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Resistance of mosses to drying, measured by the intensity of gas exchange and the content of malate and citrate

Introduction

Water stress can lead to plant dehydration, wilt, and in extreme cases to its complete death. Known as drought, it is one of the many factors limiting the occurrence of plants in the environment. In contrast, drought is an abiotic condition that occurs when plant transpiration is greater than the amount of precipitation supplied. It is closely related to the loss of water from plant tissues and cells. Climatology treats drought as a reduction in the amount of rainfall, which is significantly different from the norm. Weather conditions, such as low air humidity, high temperatures, strong winds make rainfall less effective, resulting in drought (Chojnacka-Ożga, Lorenc, 2019). Drought causes a serious disturbance in the life of plants, especially in those whose capacity to retain water for physiological processes for a long time is limited. Even if the water deficit does not cause the plant's death, it can cause significant morphological and physiological dysfunctions (Vitt et al., 2014).

Mosses are among the most primitive land plants. In contrast to vascular plants which have developed tissues for transportation and retention of water, mosses retained simple morphology and anatomy (Charron, Quatrano, 2009). Leafy gametophytes have properties that indicate their adaptation to terrestrial living conditions by developing efficient, capillary-driven water transport for maintenance of growth, efficient photosynthesis and reproductive processes (Oliver, 2009). However, poorly specialised moss leaves, often made of a single layer of cells, do not always allow to survive in conditions of water deficit. Therefore, mosses generally only tolerate some degree of cellular dehydration. After removing the liquid water from the cell surface, they quickly lose turgor and balance with the water potential of the air. This is common in many bryophytes and most species have developed different ways of surviving. For example, mosses avoid water stress by colonising wet or heavily shaded ecological niches, growing in short, dense

clusters that reduce water evaporation (Proctor, 1980; Rice et al., 2001). The evolution of mechanisms to withstand water stress presumably arose from individuals uniquely suited to occupy the outer limits of mesic niches (Olivier et al., 2005; Rzepka, 2008). Another example is the fact that many mosses have developed the ability to survive even completely drying out, returning to vital functions within a few hours of rehydration. As poikilohydric organisms, they are generally considered to be relatively resistant to desiccation (Proctor, 1990; Proctor, Pence, 2002). This allows them to survive, both short and long periods of dehydration to a level at which the entire mass of the water is lost from the cells (Oliver, 2009).

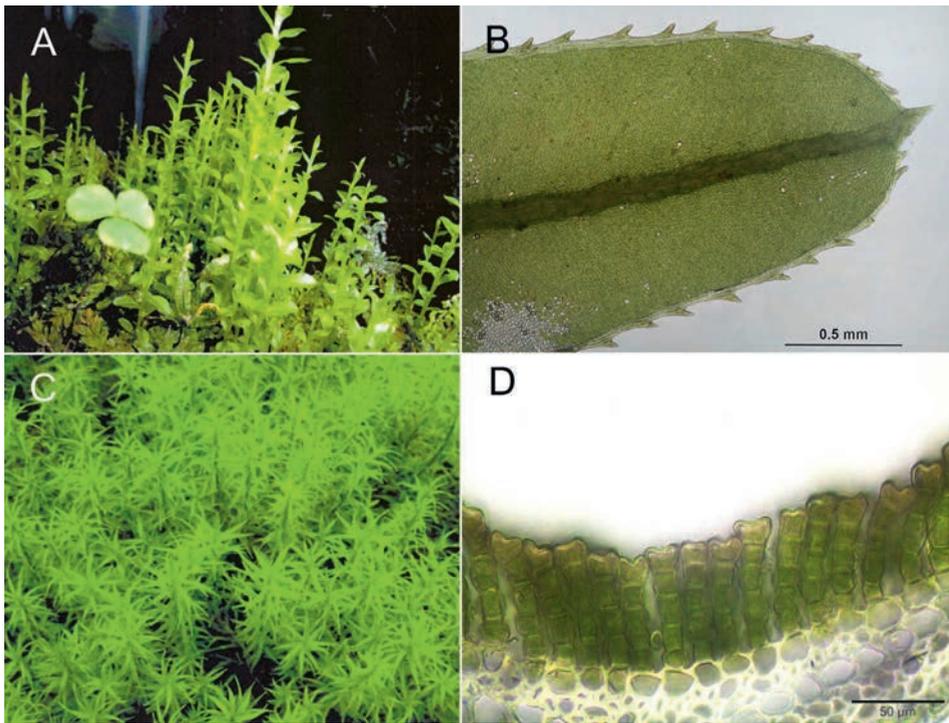


Fig. 1. *Plagiomnium undulatum* (Hedw.) T.J.Kop.: A – gametophyte appearance (Photo. W. Starmach), B – leaf fragment (Source: <https://commons.wikimedia.org/wiki/>); *Polytrichum commune* Hedw.: C – gametophyte appearance (Photo. W. Szarek), D – leaf with lamellas (Source: <https://commons.wikimedia.org/wiki/>)

