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Impact of water stress on physiological processes of moss *Polytrichum piliferum* Hedw.

Introduction

Plant responses to water deficits depend not only on their age and development phase but also on the extent and rate of water stress. A slow pace of water loss allows air conditioning and reduces damage caused by a water deficit, while fast-pace water loss can block this process. Though, a similar water deficit can cause differing responses in sensitive plants compared to plants resistant to water deficiency (Bray, 1997).

In addition to water, oxygen availability is also an important element in plant biochemical processes. Improper oxygen conditions of the soil adversely affect plants, causing root hypoxia and, consequently, inhibition of respiration. In hypoxic roots, growth is first restricted, followed by reduced water permeability and nutrient uptake. Maintenance of hypoxia and drought leads to irreversible physiological processes in both seed and spore plants, e.g. mosses (Kozłowski, 1984; Kozłowski, Pallardy, 1997; Rzepka et al., 2003; Rzepka, 2008).

Mosses (Bryophyta) are a group of plants present in various relatively humid habitats around the world (Proctor, 2000, 2001). In general, their life requirements are small, which is why they often resettle in difficult conditions, as pioneer plants. In some plant communities they cover huge areas, constituting the dominant floristic group. They are commonly found on meadows, peat bogs, in brush, set-aside, rocks, stones, trees, in ditches, fires, debris and on walls. Mosses are characterised by high resistance to variability of habitat edaphic factors, temperature and humidity (Karczmarsz, 2000; Fojcik, 2011; Możdżeń, Skoczowski, 2016; Kula et al., 2018; Sołtys-Lelek et al., 2018; Możdżeń, 2019). They collect water thanks to the imbibition forces located in the plasma of cells, membranes and mucous substances that are secreted on the surface of the stalks or gametophyte leaves. The role of rhizoids is limited to attaching the plant to the ground and is not important during intake of water. Therefore, for

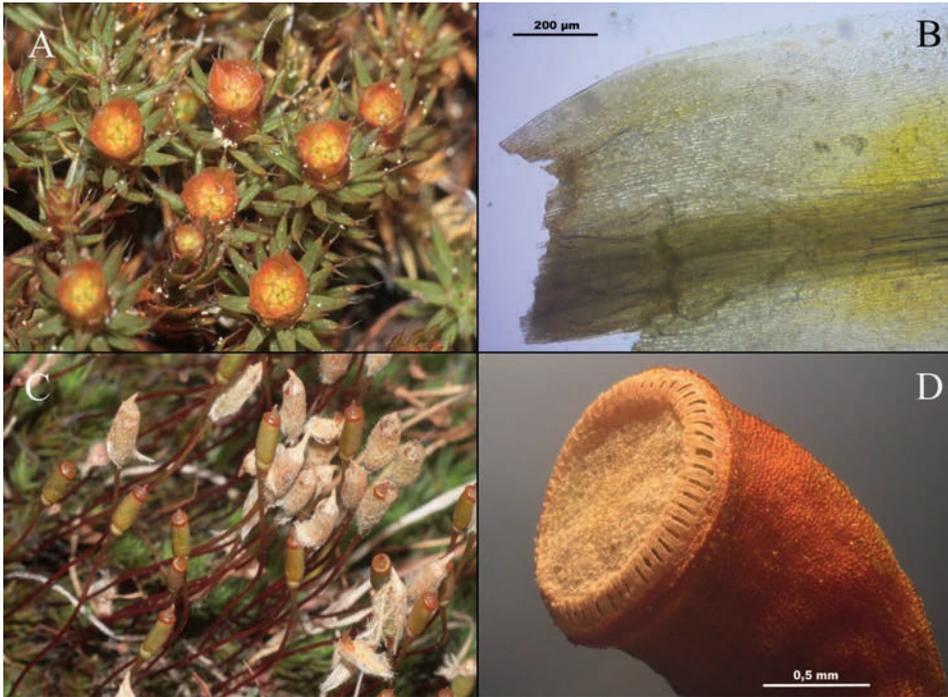


Fig. 1. *Polytrichum piliferum* Hedw.: A – gametophores, B – fragment of gametophyte leaf with rib, C – sporophytes, D – fragment of capsule with peristome (Source: <https://atlas.roslin.pl/plant/9498>)

many species of mosses, rainwater and dew are a direct source of moisture. Water conduction in mosses occurs due to the presence of layers of highly hygroscopic mucilaginous substances that draw in water and distribute over the entire surface of the turf. Water migration also takes place over the surface of leafy stalks, due to capillary forces present in the spaces between the leaves, or through primitive conductive tissue developed in the middle of the stem (Pressel et al., 2006).

