

Article

Water Holding Capacity of Some Bryophyta Species from Tundra and North Taiga of the West Siberia

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Abstract: Functional traits are a set of characteristics that are expressed in the phenotype of an individual organism as a response to the environment and their impact on the ecosystem's properties. They are positioned at the crossroads between the response and influence of the organisms, creating a certain interest in functional ecological and evolutionary fields. Due to this unique position, they are divided into two categories: effect functional traits and response functional traits. Effect traits describe the influence of the species on the environment regardless of whether such traits are an adaptive advantage to the individual or not. In Bryophyta, one of the most important effect traits is water holding capacity (WHC), which is their means of regulating ecosystem hydrology. On a global scale, mosses' WHC is manifested in the slowdown of the large water cycle, in the storage of huge volumes of fresh water by peatlands and in the enormous paludification of Western Siberia. The main goal of our research was to obtain the water holding capacity measurements of tundra and taiga moss species to establish the base and foundation for environmental monitoring in the north of Siberia—the region with the most rapidly changing climate. Both the capacity to hold water within the moss tissues (WHC) and the capacity to hold water externally between the morphological structures (leaves, branches, rhizoids, etc.) (WHCe) were measured. In total, 95 samples of 9 Sphagnum and 5 true mosses species were involved to the research; some species were collected at two or three sampling sites within two natural zones/subzones that gave us the opportunity to compare the WHC along the meridional transection. In average, the northern taiga samples showed slightly higher WHC than tundra samples, probably due to the environmental specifics of the habitat—the taiga habitats were more moist, while the tundra was drier. Overall, in the majority of species, the standard deviation calculation revealed that the variability of WHCe is significantly higher than that of WHC. Such high variability in WHCe may be explained in regard to the morphological features of each individual considerably shifting between the samples of the same species while the anatomical features retain more stable results.

Keywords: water holding capacity; bryophyte functional traits; tundra; north taiga; West Siberia



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1. Introduction

Water uptake, transport and loss are important traits that are used to describe the functioning of communities and ecosystems and have become useful tools for predicting global climate change's impact on plants. In theory, to optimize the usage of the limited resources of the environment, the acquisition of key resources, including carbon, nutrients and water, should be coupled in the plant organism, because there are linkages across

organs and coupling among resources, resulting in an integrated whole-plant economics spectrum [1].

Bryophytes have no vascular system and consist of simple tissues that provide the internal transport of water and solutions, but they play a key role in some ecosystems like tundra or mires. If abundant, moss, especially *Sphagnum*, a recognized ecosystem engineer, contributes significantly to carbon sequestration. However, climate change may lead to more frequent heat waves, droughts, water level drawdowns and fires; over the last decades, these catastrophic events have become normal in the northern Siberian permafrost zone, influencing the frozen ground's stability and damaging the peatlands. This affects the balance of carbon storage and sequestration; the carbon sinks become carbon sources.

The vegetation's response to climate warming differs according to plant groups. Among all plant groups, bryophytes may suffer significant damage due to their poikilohydric properties [2]. As of now, the rise in the average temperature is slowly shifting the climate conditions in many areas, which is taking a toll on multiple species' functioning, forcing them to adapt and change their ecological and survival strategies. The peatlands, characteristic of West Siberia, are under climate-induced threats too: one of the world's largest carbon sinks is releasing more and more dissolved carbon into the carbon cycle, which is then being transformed into CO₂ by bacterial activity [3].

To indicate and monitor future changes in the tundra and mires of the northern part of West Siberia, we propose using a special set of bryophyte functional traits. Functional traits are characteristics that are expressed in the phenotype of an individual organism or community features as a response to the environment (response functional traits) and their impact on the ecosystem's properties (effect functional traits). Effect traits describe the influence of the species on the environment, regardless of whether such traits are an adaptive advantage to the individual or not. In Bryophyta, one effect trait is water holding capacity (WHC), which is their means of regulating ecosystem hydrology. There is a link between mosses' water holding economy and carbon economics, so WHC could be a crucial tool for monitoring climate-induced changes and bryophyte community changes, as well as the response. This paper reports the first data on some high-latitude Bryophyta species' water holding capacity and discusses the potential of this trait as a climate change monitoring tool in the northern part of West Siberia.