Plagiomnium undulatum (Hedw.) T.J.Kop. = *Mnium undulatum* Hedw. (hart's-tongue thyme-moss) Plagiomniaceae T.J.Kop. family, is orthotropic moss, with creeping stolons forming large, loose and vivid green turf (Fig. 1A). It has stems up to 15 cm long, towards the top with increasing side branches. Its leaves are longitudinally lingual, strongly folded transversely, long running along the stem, rounded at the top, with a short, sharp tip and with sharp single teeth along the entire edge (Fig. 1B). Their rib is

thick, reaching the top of the leaf. There are several oval-shaped capsules on one stem, growing on reddish sets. The operculum is with a short spout. This species grows in wet deciduous forests – riparian forests and hornbeam forests – as well as on humus (Szafran, 1961; Düll, Düll-Wunder, 2012; Plášek, 2013).

Polytrichum commune Hedw. (common haircap) Polytrichaceae Schwägr. family, is an orthotropic moss that creates loose, dark green turf (Fig. 1C). Its stems are single and reach up to 20–30 cm in length (sometimes up to 40 cm). The leaves (1–2 cm long) have a sheath-like base and a lanceolate leaf blade, protruding from the stem. The edge of the leaves from the top almost to the base is sharply toothed. The leaf blade is dark green with square cells. The vaginal part of the base of leaf is white, with elongated cells (up to 10 times longer than wider). The rib is wide, with sharp serrations on the dorsal side, and shortly protruding at the top as a serrated, brown spike. Up to 70 longitudinal lamellas appear on the ventral side of the rib (Fig. 1D). The upper lamella cell is larger than the others, with a deep crescent-shaped furrow. The capsule is four, five or hexagonal, with a well-developed neck, with yellow-red, long (up to 10 cm) seta. The calyptra is dense, golden yellow hairy (remnants of the archegonium). Most often, this moss grows in peat bogs, both in the lowlands and in the mountains. It also occurs in damp forests or along the banks of streams (Szafran, 1961; Ignatov, Ignatova, 2003; Plášek, 2013).

Bryophytes belong to the homoiochlorophyllous groups and cannot maintain constant internal water content by regulating water loss (Tuba et al., 1998; Proctor et al., 2007). Previous studies on the physiological level do not fully explain the mechanisms of drought tolerance in bryophytes. Therefore, the aim of this experiment was to determine the relationship between the stressor (drought) and changes in the intensity of relative photosynthesis (1), respiration (2) and the content of malate and citrate (3) in two species of mosses – *Plagiomnium undulatum* (Hedw.) T.J.Kop. and *Polytrichum commune* Hedw.

Material and methods

Plant material

The gametophores *Plagiomnium undulatum* and *Polytrichum commune* were used in the research. The plant material was collected in southern Poland, near Krakow (Rybna, 50°03'04"N 19°38'50"E) and Tarnów (Pleśna, 49°55'19"N 20°56'43"E). Both moss stands were remote from communication routes.

The cultivate conditions

The collected moss turf was stored in 1 dm³ glass aquariums, in air-conditioned growth chambers (Fig. 2A).