Bristly haircap moss *Polytrichum piliferum* Hedw. from the Polytrichaceae Schwägr. family belongs to cosmopolitan spore plants but is more commonly found in the Northern Hemisphere. In Poland, it occurs both in the mountains and in the lowlands. It grows in sunny, sandy, dry and acidic places and creates brown-green, loose turf (Szafran, 1948). In its life cycle, like other mosses, the dominant generation is haploid gametophyte (Fig. 1A–B). The sporophyte has the form of a simple telome ending with a sporangial (Fig. 1C–D). The underground part of the gametophores are made of rhizoids up to 5 cm long, and the above-ground part of the stalk has leaves that reach 4.5 to 6 mm in length and 0.5 mm in width. They are lanceolate, whole leaf edges, extended at the bottom in a single-layer, non-green sheath. This moss has a double-layered leaf blade with a single-layer edge; a rib is present in the middle of the leaf (Fig. 1B). The ventral side of the leaf has lamellas, whose apical cells are bottle-shaped and papillary (Wójciak, 2003).

Mosses are convenient organisms for studying the reaction of plants to water stress because they are relatively primitive for terrestrial plants. They do not have an epidermis, which is why they are more sensitive to moisture changes than most other plants (Harmens et al., 2011; Schröder et al., 2014). Therefore, they are often a research object for exploring plant hydration. The aim of the study was to determine the effect of water stress on the activity of photosynthesis (*i*) and dark respiration (*ii*) in Bristly haircap moss *P. piliferum*.

Material and methods

Plant material

The turf of *Polytrichum piliferum* mosses collected in situ in spring 2010, from the natural forest habitat surrounding Rybna (50°03'04"N 19°38'50"E – Southern Poland) site was used for the research.

Conditions

Plant material was acclimated for 2 weeks in a growth chamber. Conditions for mosses during the acclimatisation were a 12 h/12 h photoperiod, density of quantum stream in the PAR range of $70 \mu\text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$ – with the fluorescent light source Fluora-Osram (Poland), a temperature of 15°C ($\pm 2^\circ\text{C}$) and a relative humidity that oscillated around 70–100%. Mosses were regularly watered with distilled water. After the acclimatisation period, similar morphological *P. piliferum* gametophores ± 1.5 cm long were selected for the study. Plants were rinsed with distilled water and dried with filter paper. Then they were placed into holes of plexiglas plates in glass vessels with a volume of 1 dm³ with 10 ml of distilled water and stored in a growth chamber.

Gas exchange

An infrared gas analyser ADC–225 MK3 (UK) operating in a closed system was used to measure photosynthesis and respiration of gametophores. The entire system consisted of an assimilation chamber with an air humidifying system and a water jacket, and its volume was 0.664 dm³. Measurements were carried out in air with an oxygen content of 21%. The temperature inside the assimilation chamber was 25°C throughout the measurements. During photosynthesis measurements, the intensity of light reaching the gametophores was $100 \mu\text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$. The concentration of carbon dioxide was 300–400 $\mu\text{mol CO}_2$ in 1 litre of air in a closed system, and the relative humidity of the air was approximately 75%, which allowed air to pass through the scrubber with distilled water.

Experimental groups

The control group for photosynthesis and dark respiration were *P. piliferum* gametophores arranged on Plexiglass plates, immediately after acclimatisation. After the fresh mass determination and gas exchange measurements, the mosses were dried for 1 hour at room temperature, and then their mass, photosynthesis and dark respiration were measured. After this treatment, the gametophores were sprayed with distilled water and allowed to rehydrate in air for 15 h. Then their mass was determined, photosynthesis and dark respiration were measured. After measurement, the gametophores were placed in a dryer (Wamed SUP-100, Poland) until completely dry to determine their dry mass (DM).

The second experiment consisted of periodic flooding of gametophores with distilled water for 1 h, after which photosynthesis and respiration parameters were determined, and then the plant material was transferred to the atmosphere for 15 h. After this time, the gas exchange parameters were determined. After completing these measurements, the plant material was placed in the dryer to completely determine the DM.

Statistical analysis

Statistical analysis was performed using one-way analysis of variance, ANOVA/MANOVA, tests. The significance of difference between means (\pm SE), $n = 5$, was determined with Tukey test at $p = 0.05$. The data was analysed with STATISTICA Data Analysis Software System (StatSoft, Inc., 2018, Version 13.1, www.statsoft.com).

