



UDC: 582.32:581.527.7+631.484

## WATER EXCHANGE OF THE FOREST ECOSYSTEMS EPIGEIC BRYOPHYTES DEPENDING ON CHANGES OF THE STRUCTURAL AND FUNCTIONAL ORGANIZATION OF THEIR TURFS AND THE INFLUENCE OF THE LOCAL GROWTH ENVIRONMENTAL CONDITIONS

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Lobachevska, O., & Karpinets, L. (2024). Water exchange of the forest ecosystems epigeic bryophytes depending on changes of the structural and functional organization of their turfs and the influence of local growth environmental conditions. *Studia Biologica*, 18(2), 139–156. doi:[10.30970/sbi.1802.766](https://doi.org/10.30970/sbi.1802.766)

**Background.** Moss cover plays a decisive role in increasing soil moisture in forest ecosystems. Bryophytes with high water content can significantly reduce water evaporation from the soil surface and retain it for an extended time. Under the influence of environmental conditions, mosses change the shape and organization of moss turfs thus regulating the efficiency of moisture absorption and retaining. Therefore, it is essential to establish the differences in the water exchange strategy of epigeic dominant moss species depending on the environmental conditions in reserved and anthropogenically disturbed forest ecosystems.

**Materials and Methods.** The research was carried out using the dominant epigeic, typical forest moss species *Plagiomnium cuspidatum* (Hedw.) T. J. Kop. and *P. ellipticum* (Brid.) T. J. Kop. from experimental plots of forest ecosystems, which differed in water and temperature regimes and light intensity. We determined the peculiarities of the influence of adaptations of moss turf morphological structure, individual plant's physiological functional traits, and their metabolic osmoprotective changes based on the leading indicators of their water exchange (coefficients of water retention, water recovery, and drought resistance).

**Results.** It was established that humidity and light intensity in forest ecosystems changed the shape and organization of moss turfs, i.e., the height of individual shoots in the turf and the density and size of leaves. The predominance of the generative or vegetative type of moss reproduction led to significant changes in the morphology of



shoots, physiological functional traits of plants, and the density of the turf structure, which was regulated due to the increase in airstream turbulence and wind penetration, absorption and evaporation of water. The hydration of moss tissues was maintained due to the rise in the total carbohydrate content as well as the soluble fraction content primarily in the vegetative shoots.

**Conclusions.** Mosses adapted to variable microclimatic conditions of forest ecosystems due to endohydricity and water retention mechanisms in external capillary spaces, i.e., changes in height, shape, and density of turfs, shoot morphology, various ratios of fertile to sterile plants, and their physiological functional traits. The internal regulation of water potential of cells was ensured by an increased concentration of osmoprotectors (carbohydrates, primarily their soluble fraction).

**Keywords:** water retention, water recovery, drought resistance, moss *Plagiomnium cuspidatum*, *P. ellipticum*, turf structure, osmoprotectors

## INTRODUCTION

Since forest ecosystems have suffered from drought in recent years (Eldridge *et al.*, 2020b; Senf *et al.*, 2020), while mosses are increasingly threatened by global warming (He *et al.*, 2016), it is of utmost importance to investigate the hydrologic impact they have on their habitats. Furthermore, the reduction of bryophyte diversity changes ecosystem structure and function, nutrient cycling, and carbon balance. Climate change is now recognized as one of the biggest threats to nature and biodiversity and the main driver of ecosystem change and degradation, which will probably result in potentially irreversible changes in various habitats (Hooper *et al.*, 2012; Eldridge *et al.*, 2020a; Senf *et al.*, 2020).

Bryophytes are harbingers of changes and indicators of conditions in forest ecosystems, not only based on changes in their genus and species affiliation but also in the ecological and biomorphological structure and indicators of metabolic processes, which may indicate specific mechanisms of adaptation of the organism in unstable environmental conditions (Müller *et al.*, 2016). Poikilohydric bryophytes are a group of plants sensitive to the influence of habitat conditions, which shows indicators different from vascular plants for early prediction of changes in the natural environment.

Moss cover plays a defining role in soil moisture gain in forest ecosystems since the rate of its evaporation is lower with bryophytes than with grasses, and they can retain a large amount of water during wet periods (Levinsh *et al.*, 2020; Ah-Peng *et al.*, 2017). Primarily during evaporation, a considerable amount of moisture is transported from bryophytes to the soil surface. Furthermore, mosses with high water content can significantly reduce evaporation from the soil surface since they often retain water for long periods (Oishi, 2018).

Usually, most bryophytes grow not as individual plants but in groups, demonstrating clonal or colonial life forms (Bates, 1998; Glime, 2019). Supposedly, the growth and morphology of individual plants in life forms are genetically determined. In that case, their structural organization results from natural selection under certain environmental conditions. It shows considerable plasticity under the influence of changes in ecological factors and the strategy of plant life-cycle (Bates, 1998; Rossi *et al.*, 2001). The development of life forms provided poikilohydric bryophytes with numerous advantages for existence on land: it compensated for the lack of specialized anatomical structures, which