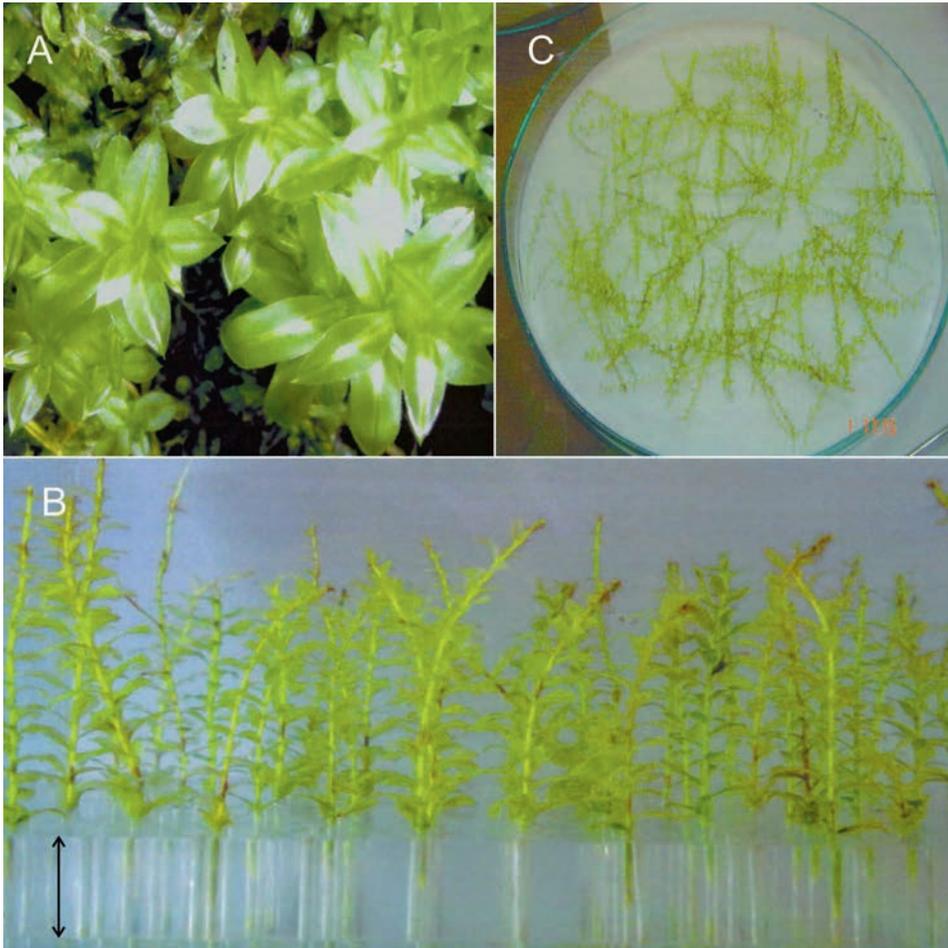


Fig. 2. Gametophores of *Plagiommium undulatum* (Hedw.) T.J.Kop.: A – placed in a glass vessel, B – placed in a plexiglass plate, C – dried on plates with filter paper (Photo. W. Szarek)

The density of the quantum stream used here in the PAR range was $70 \mu\text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$ (Fluora-Osram, Poland), with a photoperiod of 12 h day/12 h night, with temperature $15^{\circ}\text{C} (\pm 2^{\circ}\text{C})$ and relative air humidity from 70 to 100%. Mosses were watered regularly with distilled water. The digital hygrometer PWT-221 (Elmetron, Poland) was used to measure the relative air humidity. Quantum flux density in the PAR range was measured with a radiometer (LI-COR model Li-189, USA).

Course of experiments

Moss gametophores of equal length (about 4–5 cm in the case of *Plagiommium undulatum* and 1.5–2 cm in the case of *Polytrichum commune*) were rinsed with distilled water

and dried with filter paper. Then they were placed evenly in the holes of the plexiglass plates, in glass vessels with a volume of 1 dm³ (Fig. 2B).

After the control measurement of photosynthesis and respiration, the gametophores of both species were subjected to the drought. For this aim, leafy moss stalks were placed in a petri dish lined with three layers of filter paper discs, kept in air with a relative humidity of 30–40% until a loss of about 50% relative water content (Fig. 2C). The intensity of the luminous flux reaching the moss leaves during drying was 80 $\mu\text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$, and the temperature was 20°C ($\pm 1^\circ\text{C}$). Then, the gametophores were rehydrated, placed in a plexiglass plate and kept in glass aquariums in a growth chamber for 24 h. After this time, further measurements were made. Preparation of moss gametophores for malate and citrate measurements looked similar to photosynthesis and respiration measurements. Additionally, before measuring the malate content, after a period of darkness, the vessel with the gametophores was darkened and placed in the growth chamber.

Gas exchange

The infrared gas analyser ADC-225 MK-3 (Great Britain) was used to measure the intensity of photosynthesis and respiration of the moss gametophores in a closed system. The entire closed system consisted of: an assimilation chamber, a water jacket and an air humidifying system, and its volume was 0.644 dm³. The intensity of the light that reached the gametophores was 100 $\mu\text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$. The temperature inside the assimilation chamber was 25°C. Measurements were carried out in air with 21% oxygen. KOH scrubbers, together with the control kit, made it possible to obtain various concentrations of carbon dioxide. The carbon dioxide concentration was controlled using an ADC-225 MK-3 gas analyser. The CO₂ concentration during the measurement was 300–500 $\mu\text{mol} \times \text{mol}^{-1}$ in a closed system. In contrast, the relative humidity was about 75%, thanks to the air being passed through a scrubber with distilled water.