Results

Drying and rehydration

In the control group, photosynthesis intensity for *Polytrichum piliferum* gametophores was $61.3 \mu\text{mol CO}_2 \text{ g}_{\text{DM}}^{-1} \times \text{h}^{-1}$. Drying the plant material for one hour reduced the intensity of photosynthesis to $0 \mu\text{mol CO}_2 \text{ g}_{\text{DM}}^{-1} \times \text{h}^{-1}$. Rehydrating the same material for 15 hours resulted in the restoration of photosynthetic activity to $32 \mu\text{mol g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, which constituted 51% of the initial value (Fig. 2A; Tab. 1).

The dark respiration rate for the control plants was $35.5 \mu\text{mol CO}_2 \text{ g}_{\text{DM}}^{-1} \times \text{h}^{-1}$. After drying the mosses for 1 hour, respiration decreased to $34.0 \mu\text{mol CO}_2 \text{ g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, compared to the control. After subjecting the same gametophores to 15 h of rehydration, the intensity of dark respiration increased significantly to $45.6 \mu\text{mol CO}_2 \text{ g}_{\text{DM}}^{-1} \times \text{h}^{-1}$ and was 28.5% higher than the control value (Fig. 2A; Tab. 1).

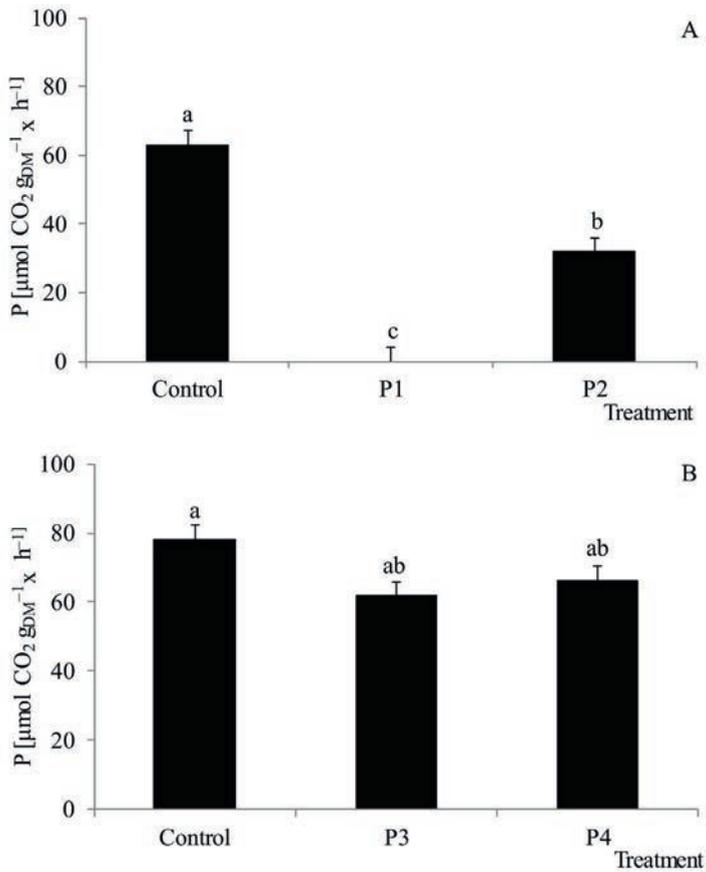


Fig. 2. Changes in photosynthesis intensity (P) in *Polytrichum piliferum* Hedw. gametophores: A: P1 – after 1 h drying at room temperature, P2 – after 1 h drying and 15 h rehydration; B: P3 – after 1 hour of flooding, P4 – after 1 hour of flooding and 15 hours of reoxygenation in the air; mean values (\pm SE) marked with different letters differ significantly according to Tukey test $p = 0.05$

Flooding and reoxygenation

Before flooding *P. piliferum* gametophores, photosynthesis intensity was $78 \mu\text{mol CO}_2 \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$ (control). Hourly (1 h) flooding of plant material reduced photosynthesis to $61.8 \mu\text{mol CO}_2 \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, i.e. 21% relative to the control. In addition, subjecting the plant material to 15 hours of reoxygenation in the air resulted in an increase in photosynthesis intensity to $66.3 \mu\text{mol CO}_2 \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, i.e. its intensity was 15% lower than the initial value (Fig. 2A; Tab. 1).