are typical for vascular plants, and provided essential functions, i.e., the mechanical stability of turf structure, water transport, and retention. Depending on the type of water transport, there are two types of bryophytes: ectohydric and endohydric. It is essential to note that both methods of water movement frequently occur in the same plant. Internal transport accounts for  $\frac{1}{3}$  of plant conductance and prevails only when the moisture content is not less than 90 % (Glime, 2019; Proctor, 2008). Nevertheless, most mosses are ectohydric plants characterized by external water transport through capillaries on the shoot surface. Such mosses usually have thin, non-waxy cuticles and can absorb water with the entire surface (Glime, 2019). Typical endohydric mosses are mainly characterized by internal water transport through conducting tissues since surfaces with waterproof cuticles reduce their ability to absorb water through leaves (Proctor, 2008). It is vital for mosses to maintain moisture inside the turf and on the plant's surface as long as possible (Vitt *et al.*, 2014). Depending on moisture conditions, mosses can adapt to environmental changes, altering the shape and organization of moss turfs for sufficient water supply. The shape of moss turf significantly affects its moisture content when interacting with wind, contributing to a more efficient catching of water droplets and their distribution to neighboring shoots (Thielen *et al.*, 2021). Water loss control strategies of mosses can be expressed at different morphological and anatomical structural levels, from the cellular to the community level (Rice & Schneider, 2004; Glime, 2019). However, much research is still needed to understand the importance of different levels and their role in controlling water loss rates in mosses, i.e., the structural characteristics of life forms, surface area to volume ratio, the influence of shoots' location on the degree of capillary integration (Rice, 2012), or the forms' surface roughness, arrangement of leaves and presence of wax coating and hyaline cells in them. It is also essential to determine the specificity of the community level (Kürschner, 2004; Zotz & Kahler, 2007). The study of the relationship of these features provides insights into bryophytes' water exchange strategy and enables assessment of the function of mosses in the water balance of forest ecosystems, i.e., precipitation interception and reduction of soil water evaporation (Rice & Schneider, 2004; Rice, 2012; Oishi, 2018; Glime, 2019).

Considering this, the study aimed to understand the adaptive features of the morphological structure of turfs and physio-biochemical reactions of dominant epigeic species of mesophytic *Plagiomnium cuspidatum* (Hedw.) T. J. Kop. and hydrophytic *P. ellipticum* (Brid.) T. J. Kop. mosses and reveal the differences in their water exchange indices under the influence of the ecological conditions in reserved and anthropogenically disturbed forest ecosystems.

## MATERIALS AND METHODS

The research objects were epigeic species of bryophytes from experimental sites that differed in water and temperature regimes and light intensity (Lobachevska *et al.*, 2023). The experimental sites were in Roztochchya Biosphere Reserve – an area of the complete conservancy of old-growth beech forests of the Vereshchytsia Nature Conservancy research department (air temperature above the moss turf: +24.0 °C to +26.3 °C, turf temperature: +20.0 °C to +23.0 °C, air humidity: 32 %, light intensity: 30,000 to 50,000 lux) on the territory of the 40-year-old felling of the Stradchiv Educational Production Forestry Plant (air temperature above the moss turf: +36.0 °C to +39.0 °C, turf temperature: +30.0 °C to +33.0 °C, air humidity: 22 %, light intensity: 80,000 to 100,000 lux) and the stationary recreation area “Vereshchytsia” of the Yavoriv

National Nature Park (air temperature: +23 °C to +27 °C, turf temperature: +19 °C to +22.5 °C, air humidity: 28 %, light intensity: 90,000 to 100,000 lux).

The names of moss species are presented according to the latest sources (Hodgetts *et al.*, 2020 and Virchenko & Nyporko, 2022).

**Morphometric analysis of plants:** measuring of the shoots' length, the size of the leaves, and their number on the stem were performed on the motorized microscope Axio Imager M1 (Carl Zeiss) using the software Carl Zeiss AxioVision 4.6 and UTHSCSA Image Tool 3.0i and the stereo binocular Stemi 2000-C (Carl Zeiss) with a photo attachment and a "Nikon" digital camera.

**The biomass in same-size samples of bryophyte cover** was determined according to the method by B. Van Tooren and co-authors (Van Tooren *et al.*, 1990). Bryophytes, including the brown section, were separated from the soil particles and washed with water. The dry mass of the sample was calculated after drying for 48 hours at a temperature of 70 °C.

**Moss samples were weighed before and after drying** in a cabinet dryer for 48 hours at a temperature of 70 °C to determine the dry mass of shoots. Field water capacity in samples was calculated as fresh weight minus dry weight divided by dry weight and expressed as a percentage. Temperatures of air, moss turf, and the substrate's 0–3 cm top layer were measured with mercury thermometers. The light intensity in experimental sites was determined using a lux meter U116.

**Determination of the hydration of the moss gametophyte** and the soil under them was conducted according to generally accepted methods. Indicators of water retention coefficient ( $Cwr_1$ ) were determined after drying shoots for 24 hours at room temperature, water recovery coefficient ( $Cwr_2$ ) – after saturation with water for 24 hours at room temperature, and drought resistance coefficient ( $Cdr$ ) – by weighing and calculation methods (Polchyna, 1991).

$$Cwr_1 = \frac{\text{shoot mass after drying}}{\text{mass of fresh shoots}} \cdot 100 \%$$

$$Cwr_2 = \frac{\text{mass of shoot after saturation with water}}{\text{mass of fresh shoots}} \cdot 100 \%$$

$$Cdr = \frac{Cwr_1 \cdot Cwr_2}{100}$$

The samples immersed in distilled water for 24 hours were taken out, soaked with a paper towel for 15 seconds, and weighed to calculate the water recovery coefficients.

**The phenol-sulfate method** was applied to determine the total and soluble carbohydrate contents (Sadasivam & Manickam, 2007). In order to study the total content of carbohydrates, 1 mL of 2.5 N hydrochloric acid solution was added to 100 mg of plant material and then extracted in a boiling water bath for 3 hours. The homogenate was cooled, and the addition of  $\text{Na}_2\text{CO}_3$  neutralized the acid until the reaction stopped. The homogenate was centrifuged for 15 min at 4000 rpm, and the supernatant was used to determine the total carbohydrate content.