Measurement of malate and citrate

A specific sample of plant material (about 100–150 mg) was triturated with distilled water in a weight ratio of 1:4 for *Plagiomnium undulatum* and 1:6 for *Polytrichum commune*, and then centrifuged for 5 minutes at 5000 g at 4°C (HERMLE Labortechnik Z 36 HK, Germany). The content of malate and citrate in the test sample was measured at the end of the day (around 5:00 pm) and at the end of the night period (around 7:00 am).

In order to determine the malate concentration, 500 μl of the buffer (0.6 M glycylglycine, 0.1 M L-glucamate pH 10), 100 μl of NAD⁺ (Sigma), 5 μl of GOT (Roché), 745 μl of redistilled water, 25 μl of the test sample and 5 μl of malate L-dehydrogenase, were mixed in the spectrophotometric cuvette (MDH, Roché). For the determination

of citrate, the following were mixed in the spectrophotometric cuvette: 180 μl of the buffer (0.6 M glycylglycine, 0.6 mM ZnCl_2 pH 7.8), 25 μl of NADH, 10 μl of MDH/LDH (Sigma), 331 μl of redistilled water, 25 μl of the test sample and 5 μl of citrate lyase.

The concentration of malate and citrate was determined spectrophotometrically (CECIL 9500, Great Britain), according to the Möllering method (1985), at the wavelength $\lambda = 340$ nm, at room temperature. The concentration of malate and citrate was expressed as the difference, according to the following formulas:

$$(\Delta) \text{ malate } (\mu\text{M}) = (\text{malate})_{\text{night}} - (\text{malate})_{\text{day}} \quad (1)$$

$$(\Delta) \text{ citrate } (\mu\text{M}) = (\text{citrate})_{\text{night}} - (\text{citrate})_{\text{day}} \quad (2)$$

Statistical analysis

The experiment was carried out in 3 repetitions. The significance of differences between mean values (\pm SE) were analysed by the parametric test using the Duncan's test ($p \leq 0.05$) in Statistica 13.0 for Windows.

Results

Changes in the intensity of gas exchange

The drying of the gametophores of both moss species to the loss of about 50% of water resulted in changes in the intensity of gas exchange (Fig. 3, 4). In the case of *Polytrichum commune*, an increase in the value of photosynthesis by $16.45 \mu\text{mol CO}_2 \times \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$ was observed, which was a difference of 21% compared to the control sample. Conversely in *Plagiomnium undulatum* – a reduction in the intensity of photosynthesis by $30.74 \mu\text{mol CO}_2 \times \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$ was shown here, which was a 25% difference in efficiency compared to the control.

The respiration rate of gametophores subjected to the stress of drying and rehydration decreased in both moss species, compared to control. This parameter in *P. commune* was $8.32 \mu\text{mol CO}_2 \times \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, and in *P. undulatum* was $16.13 \mu\text{mol CO}_2 \times \text{g}_{\text{DM}}^{-1} \times \text{h}^{-1}$, which constituted 18% and 15%, respectively, in relation to the control values.

Changes in the content of malate and citrate

As a result of the conducted experiments, differences in the content of malate in the leaves of both species of mosses and between night and day, after drying and rehydration of the leaves, were found, compared to the control (Tab. 1; Fig. 5).

In the case of the control sample in *P. commune*, the difference was $1.86 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$. In the test sample, this value was significantly higher – $3.28 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$. In *P. undulatum*