The intensity of dark respiration in the control sample was $41 \mu\text{mol CO}_2 \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$. After 1 h of flooding the plants, respiration decreased to $37.2 \mu\text{mol CO}_2 \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$ (by 9% compared to the control). After subjecting the same gametophores to air reoxygenation for 15 hours, the intensity of this process increased to $38.0 \mu\text{mol CO}_2 \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$ (by 7% of the initial value) (Fig. 2B; Tab. 1).

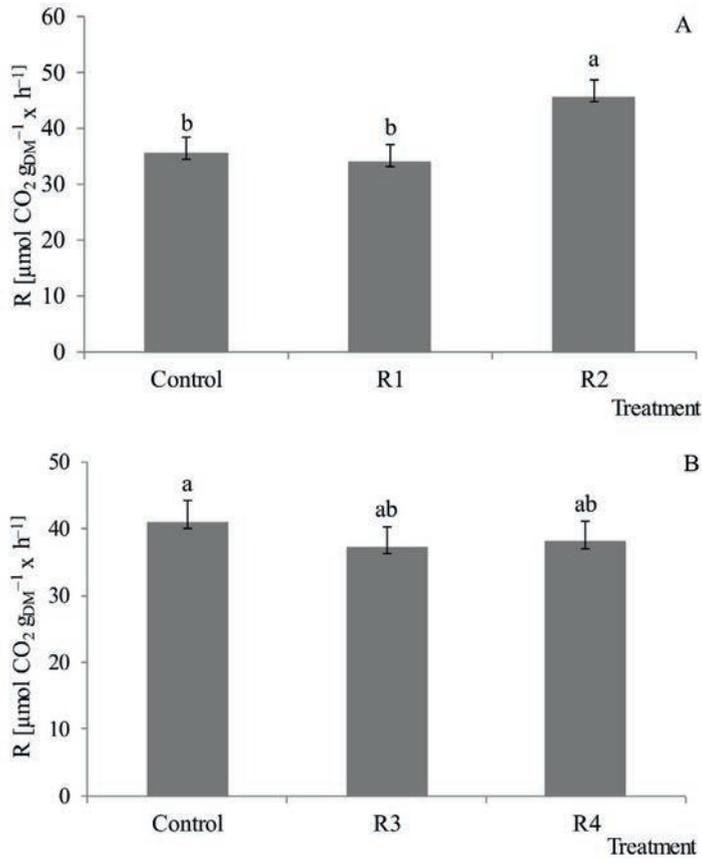


Fig. 3. Changes in dark respiration intensity (R) in *Polytrichum piliferum* Hedw. gametophores: A: R1 – after 1 h drying at room temperature, R2 – after 1 h drying and 15 h rehydration; B: R3 – after 1 hour of flooding, R4 – after 1 hour of flooding and 15 hours of reoxygenation in the air; mean values (\pm SE) marked with different letters differ significantly according to Tukey test $p = 0.05$

Tab. 1. Changes in photosynthesis and respiration processes in *Polytrichum piliferum* Hedw. gametophores during drought and water stress; values expressed in % in relation to the control

Percentage of control	Mosses treatment			
	After 1 hour of drying	After 1 hour of drying and 15 h rehydration	After 1 h flooding	After 1 hour of flooding and 15 h reoxygenation
P	0.00	51.02	79.12	85.44
R	96.01	128.50	91.14	93.25

P – photosynthesis, R – respiration; control – measurement taken at the beginning of the experiment, P1, R1 – after 1 h drying at room temperature, P2, R2 – after 1 h drying and 15 h rehydration, P3, R3 – after 1 hour of flooding, P4, R4 – after 1 hour of flooding and 15 hours of reoxygenation in the air

Discussion

As a solvent, water is an irreplaceable environment for biochemical reactions. It is a substrate for many reactions and a factor that keeps the protoplast in proper physical condition. With only a 10% water deficit, the photosynthetic process was already decreasing due to the reduction of turgor and the automatic closing of stomata. Water is also associated with the transport of organic substances. It is an important temperature regulator in plant tissues, and in the process of photosynthesis it is a source of hydrogen for assimilation force. Dehydration of the green crumb inhibits chlorophyll synthesis and accelerates its degradation. However, plasma hydration has a significant impact on the entire course of respiration (Martim et al., 2009; McElrone et al., 2013; Silva et al., 2014).