In order to determine soluble carbohydrates, 100 mg of plant material was homogenized in 10 mL of distilled water, transferred to test tubes, and extracted for 10–15 min in a boiling water bath. After extraction, the homogenate was centrifuged (15 min, 4000 g),

and the supernatant was used to determine the sugar content. Then 1 mL of filtrate was taken, 1 mL of 5 % phenol solution, and 5 mL of concentrated sulfuric acid (the density 1.84 g/mL) were added. The mixture was thoroughly mixed, and the optical density was measured after 10 min with the Specord 210 Plus spectrophotometer at a wavelength of 490 nm. Distilled water was added to the blank solution instead of the plant extract. The sugar content was determined according to the calibration curve made for sucrose and expressed in  $\text{mg} \cdot \text{g}^{-1}$  of dry weight. The experiments were carried out in threefold repetition. The Excel and Statistica programs were used to guarantee statistical processing of the obtained results. The significance of difference between the variants was evaluated according to the Student's criterion (\* $p \leq 0.05$  and \*\* $p \leq 0.01$ ).

## RESULTS AND DISCUSSION

Based on the results of the systematic analysis of the bryoflora of forest ecosystems (reserved and with different degrees of disturbance), it was determined that in the old-growth beech forests of the Vereshchytsia tract, dioecious epigeic endohydric species of the family *Polytrichaceae* Schwägr. are mainly dominant, with life forms of high or low loose turf and genus *Plagiomnium* T. J. Kop. with life forms of loose or dense turf with creeping branches (Lobachevska *et al.*, 2023). In case of *Plagiomnium* species, internal water transport is carried out in the central conducting strand with well-developed hydroids, leptoids, and even pseudo-strands of the leaf trace (Glime, 2019). Usually the moss conducting central strand has species differences, in particular, in *P. undulatum* (Hedw.) T. J. Kop., it occupies up to 2/3 of the stem diameter. It is known that mosses of the families *Polytrichaceae* and *Mniaceae* Schwägr. can transport dissolved matter 16 or even 50–100 times faster than the forest moss *Pleurozium schreberi* (Willd. ex Brid.) Mitt. (Sokołowska *et al.*, 2017). Endohydric mosses typically have surfaces with watertight cell walls that reduce water absorption. The cell walls of some moss species do not contain lignin, like in vascular plants, but waxy-like polyphenolic components. Such coating provides only low resistance to water diffusion, similar to the mesophyll of vascular plants, which may be considerably more important for repelling water and increasing  $\text{CO}_2$  diffusion (Raven, 2003; Wang & Bader, 2018).

Many bryophyte species formed morphological structures and architecture of shoots in the turf that improve water supply, absorption, storage, and/or limitation of water loss from branches and leaf surfaces (Rice & Schneider, 2004; Rice, 2012). It was found that the change of moss turf capillarity of the forest ecosystems' dominant species *Plagiomnium cuspidatum* and *P. ellipticum* is conditioned by numerous leaves on the shoots and rhizoid tomentum along the stem, particularly thick at its base. In addition to the branched rhizoids (macronemata) at the base of shoots, the axillary macronema was found situated mainly around the beginning of branches or dormant buds and rhizoid formations (micronemata) from brownish threads almost without branching that arise from the outer layer of the stem bark and are situated on its entire surface (**Fig. 1B3**). Rhizoids are considered to play an insignificant role in water absorption by bryophytes but they do prevent moisture loss. However, it is worth noting that rhizoids can contribute to water transport along the stem with the help of the capillary action phenomenon. Thus, for endohydric species *Polytrichaceae* (*Polytrichum formosum* Hedw. and *Atrichum undulatum* (Hedw.) P. Beauv.), it was established that internal water conductivity helps to avoid drying only when the rhizoids can absorb water from the substrate (Wang & Bader, 2018).

It was noted that the dominant endohydric mosses of forest ecosystems actively reproduce both generatively and vegetatively. In contrast to Polytrichaceae mosses, which form a large number of sporogoniums and underground rhizomes (Lobachevska *et al.*, 2018), *Plagiomnium* representatives, in addition to underground clonal connections from plagiotropic basitonic innovations between bases of the orthotropic shoots, are characterized by above-ground creeping shoots with characteristic macro- and micronema (Fig. 1A2, B2).



**Fig. 1.** The shoots of the epigeic dominant mosses *Plagiomnium cuspidatum* (A) and *P. ellipticum* (B): 1 – fertile shoots with macronema at stem base; 2 – orthotropic sterile shoots with the long creeping stems; 3 – the turf with relatively smooth surface; 4 – micronema from the outer layer of the stem bark

Due to the rapid growth of the orthotropic shoots, the long sterile stems form, which descend to the substrate under their weight and, having attached to the latter by rhizoids, rise again, continuing the growth. The so-called “stepping growth form” is formed, contributing to the rapid expansion of moss on the substrate and its settlement in optimal local growth conditions (Lobachevska *et al.*, 1986).

It was found that depending on the predominance of the generative or vegetative type of reproduction in the dominant species of the *Plagiomnium* mosses, the morphological structure of turfs and physiological functional traits of plants change. In mostly