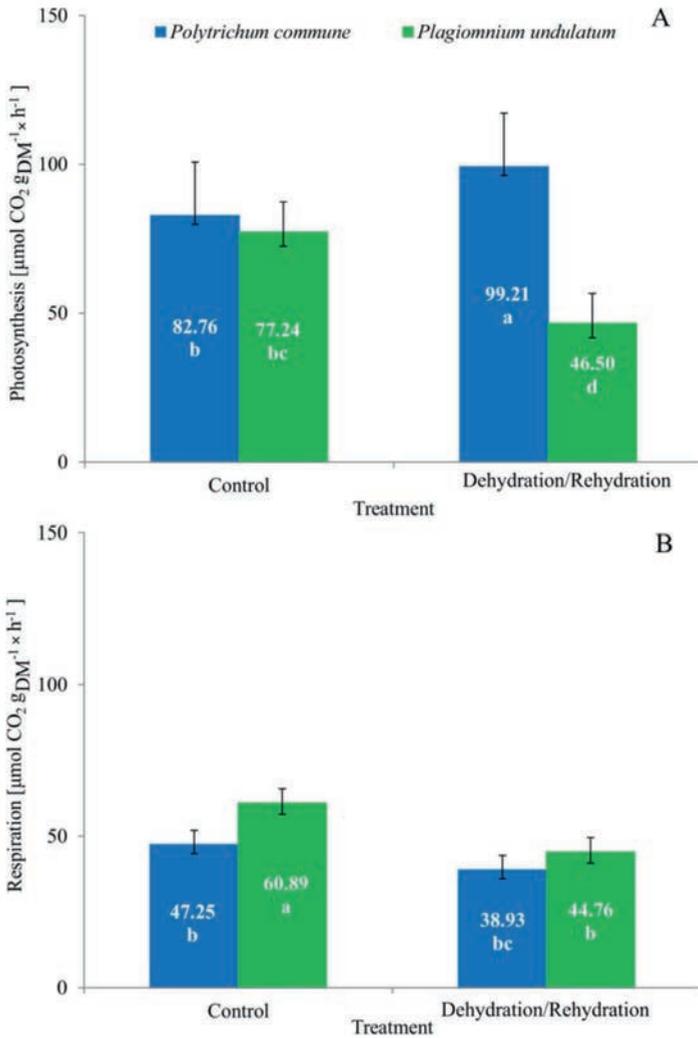


Fig. 3. Changes in the intensity of photosynthesis (A) and respiration (B) in gametophores of the *Plagiommium undulatum* (Hedw.) T.J.Kop. and *Polytrichum commune* Hedw., caused by dehydration and rehydration; mean values of 3 replicates (\pm SE), data marked with different letters differ significantly according to Duncan's test at $p \leq 0.05$

there was clearly greater accumulation of malate in the dark period. The difference between night and day for the control sample was $9.60 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$. When *P. undulatum* gametophores were dried to a loss of 50% fresh mass and then rehydrated, the difference in malate concentration between night and day increased compared to the control sample ($10.55 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$). In relation to the control, drought stress increased the malate concentration in *P. commune* by $1.42 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$, that is approximately 76%, while in *P. undulatum* – $0.95 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$, that is, approximately 10%.

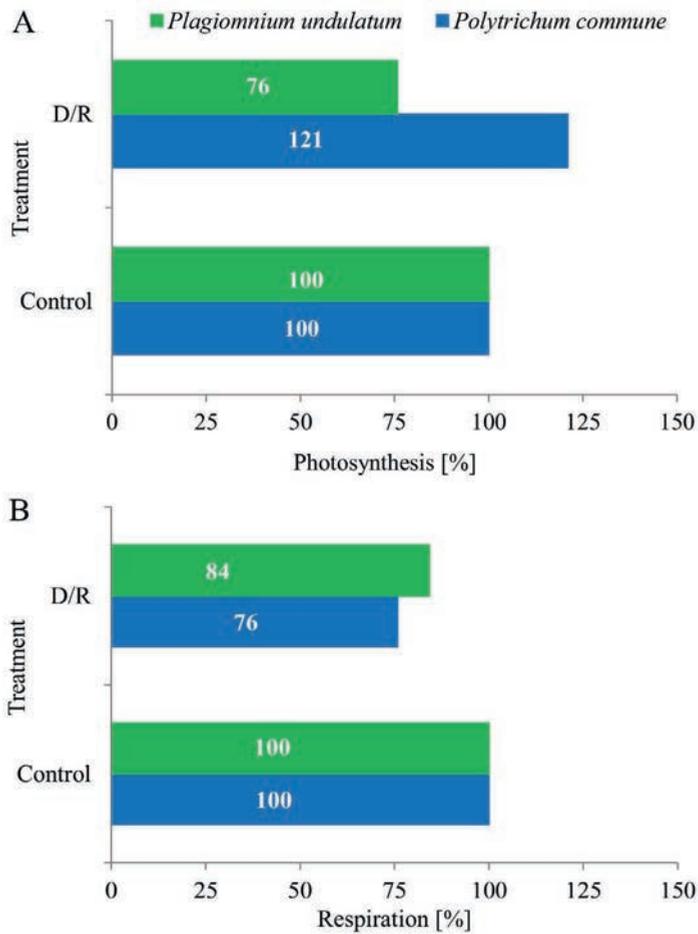


Fig. 4. Percentage changes in the intensity of photosynthesis (A) and respiration (B) in the gametophores of *Plagiomnium undulatum* (Hedw.) T.J.Kop. and *Polytrichum commune* Hedw. caused by dehydration and rehydration (D/R); mean values of 3 replicates (\pm SE), data marked with different letters differ significantly according to Duncan's test at $p \leq 0.05$

The analysis of citrate content showed differences in its concentration in the leaves of *P. commune* and *P. undulatum*, between night and day, between the control and the experimental sample (Tab. 1, Fig. 5). In *P. commune*, in the control sample, this difference was $3.36 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$. This value was higher in the test performed after drying and rehydration – $4.18 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$. In *P. undulatum* the differences in citrate content between night and day in the samples taken were smaller in comparison to *P. commune*. It reached the values of $1.75 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$ for the control sample and $1.45 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$ for the sample after drying and repeated rehydration. Dehydration and rehydration increased the amount of citrate in *P. commune* by $0.81 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$, which was 25% of

the control value. In *P. undulatum* there was a reduction in the amount of citrate by $0.32 \mu\text{M} \times \text{g}_{\text{FM}}^{-1}$, which was 21% compared to the control sample.