2. Objects, Methods and Study Sites

2.1. Bryophyta and Their Functional Traits

Mosses are poikilohydric plants, with their photosynthesis being highly dependent on water availability. Their strategies of adapting photosynthesis to water surpluses and shortages vary strongly between species. A better understanding of the relationships between water relations and photosynthetic traits across a wide range of moss species would provide important insight into their unique ecophysiological adaptations and thereby into the general principles of plant strategies for coordinating carbon and water relations [4,5].

Bryophytes' water content is heavily dependent on their external environment and decreases rapidly if the temperatures rise and humidity drops [6]. A lack of water content induces drought stress, severely lowers metabolic activity and causes tissue damage [7].

The poikilohydric properties of the bryophytes grant them the ability to retain huge amounts of water content within the community. They may retain an enormous water volume ranging from 200% to 3000% of their dry mass [8]. Nonetheless, full water saturation reduces the water storage capacity [9].

2.2. Water Holding Capacity Supporting Traits on the Example of *Sphagnum*

WHC is defined as maximum water held per gram of dry mass of bryophyte shoots or monospecific bryophyte colonies and is integrally realized at several levels in the case of Bryophyta and their communities: individual anatomy, individual morphology, colonial growth (turf) and microtopography of the habitat. Among bryophytes, special anatomical,

morphological and social structural features, resulting in increased WHC rates, distinguish representatives of the *Sphagnum* genus.

Sphagnum shoots grow in colonies of more or less tightly packed shoots with their tops growing at equal heights, creating a more or less even surface of photosynthetic tissue (Figure 1).



Figure 1. *Sphagnum warnstorffii* Russow at the palsa mire in the vicinities of Khanymey Field Research Station of Tomsk State University (northern taiga). Photo by Igor Volkov.

The surface roughness of the colony is affected by how shoots are packed. A smoother surface created by smaller shoots evaporates less and increases the colony's water retention [8]. Hence, the shoot numerical density is considered a key functional trait for *Sphagnum* water balance [8,10], as 90% of the *Sphagnum* colony's water holding capacity depends on how tightly shoots are packed [11]. A larger volume of smaller spaces enhances capillary forces and is reflected in a higher bulk density (BD; weight per volume). Consequently, BD is a key trait of *Sphagnum* water economy and the maintenance of a high water table [11–13]. The water content in the capitulum must stay above 50% of the water content for photosynthesis optimum in order for the moss to maintain photosynthesis and growth [14,15]. Relative to other bryophytes, sphagna are desiccation avoiders rather than desiccation-tolerant plants [16,17]. However, there is evidence of tolerance and evidence that some species can develop tolerance during slow desiccation processes [18,19].

The branches within a bunch are clearly differentiated in some species into spreading and pendant branches, where the pendant branches are thought to “wick” water from lower down the water table [11]. Along the branches, leaves are spirally arranged. The leaves of some species, particularly from the subgenus *Sphagnum*, are curved (i.e., convex), which increases their water holding capacity [20,21].

The branch leaves are one cell layer thick and constitute two different types of cells: hyaline and chlorophyllous cells. Each of the narrow chlorophyllous cells borders a hyaline cell, which is a large and (when mature) dead cell [11]. These hollow cells have structurally rigid cell walls and capacity to store water. This is where the last water resources are kept. The hyaline cells are responsible for 10% of the water holding capacity [11].

The hyaline cells use pores to allow passive flow of water in and out of the cell [21]. Total area of pores affects water economy, as well as the radius of a single pore. Smaller pores help the cell hold onto water [22].

In addition to shoot morphology and leaf anatomy, colony structure also affects the water economy, i.e., water holding, water retention and desiccation avoidance of *Sphagnum*.

The structure of colonies differs along the microtopography elements within the mire surface pattern (hollows, loans, hummocks, ridges, etc.) (Figure 2).