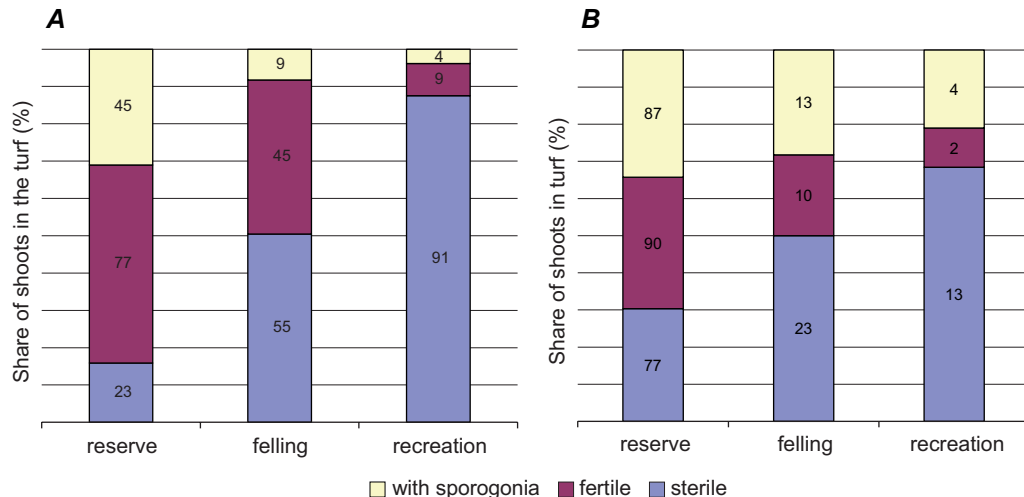
loose turfs of the bisexual mesophytic moss *P. cuspidatum*, fertile shoots are erect (2.2 to 4 cm high), densely leaved, with rosette-like leaves clustered at the top (**Fig. 1A1**). Leaves are distantly spaced on sterile stems (3.4 to 8.3 cm), erect or arcuately bent down, or lying with a rhizoid fascicle at the top; the leaves are flattened on the ends of the shoots. (**Fig. 1A2**). All leaves are broad and far decurrent.

The shoots of the dioecious hygrophytic moss *P. ellipticum* with thick rhizoid tomentum form significantly dense turfs with evenly leaved erect (3.2 to 4.0 cm) fertile shoots and sterile erect or lying (5.1 to 8.4 cm) shoots and all-round distantly placed short decurrent leaves (**Fig. 1B**).

Cells that are moving downward the base angles of the decurrent leaves by more or less wide (*P. cuspidatum*) or narrow (*P. ellipticum*) strip along the stem is a manifestation of adaptation that promotes ectohydric transport of water and dissolved nutrients from the upper part of the leaf plate with a waxy coating to its base and guarantees more effective absorption of those.

The results of the analysis of the moss turf sexual structure evidence that at the territory of old-growth forests in the loose low turfs of the bisexual moss *R. cuspidatum* fertile shoots predominate (up to 77 %), while the number of fertile shoots considerably decreased in the areas that underwent felling and recreational loads.

The number of sterile shoots fundamentally increased (up to 91 %) with significant moisture deficiency in the soil. There were no male plants identified in the samples of the dioecious moss *P. ellipticum* in all areas of forest ecosystems; the sterile shoots were usually found in the turf. The the largest number of female plants and turfs with sporogonia was found on the territory of the old-growth beech (**Fig. 2**).



**Fig. 2.** Analysis of the sexual structure of the moss turfs *Plagiomnium cuspidatum* (A) and *P. ellipticum* (B) from the forest ecosystems of Ukrainian Roztochchya

In the shaded, humid conditions of old-growth forests, the unequal height of the fertile and sterile shoots in the turf of the *Plagiomnium* mosses increased the roughness of its surface, which could significantly affect the regulation of moisture content and the activity of photosynthesis due to the increase of the evaporation intensity as a result of

the stimulation of airflow turbulence and wind penetration. While the humid upper leaves of the shoots were photosynthetically active, the lower leaves received low lighting, but were still thoroughly involved in photosynthesis during dry periods. Under dry conditions, leaves of *P. cuspidatum* and *P. ellipticum* were firmly curled, facilitating more light to enter deeper into the humid inner part of moss turf and increasing CO<sub>2</sub> absorption.

Consequently, changes in the shoot morphology and the density of moss turf structure in the vertical plane played a dual role – they regulated the airflow turbulence and intensified the interception of light in humid conditions. When the tops of the shoots dried up, the water loss rate of lower shoots, which became more photosynthetically active, decreased.

It was determined that in the *Plagiomnium* turfs, depending on ecological conditions, primarily on humidity and light intensity, the height of the individual shoots in the turf, the density and size of leaves, and their density (by biomass) change primarily due to the lying creeping shoots (Table 1). On the anthropogenically disturbed sites, a significant increase occurred in the length of the sterile shoots of *P. cuspidatum* (1.8–2 times) and *P. ellipticum* (1.4–1.5 times), compared to the old-growth site, whereas the length of fertile shoots significantly increased (1.4–1.5 times) only in the case of *P. cuspidatum*. It was noted that for both types of mosses, the slight increase of the indicators of leaves frequency and sizes and the biomass of turfs was a manifestation of adaptation to high levels of solar radiation and a decrease of the local growth humidity (Table 1).

**Table 1. The morphometric indicators of the sterile and fertile shoots and their density in turfs *Plagiomnium cuspidatum* and *P. ellipticum*, depending on local growth conditions**

Local growth	Type of shoot	The length of shoots (cm)	The number of leaves per 1 cm of length in the middle part of shoot (pcs)	Leave sizes (mm)		The biomass of turfs (mg/cm <sup>2</sup> )
				the length	the width	
<i>Plagiomnium cuspidatum</i>						
Reserved beech forests	Sterile	3.9 ± 0.5	12.4 ± 1.0	3.6 ± 0.1	2.1 ± 0.2	42.6 ± 3.1
	Fertile	2.5 ± 0.3	11.0 ± 1.1	6.1 ± 0.2	3.9 ± 0.2	
Felling area	Sterile	7.7 ± 0.6**	15.5 ± 1.1*	3.8 ± 0.3	2.9 ± 0.3*	43.6 ± 2.4
	Fertile	3.8 ± 0.2**	14.3 ± 1.2*	6.0 ± 0.1	4.1 ± 0.2	
Recreation area	Sterile	7.1 ± 0.7**	15.1 ± 0.8*	3.2 ± 0.1**	2.8 ± 0.2*	53.2 ± 4.2*
	Fertile	3.4 ± 0.3*	14.1 ± 1.0*	5.8 ± 0.2	4.0 ± 0.3	
<i>Plagiomnium ellipticum</i>						
Reserved beech forests	Sterile	5.4 ± 0.3	12.7 ± 1.4	3.9 ± 0.2	2.8 ± 0.2	52.1 ± 1.5
	Female	3.3 ± 0.1	15.0 ± 1.2	6.4 ± 0.2	4.1 ± 0.3	
Felling area	Sterile	7.9 ± 0.5**	14.5 ± 1.3	2.3 ± 0.3**	2.0 ± 0.2**	47.9 ± 1.8*
	Female	3.8 ± 0.2*	15.0 ± 1.9	3.2 ± 0.2**	2.1 ± 0.2**	
Recreation area	Sterile	7.4 ± 0.4**	8.0 ± 1.5*	4.5 ± 0.2*	3.2 ± 0.2	51.1 ± 3.3
	Female	3.6 ± 0.1*	9.2 ± 2.3*	5.1 ± 0.3**	4.0 ± 0.3	

