz salda promieniowania w pełnym zakresie widma nad roślinnością. Pomierzono temperaturę powietrza, wody oraz na powierzchni i wewnątrz roślin. Zebrany materiał biologiczny poddano analizom laboratoryjnym. Świeża masa gametofitów była istotnie największa u roślin rosnących na stanowisku 5 (pośrednie wartości parametrów światła i temperatury), a najmniejsza u mchów ze stanowisk 1, 2 (m.in. najniższe temperatury powietrza). Sucha masa zmieniała się w zależności od gatunku i siedliska. Procentowa zawartość wody u *B. rivulare* była największa dla okazów ze stanowiska 4 (najwyższa temperatura powietrza i wody), a u *C. filicinum* ze stanowiska 5. Istotnie najmniejsze wartości tego parametru stwierdzono dla roślin rosnących na stanowisku 2 (najniższa temperatura wody). Wpływ elektrolitów z komórek mchów był specyficzny i zależał od gatunku. Największą destabilizację błon komórkowych wykazano u roślin zebranych ze stanowisk 1 i 2, gdzie było najchłodniej. Fluorescencja chlorofilu *a* zmieniała się w zależności od gatunku mchu i źródliska. Niniejsza praca prezentująca pilotażowe wyniki, stanowi niejako wstęp do szerszej zakrojonych badań w tym zakresie.

**Słowa kluczowe:** albedo, biomasa, *Brachythecium rivulare*, *Cratoneuron filicinum*, fluorescencja chlorofilu *a*, wpływ elektrolitów, saldo promieniowania krótko i długofalowego

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