Most mosses are very sensitive to changes in water conditions (Rzepka et al., 2003, 2005), dependent on surface water and capillary forces action, which are often supported by setting gametophore leaves (Wójciak, 2003). Mosses belong to poikilohydric plants, i.e. they are characterised by variable hydration. In drought conditions, these plants can dry out completely, but their structure is not completely destroyed (Lou, 2006; Ruibal et al., 2012; Zhou et al., 2011). Increasing the availability of water, e.g. as a result of atmospheric precipitation, causes rapid hydration of their tissues and activates metabolic processes that gradually dried up during drying. Poikilohydric plants are hydrolabile, which means that their water balance can be negative for a long period. This is the result of the low sensitivity of the stomata to dehydration, as only very low environmental humidity causes their gradual closing and limiting of transpiration. The protoplasm of these plants is resistant to significant and rapid fluctuations in water potential (Rock et al., 2009).

Experiments carried out on *Polytrichum piliferum* gametophores have shown that mosses adapt relatively quickly to changing water conditions (Fig. 2–3; Tab. 1). The rate of photosynthesis of gametophores dried for 1 h was $0 \mu\text{mol CO}_2 \text{ g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, and after 15 h of rehydration it constituted 51% of the control sample. The dark respiration rate measured in *P. piliferum*, after 1 h of drying, decreased by 4% of the original value. After 15 h of rehydration, this process increased by 28.5% relative to the control sample. This clearly illustrates a lower sensitivity of the dark respiration process than photosynthesis to a periodic lack of water (Rzepka, 1990). The process of drying and then rehydrating mosses can be repeated several times, without lethal changes to the body (Proctor et al., 2007). One of the properties of mosses that allows them to survive difficult periods of drought is the ability to preserve undamaged ribosomes. This provides the opportunity to quickly regain the ability to synthesise proteins when the cells are rehydrated. It is an ecological adaptive feature not found in other plants because irreversible destruction of the protein synthesis apparatus occurs during drying (Krupa, 1974; Zeng et al., 2002). Another feature of mosses is their relatively high level

of sucrose (~10% of dry mass), which remains constant during dehydration and rehydration (Bewley et al., 1978; Alpert, Oliver, 2002). During rehydration, the moss cells quickly return to homeostasis and become convex, and the cell organelles gradually return to their normal shape and function (Pressel et al., 2006; Proctor et al., 2007).

Dehydration causes general condensation of cell content, fragmentation of the central vacuole system, increased viscosity of the cytoplasm, condensation of chromatin and dense packing of ribosomes (Pressel et al., 2006; Proctor et al., 2007). The plasma membranes of dried cells, e.g. *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr (= *Tortula ruralis*), look like typical lipid bilayer membranes, with scattered endothelial particles. Nuclei, chloroplasts and mitochondria lose their elongated shape and become round or ovate, probably due to the loss of the depolymerised microtubule cytoskeleton (Platt et al., 1993; Ligrone, Duckett, 1996, 1998; Hoekstra et al., 2001). The effects of water deficit are revealed in almost every cellular process. One such response may be the appearance of oxidative stress. Reactive oxygen species are formed, which can trigger reactions leading to damage to cellular structures (Rzepka, 2008). This stress leads, e.g. for lipid peroxidation, to changes in thylakoid structure, inhibition of photosystem activity of PSI and PSII and electron transport chain and inhibition of photosynthesis due to the inactivation of thiol groups of the Rubisco enzyme. Reactive oxygen forms are removed using oxidants, e.g. catalase, peroxidase and superoxide dismutase (Hoekstra et al., 2001; Franca et al., 2007). Under conditions of water deficit, the processes of incorporating carbon are clearly modified, RuBP carboxylase activity is reduced and the incorporation of carbon into organic compounds is decreased. Inhibition of photosynthesis activity is also caused by partially closed stomata. The dark respiration process is less sensitive to periodic lack of water than photosynthesis and continues even when the potential values are low. Experiments carried out on various species of bryophytes capable of withstanding periods of drought prove that the respiration rate, as these organisms are dried, clearly decreases (Krupa, 1974; Rzepka, Krupa, 1996; Rzepka et al., 2001).