**Comments:** the difference between samples of the same species of moss compared to the indicators in the condition of the complete conservancy, is statistically significant at \*p < 0.05; \*\* at p < 0.01. Sterile and fertile shoots of monoicous moss *Plagiomnium cuspidatum*. Sterile and female shoots of dioecious moss *P. ellipticum*



The studies of the sensitivity to dehydration in mosses with different water relations (1 aquatic *Fontinalis antipyretica* Hedw. and 3 terrestrial *Pleurochaete squarrosa* (Brid.) Lindb., *Tortella tortuosa* (Hedw.) Limpr., *Campylopus pyriformis* (Schultz) Brid.) proved that shoot morphology and life form can be the defining features in the adaptation of bryophytes to habitats precisely due to control of the dehydration rate and induction of tolerance mechanisms to desiccation (Cruz de Carvalho *et al.*, 2019).

Thus, mosses formed the loosest turfs in the most humid local growth with increased roughness due to the different heights of the fertile and sterile shoots. Such life forms are likely to be more efficient for obtaining nutrients from the environment, facilitating CO<sub>2</sub> diffusion into the chloroplasts, and the ability to compete for space with other plant organisms (Bates, 1998). In the case of moisture deficiency, turfs with relatively smooth surfaces were formed due to the predominance of sterile shoots, limiting airflow turbulence and significant wind penetration (**Fig. 1A3**). Under such conditions, an essential factor of influence on the indicators of water retention is the turf capillary spaces, which are usually highly diverse and quite complex and, therefore, difficult to quantify (Rice, 2012). Enhancing the sterile shoot length, density, and sizes of leaves due to increased light intensity and temperature possibly improves water retention by moss turfs in anthropogenically disturbed forest areas. It is believed that capillary spaces between shoots and leaves, compared to solely between shoots, may be more relevant for water retention (Voortman *et al.*, 2013; Thielen *et al.*, 2021).

Mosses can adapt to changes in the environment, altering the shape and organization of the turf depending on the moisture conditions. The above was observed in *Polytrichum alpestre*, an endohydric moss, which shows a looser structure of turfs and their increased roughness in humid habitats (Zajączkowska *et al.*, 2017).

Thus, mosses showed the ability to adapt to variable microclimatic conditions of the environment due to the different ratios of fertile and sterile shoots, changing the height, shape, and density of turfs depending primarily on the water regime, temperature, and light intensity.

In reserved areas, the Cdr were higher for *P. cuspidatum* compared to *P. ellipticum*; in particular, higher indicators for both mosses were determined for vegetative shoots; the Cdr of female plants differed more significantly. The Cwr<sub>1</sub> and Cwr<sub>2</sub> for sterile shoots of monoecious species of *R. cuspidatum* moss were higher compared to fertile shoots, which were determined to contain 1.4 times more moisture. It was established that in female plants of the dioecious moss *P. ellipticum* from the old-growth forest, the relative moisture content (1.9–2.1 times) and Cwr<sub>2</sub> were higher than in sterile plants and the water deficiency indicators differed insignificantly. However, for sterile plants, Cwr<sub>1</sub> were 1.2 times higher than for female plants (**Table 2**).

For forest ecosystems with different degrees of disturbance, the territory of stationary recreation and the 40-year-old felling, an increase in the air and moss turf temperature and light intensity indicators caused a significant reduction of the environment humidity (by 4–10 %). In separate humid (27.8 %) parts of the recreation area, the moisture-loving moss *P. ellipticum* was found more often in the turfs where sterile shoots predominated. It was found that in these areas, female and sterile shoots differed insignificantly according to the following indicators: moisture content, water deficit, Cwr<sub>1</sub>. The same indicator of water deficit (75.3 %) was determined in the lower parts of shoots of both types; however, as it turned out, they differed by higher Cwr<sub>2</sub> in the upper part of sterile shoots, which caused slightly higher Cdr of the latter compared to Cdr for female plants (**Table 2, 3**).

**Table 2. Changes in water exchange indicators of the *Plagiomnium cuspidatum* and *P. ellipticum* depending on humidity conditions in forest ecosystems**