Tab. 1. Changes in the concentration of malate and citrate in the leaves of *Plagiomnium undulatum* (Hedw.) T.J.Kop. (A) and *Polytrichum commune* Hedw. (B), measured at the end of night and day, due to dehydration and rehydration; mean values of 3 replicates (\pm SE), data marked with different letters (within one species) differ significantly according to Duncan's test at $p \leq 0.05$

Treatment	Malate [$\mu\text{M} \times \text{g}_{\text{FM}}^{-1}$]					
	Day (17:00)		Night (7:00)		(Δ)	
	A	B	A	B	A	B
Control	16.70 b ± 3.90	20.70 b ± 0.70	26.30 a ± 6.50	22.56 a ± 0.47	9.60 b ± 2.67	1.86 d ± 0.23
Dehydration/ Rehydration	16.02 b ± 7.71	20.18 b ± 0.84	26.57 a ± 9.82	23.46 a ± 0.91	10.55 a ± 2.67	3.28 c ± 0.07
	Citrate [$\mu\text{M} \times \text{g}_{\text{FM}}^{-1}$]					
Control	10.55 b ± 1.27	11.85 b ± 0.64	12.30 a ± 1.67	15.21 a ± 0.73	1.75 c ± 0.41	3.36 b ± 0.09
Dehydration/ Rehydration	10.98 b ± 1.81	11.61 b ± 0.78	12.41 a ± 2.69	15.79 a ± 1.36	1.43 cd ± 0.87	4.17 a ± 0.57

Note: (Δ) – malate or citrate content measured as the concentration difference between the end of night and day

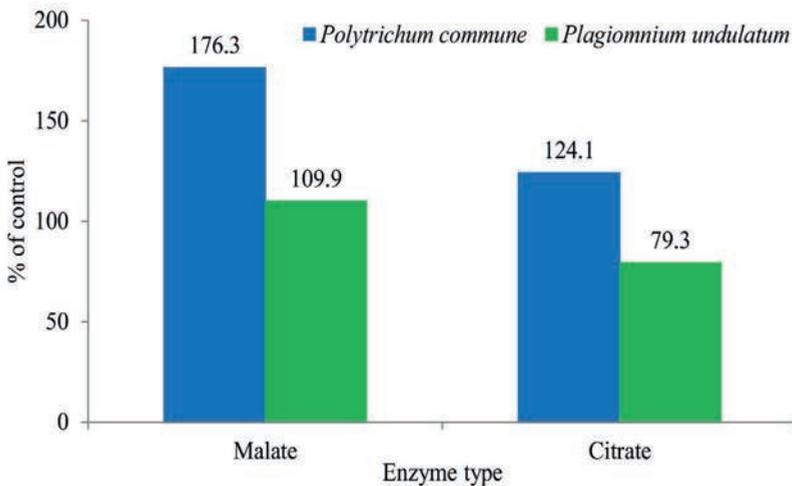


Fig. 5. Changes in the concentration of malate and citrate, expressed in % of control, in leaves of *Plagiomnium undulatum* (Hedw.) T.J.Kop. and *Polytrichum commune* Hedw. measured at the end of the night and day, due to dehydration and rehydration

The proper functioning of mosses in a natural environment depends on many external factors (Rzepka, Krupa, 2008; Możdżeń, 2019). Access to water is a particularly important parameter in land conditions. A slight water deficit can cause significant changes in metabolism and in the biochemical transformation occurring in moss cells, which were already mentioned in the introduction (Green et al., 2011; De Carvalho et al., 2014; Romańska, 2020).

Mosses have the ability to completely dry out by balancing the internal potential of water with extremely dry air and resume normal functioning when rehydrated (Alpert, 2000). Desiccation tolerance has been experimentally confirmed in over 200 species of mosses (Wood, 2007). Biological soil crusts are frequently subjected to cyclical desiccation-rehydration events and mosses have developed unusual constitutive and inducible desiccation tolerance mechanisms (Wood, 2007; Zheng et al., 2011; Li et al., 2014). Leafy stalks of mosses quickly balance with the potential of the surrounding water and can usually be fully hydrated or dry and metabolically inactive. When, the time required to recover from desiccation increases, the degree of regeneration decreases with the length of drying (Proctor et al., 2007).