In the experiment conducted with *P. piliferum*, flooding with water followed by reoxygenation in the air caused changes in the photosynthesis and the dark respiration processes of gametophores. After 1 hour of flooding, photosynthesis activity decreased by 21% and dark respiration by 9%, compared to the control. After 15 h of reoxygenation in the air, the reduction of photosynthesis had reached approximately 15% and respiration 7%, compared to these processes in the control (Tab. 1). Hypoxia can induce various plant responses (Rzepka, 2008; Rzepka et al., 2003, 2005). Many changes that adapt plants to oxygen deficiency are preceded by the activation or repression of specific genes (McDaniel et al., 2007; Trouiller et al., 2007). According to recent hypotheses, morphological adjustment consists of the development of aerenchyma, whose large intercellular spaces cause the movement of oxygen from shoots to

underground organs and these flooded organs (Kopcewicz, Lewak, 2005). Osakabe et al. (2014) wrote that water stress is an important factor limiting plant growth and productivity. Longer exposure to the stress factor causes weakness and loss of vigour of the body's cells, which in turn increases susceptibility to diseases caused by pests and pathogens. This leads to disturbances in the functioning of the plant and a decrease in its biological value.

The plant cell regains full physiological activity after being saturated with water. The speed of recovery is generally inversely proportional to the rate and intensity of stress, but most mosses regain their normal morphology in a few minutes and rebuild their architecture in 1–2 days (Proctor, 2001; Pressel et al., 2006; Proctor et al., 2007). The experiments carried out here showed that subjecting *P. piliferum* gametophores to water stress causes an imbalance of physiological processes such as photosynthesis and dark respiration. It can be argued that the plant's ability to maintain homeostasis in the circumstances of the stressor or change homeostasis through adaptation determines the resistance of plants to stress and allows them to survive or overcome prolonged stress.

Conclusion

Mosses are poikilohydric organisms and resistant to various environmental stress factors. Tolerance to drying or flooding is a relatively common phenomenon in moss plants. It helps them survive adverse environmental conditions. (i) Drought stress caused complete inhibition of photosynthetic activity of *Polytrichum piliferum* gametophores. However, rehydration for 15 h resulted in the restoration of the photosynthetic activity of the plants. This is in contrast to hypoxia stress, which did not significantly affect photosynthesis or drying. (ii) Dark respiration in the tested mosses was clearly less sensitive to drought stress or hypoxia, compared to photosynthesis. There were slight differences in the activity of dark respiration, compared to the controls. Perhaps, the ability to change homeostasis by adapting, surviving or overcoming adverse living conditions plays an important role. Global climate change causes a rise in temperature, carbon dioxide and variable distribution of atmospheric precipitation. It is these factors that increase the demand for the monitoring and testing, including photosynthesis and dark respiration, of mosses and other plant species in the eco-physiology field.

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Conflict of interest

The author declares no conflict of interest related to this article.

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Abstract

Mosses are convenient organisms for studying the reaction to water stress because they do not have an epidermis, which makes them more sensitive to changes in humidity than most other plants. The aim of the study was to determine the effect of water stress on the course of physiological processes of mosses using *Polytrichum piliferum* Hedw. The present study showed that the action of the abiotic stressor, which is water, adversely affects the photosynthesis and dark respiration processes by reducing their intensity. However, it is worth noting that the respiration process is less dependent on tissue hydration than the photosynthesis, which is clearly demonstrated by the study results. The bryophytes' resistance to stress factors is responsible for the plant's ability to maintain homeostasis under stress conditions. The ability to change homeostasis by adapting, surviving or overcoming adverse living conditions also plays an important role.

Key words: dark respiration, hypoxia, photosynthesis, *Polytrichum piliferum*, rehydration

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Wpływ stresu wodnego na przebieg procesów fizjologicznych u mchów

Streszczenie

Mchy są organizmami dogodnymi do badania reakcji na stres wodny, ponieważ nie posiadają epidermy, przez co odznaczają się większą wrażliwością na zmiany wilgotności niż większość innych roślin. Celem pracy było określenie wpływu stresu wodnego na przebieg procesów fizjologicznych mchów na przykładzie *Polytrichum piliferum* Hedw. Przeprowadzone badania pokazały, że działanie abiotycznego stresora, jakim jest woda, wpływa niekorzystnie na przebieg procesów fotosyntezy i oddychania, poprzez zmniejszenie ich natężenia. Jednak warto zaznaczyć, że proces oddychania jest w mniejszym stopniu uzależniony od uwodnienia tkanek niż proces fotosyntezy, co wyraźnie widać w przeprowadzonych tu badaniach. Za odporność mszaków na czynniki stresowe odpowiada zdolność rośliny do utrzymania homeostazy w czasie działania stresora. Również ważną rolę odgrywa zdolność zmiany homeostazy przez adaptację, przetrwanie albo pokonanie niekorzystnych warunków życiowych.

Słowa kluczowe: oddychanie ciemniowe, hipoksja, fotosynteza, *Polytrichum piliferum*, rehydratacja

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