Local growth	The type of sample	The moisture content (%)	The water deficiency (%)	The coefficients (%)		
				of water retention (Cwr <sub>1</sub> )	of water recovery (Cwr <sub>2</sub> )	of drought resistance (Cdr)
<i>Plagiomnium cuspidatum</i>						
Reserved beech forests	Sterile	10.7 ± 0.3	76.9 ± 1.2	89.5 ± 1.3	433.7 ± 15.7	388.1 ± 12.5
	Fertile	15.0 ± 0.3	76.6 ± 1.3	84.9 ± 1.3	427.5 ± 13.3	363.2 ± 10.1
	Soil	41.3 ± 6.3				
Felling area	Sterile	9.4 ± 0.3**	72.2 ± 1.4*	90.6 ± 1.5	364.7 ± 21.0*	330.3 ± 15.4*
	Fertile	9.8 ± 0.4**	75.7 ± 1.5	90.2 ± 1.4*	363.8 ± 14.3*	328.1 ± 10.0*
	Soil	9.4 ± 3.2**				
Recreation area	Sterile	11.5 ± 0.2*	71.9 ± 1.4*	88.5 ± 1.5	414.9 ± 23.1	367.2 ± 13.7
	Fertile	14.1 ± 0.3*	75.9 ± 1.3	85.9 ± 1.2	355.9 ± 15.7*	305.7 ± 14.6*
	Soil	3.5 ± 2.1**				
<i>Plagiomnium ellipticum</i>						
Reserved beech forests	Sterile	13.1 ± 0.4	75.2 ± 3.7	86.9 ± 1.5	404.4 ± 9.3	351.4 ± 11.3
	Female	25.7 ± 1.7	76.2 ± 3.0	74.3 ± 2.0	420.0 ± 8.0	312.7 ± 9.1
	Soil	27.2 ± 2.0				
Felling area	Sterile	5.3 ± 0.3**	76.9 ± 3.1	94.7 ± 2.1*	432.9 ± 10.5	409.8 ± 13.1*
	Female	10.4 ± 1.1**	77.8 ± 3.3	89.6 ± 2.3**	449.9 ± 9.2*	402.8 ± 12.5**
	Soil	19.7 ± 1.3*				
Recreation area	Sterile	7.2 ± 0.4**	77.7 ± 3.3	92.8 ± 1.7*	448.7 ± 13.1*	416.4 ± 12.0*
	Female	7.9 ± 0.5**	76.9 ± 3.4	92.1 ± 2.4**	433.0 ± 13.0	398.8 ± 13.2**
	Soil	17.8 ± 1.5*				

**Comments:** the difference between samples of the same species of moss and the soil below it, compared to the indicators in the condition of the complete conservancy, is statistically significant at \* p < 0.05; \*\* at p < 0.01

The drought-resistant moss *P. cuspidatum* was more often found on the territory of the felling, in the turfs of which almost the same number of fertile and vegetative shoots was detected (**Fig. 2A**). In conditions of moisture lack, higher indicators of water deficit were noted for fertile shoots, especially in the lower part of the shoots (**Table 3**). The highest indicators of Cwr<sub>1</sub>, over 90 %, were determined for fertile and sterile moss shoots, and indicators of Cdr were almost the same: 328.0 % and 330.3 %. Apparently, in conditions of the significant lack of moisture in the moss turf of *P. cuspidatum* the differences between the physiological functional traits of plants were leveled, which contributed to the implementation of the strategy of “social organization” of bryophytes, namely facilitation (positive interaction) (Mishler, 2001; Glime, 2019), which ensured the mutual preservation of water reserves as a result of a more or less equable distribution of water between the shoots. In order to change the surface area of heat exchange and reduce water loss, bryophyte turfs become similar in size and structure, thus improving

control over the surface layer properties and evaporation (Glime, 2019). The analysis of the water deficiency and water recovery ability indicators in different parts of shoots shows significant adaptive differences between turfs of the mesophytic *P. cuspidatum* and the hygrophytic *P. ellipticum* mosses (Table 3).

Table 3. Variability of water deficit indicators and water recovery ability in different parts of shoots of *Plagiomnium cuspidatum* and *P. ellipticum*

Ecosystem areas	Type of shoots	Stem parts	Moisture deficiency (%)	Coefficient of water recovery ( $Cwr_2$ ) (%)
<i>Plagiomnium cuspidatum</i>				
Reserved beech forests	Sterile	upper	74.9 ± 1.0	398.3 ± 11.5
		lower	76.1 ± 0.8	418.6 ± 9.0
	Fertile	upper	73.0 ± 0.9	370.2 ± 11.2
		lower	70.1 ± 0.7	334.6 ± 9.3
Felling area	Sterile	upper	70.5 ± 1.1*	338.9 ± 12.3*
		lower	73.4 ± 0.8*	375.5 ± 9.0*
	Fertile	upper	71.3 ± 1.2	348.2 ± 10.3
		lower	74.1 ± 0.9*	386.8 ± 10.0*
Recreation area	Sterile	upper	70.4 ± 0.9*	365.2 ± 13.0
		lower	73.0 ± 0.9*	390.1 ± 9.1
	Fertile	upper	70.0 ± 0.8*	371.3 ± 12.7
		lower	73.0 ± 1.0	391.0 ± 10.5**
<i>Plagiomnium ellipticum</i>				
Reserved beech forests	Sterile	upper	73.76 ± 0.8	340.2 ± 10.2
		lower	77.0 ± 0.9	371.6 ± 9.1
	Female	upper	76.6 ± 0.9	349.0 ± 12.5
		lower	77.0 ± 0.8	391.1 ± 12.7
Felling area	Sterile	upper	78.9 ± 1.1*	486.5 ± 13.3**
		lower	76.1 ± 1.1	411.1 ± 9.3*
	Female	upper	79.0 ± 0.9	469.4 ± 13.7**
		lower	75.5 ± 1.0	409.0 ± 12.30
Recreation area	Sterile	upper	79.9 ± 0.9**	496.1 ± 14.2**
		lower	75.3 ± 0.9	404.4 ± 9.0*
	Female	upper	78.9 ± 1.2	473.9 ± 13.9**
		lower	75.3 ± 0.8	403.5 ± 12.0

**Comments:** the difference between samples of the same species moss, compared to the indicators in the condition of the complete conservancy, is statistically significant at \* p < 0.05; \*\* at p < 0.01