In the present experiment it was shown that the *Plagiomnium undulatum* and *Polytrichum commune* gametophores reacted differently to dehydration and rehydration of cells. (Fig. 3, 4; Tab. 1). *P. commune* showed less changes in metabolic activity due to the stressor than *P. undulatum* (Fig. 3, 4). Both species regenerated very quickly upon rehydration. The photosynthesis process was much more sensitive to slight disturbances in the water balance than dark respiration. The reaction to partial dehydration is to reduce photosynthesis, while periodically increasing the respiration process (Krupa, 1974). This kind of response could be due to the fact that mosses are evergreen and perennial plants that show seasonal changes in metabolic activity related to the variation in temperature and water relations throughout the year (Rzepka, 2008). In mosses, full photosynthesis, respiration and protein synthesis activity is restored within minutes and sometimes one or two hours; it may take 24 hours or more to activate the cell cycle, food transport and rebuild the cytoskeleton (Pressel et al., 2006; Proctor et al., 2007). The time needed to reactivate the photosynthetic process depends largely on the amount of water lost, the dehydration time and the natural conditions in which the species lives. Many mosses respiration intensity increases over time after rehydration, and eventually reaches a value similar to that prior to dehydration (Krupa, 1974).

In addition to the physiological tolerance to drying, mosses have anatomical and morphological features that allow you to effectively combat drought (Vitt et al., 2014). Therefore, it can be assumed that the differences in the response of the studied mosses to the stress of drought could result from the different shape, structure, arrangement

of the leaflets and the heterogeneous number and type of cells that build them (Pressel et al., 2006). In some species of moss, the leaves are sharpened and positioned laterally and overlap along the edges. This may suggest that the capillary movement of water occurs from the base to the top of the plant (Stark et al., 2017). At the narrower, more closed system leaves, reduces the rate of evaporation of water from the cells. Therefore, short periods of drought are better tolerated by mosses. Other mosses have single-layer, symmetrically arranged leaves, growing from the stalks attached to the ground with a densely branched system of rhizoids. In this case, the water may be held in capillary spaces between individual gametophores or their elevations on the substrate. Some mosses create tightly intertwined, while others form loosely layering turf, which also protects against water loss (Vitt et al., 2014).

Anatomically, the leaflets of *P. commune* are more diverse than *P. undulatum*. The *P. commune* has lamellas, composed of a series of cells arranged along the rib of the leaf, with apical cells devoid of chloroplasts and with thickened walls (Szafran, 1963) – Fig. 1D. Often the outer part of the thickened wall is warty, which protects against water loss from the remaining lamella cells or acts as a light filter. In this case, the presence of rows of lamella cells next to each other on the leaf surface determines the increase of the assimilation and the gas exchange areas (Krupa, 1974; Rzepka et al., 2005; Rzepka, 2008). Whereas *P. undulatum* has a single-layer leaf blade with a multi-layer rib, and the upper surface of the leaf is smooth (Szafran, 1961, 1963) – Fig. 1B. The lack of anatomical structures in the leaves, protecting the assimilation organ against water loss, makes their metabolic activity dependent on water conditions in the environment. This diversity in the anatomy of the leaflets plays an essential role in photosynthetic production, closely related to water management. The differences in the structure of the leaflets are most often related to qualitative changes and are associated with a different assimilation surface and the size of the leaf blade. Probably the structural diversity of moss leaves is an expression of evolutionary trends and their adaptation to terrestrial living conditions (Krupa, 1974). This is one of the many factors responsible for the different reactions in photosynthetic and respiration activity in the analysed mosses.

Differences in the gas exchange of *P. undulatum* and *P. commune* gametophores subjected to dehydration and rehydration, could also result from changes in the activity of malate and citrate (Table 1; Fig. 5). Malate is involved in processes related to the biosynthesis of organic compounds, energy transformation and mineral nutrition. It plays an important role as a factor regulating photosynthesis and glycolysis. The concentration of citrate is related to the synthesis and accumulation of ATP (Rzepka, 2008). Mosses have developed various systems to counteract water loss as previously mentioned (Olivier et al., 2005). Under stress, they show the ability of expression of LEA proteins, high content of non-reducing sugars and effective antioxidant and photo-protection,

are at least partly constitutive, allowing survival of rapid drying, but changes in gene expression resulting from mRNA sequestration and alterations in translational controls elicited upon rehydration are also important to repair processes following re-wetting (Bewley et al., 1978, 1993; Proctor et al., 2007). The results obtained in this experiment suggest that changes in the concentration of malate and citrate in mosses under stressful conditions could be an element of an adaptation strategy to water deficit and allowed for high plasticity of changes in metabolism (Rut et al., 2010).