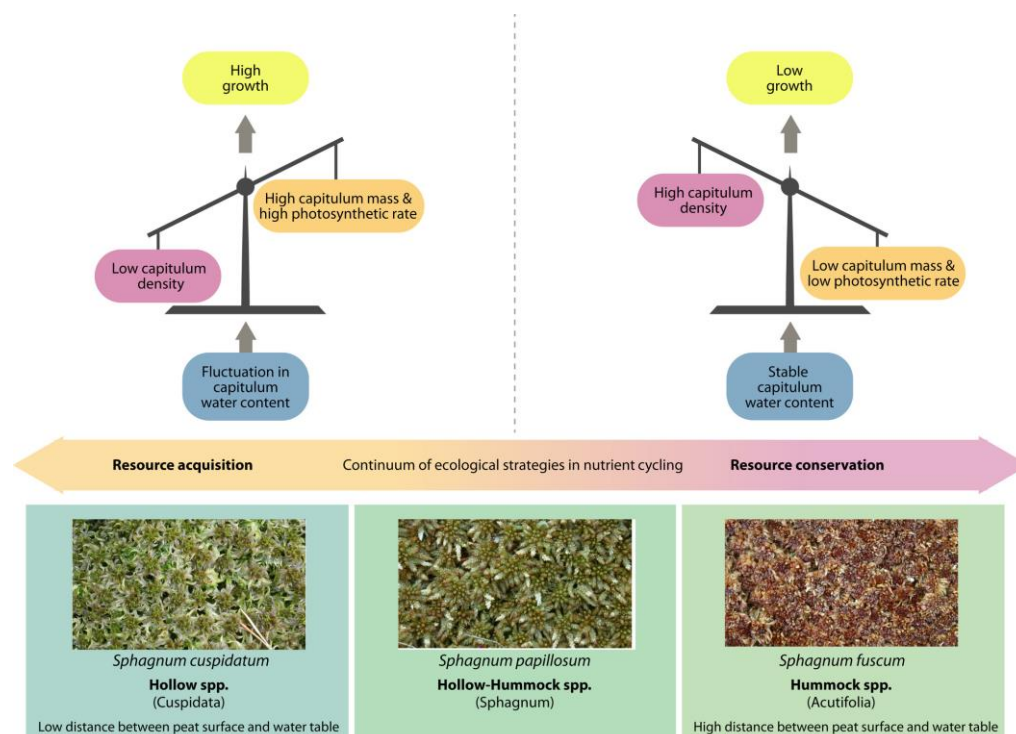


Figure 2. The continuum of ecological strategies driving trait trade-offs in the *Sphagnum* economic spectrum. Hollow species with fast nutrient cycling have short distance from the groundwater, fluctuating water content in the capitulum, large capitulum, low capitulum density, high maximum photosynthetic rate and fast growth; slow nutrient cycling hummock species have high distance from the groundwater, a stable water content in the capitulum, small capitulum, dense canopy, low photosynthetic activity and slow growth. In-between rates for species with large microtopographical variability [2].

In short, the *Sphagnum* moss traits that help water economy are:

- Leaf anatomy: hyaline cells amount and size, amount and size of pores;
- Stem anatomy (hyalodermis);
- Shoot morphology: overall height, branch and leaf density, fuzz on stem and branches, leaf size and shape;
- Colony structure: loose or dense, proximity of growing;
- Confinement to a certain element of the microtopographical element: hummock, loan or hollow at the mire, raised or lowered elements of the tundra microrelief, etc.

2.3. Study Area

The sampling covered habitats in the north of Western Siberia within geographical subzones of the northern taiga (mire and coniferous forest habitats in the vicinities of Noyabrsk City and Khanymey Field Research Station of Tomsk State University), the typical tundra and the southern tundra (Gydan Peninsula and Taz Peninsula) (Figures 3 and 4):

1. Gydan Peninsula: dryas tundra flat uplands—herb-dwarf shrub-moss tundra plant community;
2. Taz Peninsula south (shrubby) tundra: mossy frozen mounds and hollows in palsa mire, palsa mound slopes, high terrace of Taz River—shrub-dwarf shrub-moss tundra plant community;
3. Khanymey Field Research Station: bogs, palsa mire, tall frozen mounds, coniferous forest—shrub-moss-lichen communities;