On the territory of the old-growth forest, significantly higher indicators were established for the upper parts of fertile plants and lower parts of sterile shoots in the *P. cuspidatum* turfs, and, compared to anthropogenically disturbed forest areas, where higher indicators of water deficiency in the lower parts of both types of shoots for *P. cuspidatum*

have been established. In case of *P. ellipticum*, on the contrary, higher indicators of water deficit and the coefficient of water recovery were noted in the disturbed areas, compared to the old-growth forest, namely in the upper parts of both sterile and fertile plants. The detected differences in the water content can be explained primarily by differences in the morphology of the turfs of the studied mosses and their different requirements for habitat humidity. The *R. cuspidatum* turfs with a rougher surface and area in contact with air, on the one hand, intercept water better, but, on the other hand, use it with less effort and, therefore, having lost the capillary action force they cannot accumulate it at the base of shoots. With a high density of sterile shoots, *P. ellipticum* retains water longer inside turfs. In addition to the capillarity of each stem, water distributes between adjacent shoots, forming an additional level in the capillary system of turf moss. However, hygrophytic moss has no adaptations limiting water consumption, whereas it prefers humid soil conditions and high air humidity. Therefore, adaptive relations between habitats, water relations, and the morphology of moss turfs increased indicators of moisture deficiency and  $Cwr_2$  of moss plants in the upper part of shoots. Bryophytes usually maintain constant endohydric water content, absorbing water from the external capillary spaces if necessary. This is more important for the plant's general functioning than for internal functioning, whereas cell functions remain unchangeable at almost zero water potentials (Coelho *et al.*, 2023; Jauregui-Lazo *et al.*, 2023).

The results of analysis of the water exchange indicators of *Plagiomnium cuspidatum*'s and *P. ellipticum*'s shoots show that indicators of water deficit were related to the water-retaining ability of plants, which is the primary indicator of drought resistance and plays a leading role in the regulation of water exchange of dominant epigeic mosses.

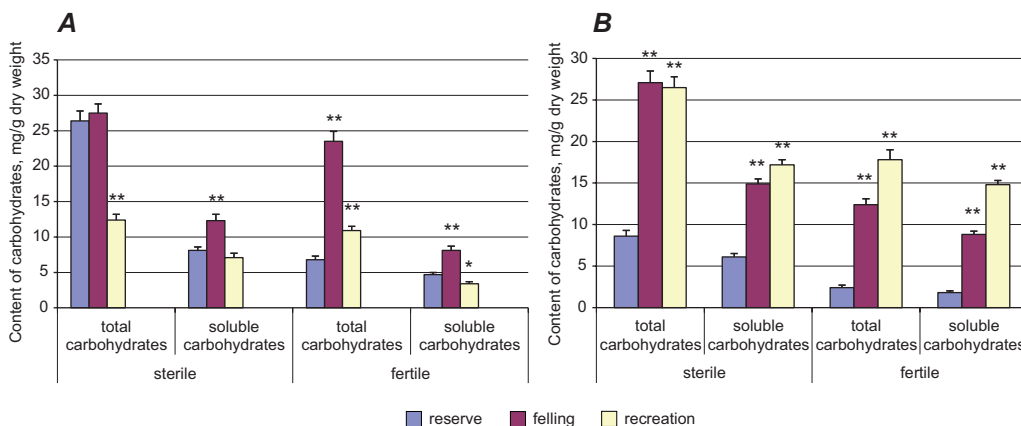
Water-retaining forces caused mainly by the content of the osmotically active substances in cells and the ability of the colloids to swell play an essential role in regulating water exchange in mosses.

Structural and soluble carbohydrates accumulate at the metabolic level to prevent cell membranes' disintegration, increase intracellular osmolarity, and compensate for water loss.

It was found that in moss samples from anthropogenically disturbed forest ecosystems, apparently in response to high light intensity and moisture deficiency, the total content of carbohydrates and their soluble fraction significantly increases (**Fig. 3**). It is known that the accumulation of carbohydrates ensures the internal regulation of water potential and promotes active water absorption by plants (Zúñiga González *et al.*, 2016). It was found that in the studied *Plagiomnium* mosses from all localities, more carbohydrates accumulated in vegetative than in fertile shoots (**Fig. 3**). In old-growth forests, the total content of carbohydrates in sterile *P. cuspidatum* shoots was 3.9 times higher, and in *P. ellipticum*, soluble sugars were 3.4 times higher than in fertile shoots. If female plants of *P. ellipticum* were determined to have a higher percentage (more than 70.82 %) of soluble sugars from the total content of the carbohydrates in all studied areas, for *P. cuspidatum* a higher percentage (68.78 %) was found only in the area of old-growth forests. The lower the substrate's moisture level and the higher the temperature regime of local growth were recorded, the higher the indicators of total carbohydrate content in plants were determined.

The maximum amount of carbohydrates in the sterile shoots of *P. cuspidatum* and *P. ellipticum* accumulated in localities on the territory of felling. The highest content of soluble sugars in female plants and in sterile was detected for *P. ellipticum* from the recreation area (**Fig. 3**).

Adaptive morpho-physiological responses of mosses from anthropogenically disturbed areas show two mechanisms for the simultaneous effects of drought and high-temperature stress. Mechanisms of avoidance are mainly morphological adaptive changes that ensure a reduction of water use, in particular, an increase in the number of macro- and microneme rhizoids, waxy coating on the decurrent leaves, and their twisting for reduction of evaporation. The signs of tolerance include maintenance of tissue hydration due to cellular and biochemical modifications, mainly resulting from an increase in the content of osmotically active substances. Resistant species of mosses are characterized by high concentrations of sucrose, which, functioning as the main osmoprotectant, can replace proline as in *Arabidopsis thaliana* (L.) Heynh. plants under drought conditions and high-temperature stress (Zúñiga González *et al.*, 2016; Kiriziy & Stasik, 2022).