Gabriel et al. (2005) described the tolerance to drying out in bryophytes as a reversible plastic feature. Even drying and rehydrating a few times does not cause any serious changes in the functioning of the whole organism (Krupa, 1974; Mayaba et al., 2001). Dehydration tolerant mosses can survive in dry atmospheres – with 50% and lower humidity values (Alpert, Oliver, 2002; Wood, 2007). Many species are able to withstand drying to a water content of 5–10% of their dry mass and return to normal metabolism and growth when rehydrated (Alpert, 2006). Such a way of surviving drought probably depends on: the speed of drying the plants, the relative water content of the surrounding environment and the drying time (Green et al., 2011; Stark, Brinda, 2015; Brinda et al., 2016). High resistance to drying of mosses and their ability to regenerate physiological processes after rehydration is a characteristic feature that distinguishes them from vascular plants. The lack of mechanisms protecting them against excessive water loss allows us to assume that there are physiological adaptations to the changing water content in cells (Krupa, 1974). The resistance of plants on the stress factor determines the plasticity of the cellular structures resulting from genetic conditions, the body's ability to repair damage caused and the ability to adapt to the changing conditions of stress (Levitt, 1980; Bohnert et al., 1995).

Conclusion

The results of the experiment showed that drying to 50% of the relative water content and then rehydration of the *Plagiomnium undulatum* and *Polytrichum commune* gametophores affected changes in the daily activity of gas exchange and the content of malate and citrate.

(1, 2) *P. commune* responded to the stressor to a lesser extent than *P. undulatum*. The photosynthesis process was much more sensitive to changes in the amount of water than respiration.

(3) Changes in the content of malate and citrate indicated a close relationship between cell hydration and their metabolic efficiency. This reaction was specific and depended on the species and anatomical and morphological structure of moss leaves.

Acknowledgments

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Conflict of interest

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

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Abstract

Desiccation tolerance, the ability to lose virtually all of its free intracellular water and then restore normal function when rehydrated, is one of the most remarkable features of bryophytes. The aim of the study was to determine the resistance of two species of *Plagiomnium undulatum* (Hedw.) T.J.Kop. and *Polytrichum commune* Hedw. to drying to 50% relative water content of the air and rehydration. Changes in the intensity of photosynthesis and respiration, as well as the content of malate and citrate in leafy moss stems were analysed. *P. commune* gametophores showed greater resistance to drought stress than *P. undulatum*. In both species, photosynthesis was much more sensitive to drought than respiration. Changes in the content of malate and citrate indicated a high plasticity of moss metabolism in conditions of water shortage and may be one of many important elements of the adaptation strategy to water deficit. The reactions of the tested mosses to dehydration and rehydration confirmed their adaptation to specific land conditions.

Key words: dehydration and rehydration, enzymatic activity, photosynthesis, respiration

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Odporność mchów na wysychanie, mierzona intensywnością wymiany gazowej oraz zawartością jabłczanu i cytrynianu

Streszczenie

Tolerancja na wysychanie, czyli zdolność do utraty praktycznie całej wolnej wody wewnątrzkomórkowej, a następnie przywrócenia normalnego funkcjonowania po nawodnieniu, jest jedną z najbardziej niezwykłych cech mszaków. Celem eksperymentu było określenie odporności dwóch gatunków *Plagiomnium undulatum* (Hedw.) T.J.Kop. i *Polytrichum commune* Hedw. na wysuszenie do 50% względnej zawartości wody w powietrzu i ponownemu uwodnieniu. Przeanalizowano zmiany intensywności fotosyntezy i oddychania oraz zawartości jabłczanu i cytrynianu w ulistnionych łodyżkach mchów. Gametofory *P. commune* wykazały większą odporność na stres suszy niż *P. undulatum*. U obu gatunków proces fotosyntezy był znacznie bardziej wrażliwy na działanie suszy niż oddychanie. Zmiany w zawartości jabłczanu i cytrynianu wskazywały na dużą plastyczność metabolizmu mchów w warunkach niedoboru wody. Mogą one być jednym z wielu ważnych elementów strategii przystosowawczej do deficytu wody. Reakcje badanych mchów na wysuszenie i ponowne

uwadnianie potwierdziły ich adaptację do specyficznych warunków lądowych.

Słowa kluczowe: wysuszenie i uwadnianie, aktywność enzymatyczna, fotosynteza, oddychanie

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His research interests are related to the response of plants, especially mosses, to abiotic and biotic stress factors. The analyses include changes in selected metabolites, as well as the intensity of photosynthesis, respiration, transpiration, stomatal conductance and chlorophyll a fluorescence.

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