4. Vicinities of Noyabrsk: small mounds in palsa mire—herb-dwarf shrub-moss plant community.

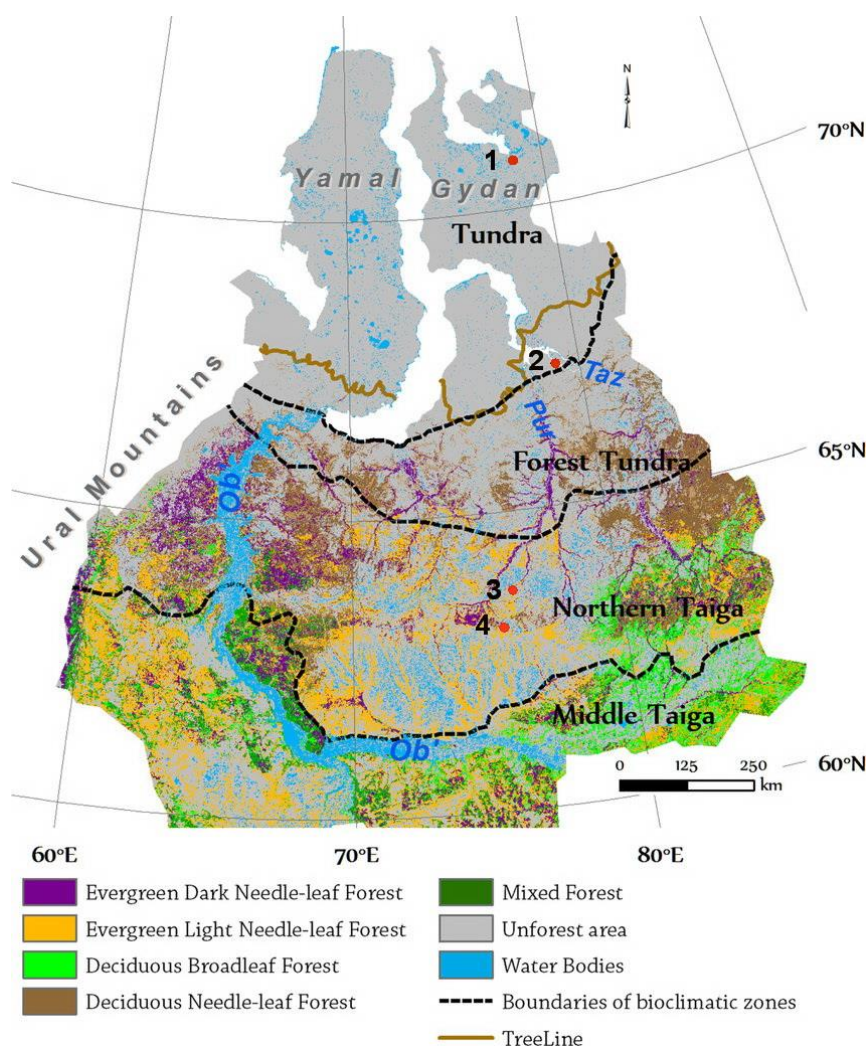


Figure 3. Sampling sites location: 1—Gyda, 2—Taz, 3—Khanymey, 4—Noyabrsk. The map of the northern West Siberia land-surface cover and bioclimatic zones taken from [23].

2.3.1. Northern Taiga Bioclimatic Subzone (Khanymey, Noyabrsk)

The vegetation of the subzone is represented by northern taiga forests. Large areas are occupied by Sphagnum or Sphagnum-lichen palsa mires—peatlands with flat or domed large frozen mounds.

The entire subzone is characterized by a harsh climate: average annual temperatures range from -4 to -9° ; average July temperatures reach up to 16° . Cooling often occurs in summer [24]. Winter is the longest season of the year. Average January temperatures in the south are -23.5° ; the minimum temperatures reach -56° . In winter, blizzards are often observed—featuring snowfalls with strong winds. The snow cover appears in early October, melts in late May–early June and lasts 208–233 days. Despite its inland position, taiga receives more precipitation than forest-tundra or tundra. The annual amount of precipitation is about 600–300 mm, mainly in the form of snow.



Figure 4. Sampling sites: dwarf shrub (“typical”) tundra at the north of Gydan Peninsula (**top left**); shrub (“south”) tundra at the Taz River valley (**top right**); northern taiga in the vicinities of Khanymey settlement, near the Tomsk State University Field Research Station (**bottom left**); flat-mound plaza mire in the vicinities of Noyabrsk City (**bottom right**).

Throughout the last quarter of the twentieth century, some of the greatest temperature increases have taken effect on the latitude zone occupied by the boreal forests [25] and even more on the Arctic and sub-Arctic zones (tundra). The temperatures increased both in summer and in winter, but winter temperatures increased more than summer temperatures.

2.3.2. Tundra Bioclimatic Subzone (Taz, Gyda)

The climatic conditions of the Western Siberian tundra are harsh. The summer is short and cold, followed by a long, windy and frosty winter. The severity of the tundra climate is associated with the wide distribution of permafrost, which occurs at a shallow depth. Permafrost has a profound effect on all natural processes.