**Fig. 3.** The total content of carbohydrates and the content of their soluble fraction in the shoots of *Plagiomnium cuspidatum* and *P. ellipticum* depending on the conditions of local growth of forest ecosystems  
**Comments:** \*  $p < 0.05$ ; \*\* at  $p < 0.01$

Therefore, an increase in the concentration of osmoprotective compounds testifies to the resistance of mosses to abiotic stresses due to the provision of tissue hydration and maintenance of cellular turgor, protection of protein structures, and stabilization of cell membranes as the cells dehydrate.

## CONCLUSIONS

In the turfs of *Plagiomnium cuspidatum* and *P. ellipticum*, depending on ecological conditions, primarily humidity and light intensity, both the length of shoots, the frequency and size of leaves, and their density (in terms of biomass) changed mainly due to sterile creeping shoots.

On the territory of the old-growth forests, fertile shoots prevailed in moss turfs. In contrast, in areas that experienced felling and recreational loads, the number of fertile shoots decreased significantly; with a significant moisture deficit in the soil, the number of sterile shoots reached 91 %. In the wettest local growth, mosses formed the loosest turfs with increased roughness due to different heights of fertile and sterile shoots; with lack of moisture and in conditions of high light intensity, mosses formed turfs with relatively

smooth surfaces mainly from sterile lying shoots which limited airflow turbulence and moisture evaporation.

The results of the analysis of water deficiency indicators and water-recovery ability in different parts of shoots indicate significant adaptive differences in turfs of mesophytic and hygrophytic mosses. In anthropogenically disturbed forest areas, higher indicators were found for *P. ellipticum* in the upper part of both sterile and fertile plants and for *P. cuspidatum* – in the lower parts of both shoots.

It was established that water deficit indicators were related to the water-retention ability of plants, which is the primary indicator of drought resistance and plays a leading role in regulating the water exchange of dominant epigeic mosses.

Therefore, mosses adapted to the changing microclimatic conditions of forest ecosystems due to endohydricity and morphological adaptive mechanisms of water-retention in the external capillary space: change of height, shape, and density of turfs, the morphology of shoots, different ratios of fertile to sterile plants and their physiological functional traits. The internal regulation of cell water potential was provided by an increased osmoprotectant concentration (carbohydrates, primarily their soluble fraction).

## COMPLIANCE WITH ETHICAL STANDARDS

**Conflict of Interest.** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Animal Rights.** This article does not contain any studies with animal subjects performed by any of the authors.

## AUTHOR CONTRIBUTIONS

Conceptualization, [O.L.]; methodology, [O.L.; L.K.]; investigation, [O.L.; L.K.]; data analysis, [O.L.; L.K.]; writing – original draft preparation, [O.L.; L.K.]; writing – review and editing, [O.L.; L.K.]; visualization, [O.L.; L.K.]; supervision, [O.L.]; project administration, [O.L.]; funding acquisition, [-].

All authors have read and agreed to the published version of the manuscript.

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## ВОДНИЙ ОБМІН ЕПІГЕЙНИХ МОХОПОДІБНИХ ЛІСОВИХ ЕКОСИСТЕМ ЗАЛЕЖНО ВІД ЗМІН СТРУКТУРНО-ФУНКЦІОНАЛЬНОЇ ОРГАНІЗАЦІЇ ЇХНІХ ДЕРНИНОК І ВПЛИВУ ЕКОЛОГІЧНИХ УМОВ МІСЦЕВИРОСТАНЬ

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**Вступ.** Моховий покрив бере визначальну участь у збільшенні вологості ґрунту в лісових екосистемах. Мохоподібні з високим вмістом води можуть набагато зменшувати випаровування води з поверхні ґрунту й утримувати її протягом тривалого часу. Під впливом умов навколишнього середовища мохи змінюють форму та організацію мохових дернин для ефективного поглинання й утримання вологи. Тому важливо з'ясувати відмінності стратегії водного обміну епігейних домінуючих видів мохів залежно від екологічних умов у заповідних і антропогенно порушених лісових екосистемах.

**Матеріали та методи.** Дослідження здійснювали з використанням епігейних видів *Plagiomnium cuspidatum* і *P. ellipticum* із дослідних ділянок лісових екосистем, що відрізнялися за водним і температурним режимами й інтенсивністю освітлення. Визначали особливості впливу пристосувань морфологічної структури мохових дернин, фізіологічних функціональних ознак окремих рослин та їхніх метаболічних осмопротекторних змін на основні показники водного обміну (коефіцієнти водоутримання, водовідновлення та посухостійкості).

**Результати.** Встановлено, що залежно від вологості й інтенсивності освітлення в лісових екосистемах змінювалася форма та організація мохових дернин: висота окремих пагонів у дернині, частота і розміри листків. Переважання генеративного чи вегетативного типу розмноження мохів зумовлювало істотні зміни морфології пагонів, фізіологічних функціональних ознак рослин і щільності структури дернинок, що регулювало завдяки збільшенню турбулентності повітряного потоку і проникненню вітру в їхню середину поглинання та випаровування води. Визначено, що обводненість тканин мохів підтримується завдяки збільшенню загального вмісту вуглеводів і вмісту їхньої розчинної фракції, насамперед у вегетативних пагонах.

**Висновки.** Мохи пристосовувалися до мінливих мікрокліматичних умов лісових екосистем завдяки ендогідричності й механізмам водоутримування в зовнішньому капілярному просторі: зміні висоти, форми та щільності дернинок, морфології пагонів, різному співвідношенню фертильних і стерильних рослин та їхніх фізіологічних функціональних ознак. Внутрішню регуляцію водного потенціалу клітин забезпечувало збільшення концентрації осмопротекторів (вуглеводів, насамперед їхньої розчинної фракції).

**Ключові слова:** водоутримання, водовідновлення, посухостійкість, *Plagiomnium cuspidatum*, *P. ellipticum*, структура мохової дернинки, осмопротектори