The humidity is relatively high, coastal areas are extremely cloudy. The total annual precipitation is low—about 250–300 mm. Northwest cyclones often come to the tundra. In winter, they are accompanied by snowfalls and blizzards and a sharp rise in temperature.

The Gydan Peninsula has a fairly flat relief. Its highest heights do not exceed 160 m above sea level. The northern part of the peninsula is a flat and, in some places, hilly plain up to 70–80 m high, while middle part of relief is tumulous. The location of the Gydan Peninsula in high latitudes, in the continuous permafrost zone and in the immediate vicinity of the cold Arctic seas determines the severity of its natural conditions.

The subzone of typical (moss and lichen) tundras occupies most of the Gydan Peninsula. It is dominated by moss and lichen tundras in combination with moss-herbaceous and Dicranum-lichen-Sphagnum mires.

The subzone of shrub tundra occupies most of the Taz Peninsula. Shrub tundras of dwarf birch in combination with Sphagnum and lichen-Sphagnum bogs and in places with willow shrubland are a characteristic formation of the subzone. The height of the shrub layer of the dwarf birch tundra ranges from 25 to 100 cm. Willows (*Salix lanata* L.,

Salix lapponum L.) are usually mixed with dwarf birch. The grass layer usually contains sedges—*Carex bigelowii* Torr. ex. Schwein, *Carex concolor* R. Br., *Arctagrostis latifolia* Griseb., *Calamagrostis groenlandica* (Schrunk) Kunth, *Pedicularis lapponica* L. and other species.

2.4. WHC Data Collection and Analysis

We collected 19 moss single-species turf samples from above-described habitats within tundra and northern taiga zones (Table 1). Samples were kept wet until the moment of the lab processing.

Table 1. The collected water holding capacity data with standard deviation (std. dev.) (G—Gyda, Taz—Taz tundra, N—Noyabrsk, Kha—Khanymey).

	Species	Average WHC _e	Average WHC	WHC _e Std. Dev.	WHC Std. Dev.	Origin	Habitat
1	<i>Aulacomnium palustre</i> (Hedw.) Schwägr.	32.72	7.87	20.68	3.56	Kha	Wooded bog
2	<i>Aulacomnium palustre</i> (Hedw.) Schwägr.	17.19	3.95	2.15	0.97	G	Herb-dwarf shrub-moss tundra
3	<i>Dicranum angustifolium</i> Kindb.	32.52	6.15	7.58	1	Taz	Dryas tundra
4	<i>Dicranum spadiceum</i> J.E.Zetterst.	16.06	4.54	6.19	0.96	G	Herb-dwarf shrub-moss tundra
5	<i>Dicranum spadiceum</i> J.E.Zetterst.	31.67	5.19	11.21	1.79	Kha	Wooded bog
6	<i>Dicranum elongatum</i> Schleich. ex Schwägr.	17	3.21	4.04	4.14	G	Dryas tundra
7	<i>Pleurozium schreberi</i> (Brid.) Mitt.	24.67	7.6	2.43	0.87	Taz	Shrub-dwarf shrub-moss tundra
8	<i>Sphagnum angustifolium</i> (C.E.O.Jensen ex Russow) C.E.O.Jensen	26.75	9.63	13.9	5.06	Kha	Wooded bog
9	<i>Sphagnum balticum</i> (Russow) C.E.O.Jensen	32.62	9.07	7.3	0.91	Taz	Shrub-dwarf shrub-moss tundra
10	<i>Sphagnum capillifolium</i> (Ehrh.) Hedw.	32.51	8.57	4.15	1.28	N	Dwarf shrub-moss-lichen community
11	<i>Sphagnum fuscum</i> (Schimp.) H.Klinggr.	30.94	11.78	2.8	2.5	Kha	Bog near its border
12	<i>Sphagnum fuscum</i> (Schimp.) H.Klinggr.	27.53	11.11	2.19	2.11	N	Dwarf shrub-moss-lichen community
13	<i>Sphagnum fuscum</i> (Schimp.) H.Klinggr.	31.05	11.24	2.24	2.42	Taz	Shrub-dwarf shrub-moss tundra
14	<i>Sphagnum jensenii</i> H. Lindb.	35.41	13.85	11.79	2.9	Kha	Pine forest, dwarf shrub moss-lichen community
15	<i>Sphagnum lenense</i> H.Lindb. ex L.I.Savicz	8.51	3.62	8.88	3.59	N	Dwarf shrub-moss-lichen community
16	<i>Sphagnum lindbergii</i> Schimp.	30.34	12.55	4.62	1.98	Kha	Wooded bog
17	<i>Sphagnum lindbergii</i> Schimp.	28.73	10.97	3.17	2.26	Taz	Shrub-dwarf shrub-moss tundra
18	<i>Sphagnum magellanicum</i> Brid. s. l. *	38.87	21.24	5.59	4.94	Kha	Palsa mire, mossy frozen mound
19	<i>Sphagnum warnstorffii</i> Russow	24.41	13.82	1.22	0.82	Kha	Palsa mire, mossy frozen mound

Notes: * the species were recently revised and divided into three species by Hassel et al. [26]; our samples most likely are cf. *Sphagnum divinum* Flatberg and K. Hassel. Nevertheless, in this paper, we are referring to the species sensu lato (*Sphagnum magellanicum* Brid. s. l.). Additional detailed investigations of taxonomy and distribution in Siberia are needed.

Before the start of WHC measurements, we determined the species of the Bryophyta present in samples. Overall, 12 samples of *Sphagnum* mosses were identified alongside 4 *Dicranum* samples and 3 other various moss species. Each species was carefully examined under a microscope to identify anatomical and morphological features that are important for water holding capacity.

The methodology for the WHC measurement was adopted from similar research [8] and slightly adjusted for our experiment. A total of 10 separate shoots of each of 19 samples were taken to measure WHC, making it 190 single plant samples taken. In total, 95 pairs of moss shoots were processed and weighed three times for each pair. Samples were remoistened beforehand in deionized water for 24 h to reach full turgor. Each pair of moss shoots was taken per weighting with all-accessible external water. Then, shoots were left to dry for less than two minutes on blotter paper and weighed again without external water. After that, every pair of shoots was placed into a ceramic bowl marked with pair's unique number, dried in the cabinet at 60 °C for at least 24 h and then weighed for the third time for an absolutely dry weight.

The weighing occurred by common methodology for analytical balance, with the sliding door closed.

WHC manifests not only through anatomy (pores in hyaline cells and stem hyaloderm structure of *Sphagnum*) but also through morphological fixtures of an individual, such as hanging *Sphagnum* branches, lamellae on leaves, stem paraphyllia and behavioral tendencies such as moss growing in a group. Following the specifics of the trait, water holding capacity for samples was calculated twice: for weight with (WHC_e) and without external water (WHC). WHC_e reflects morphological features, while WHC is based mainly on the anatomical structure of the bryophyte. Then, the calculations were brought to average, and the dispersion and standard deviation were established for groups of samples of the same species. Water holding capacity formula was taken from relative research [27]:

$$WHC = \frac{(\text{wet moss weight} - \text{dry moss weight})}{\text{dry moss weight}}.$$

3. Results and Discussion

More than half of our samples were shoots of the *Sphagnum* genus. Other samples included species from Aulacomniaceae, Dicranaceae and Hylocomiaceae families. The results of the measurements are given in Table 1 and Figure 5.

As can be seen from the table above, the measurements of the same species sampled from a different origin were separated from each other. The differentiation is necessary because the water holding capacity depends on the anatomical and morphological features of the moss and different habitats affect the growth of a moss colony as well as the anatomical and morphological features of the moss specimen in distinct ways. This separation also brings a chance to compare the water holding capacity of the same species from various habitats.

3.1. The Comparison of the Water Holding Capacity between the Species

The maximum WHC_e of all moss samples belongs to *Sphagnum magellanicum* Brid. (Figure 5). *Sphagnum magellanicum* is a moss species that is able to reach big heights. The length of the shoots may be the first reason for *S. magellanicum* dominating the table. Also, the hyaloderm of the stem is more often a construction of 3–5 layers, and its outer cells usually have 1–2 or, less often, 3–6 pores with a different number of fibers. The stem leaves are relatively large (0.8–2 mm in length and 0.5–0.8 mm in width) and include hyaline cells with pores and lumens of the membrane, with fibers. Branching leaves are tiled-overlapping, broadly ovoid and also large, measuring 1.4–2.5 mm in length and 1.1–1.3 mm in width. There are hyaline cells on the convex (ventral) surface of the branch leaves with numerous elliptical pores. *Sphagnum magellanicum* tufts in the tundra are low and dense, with short and densely branched shoots.

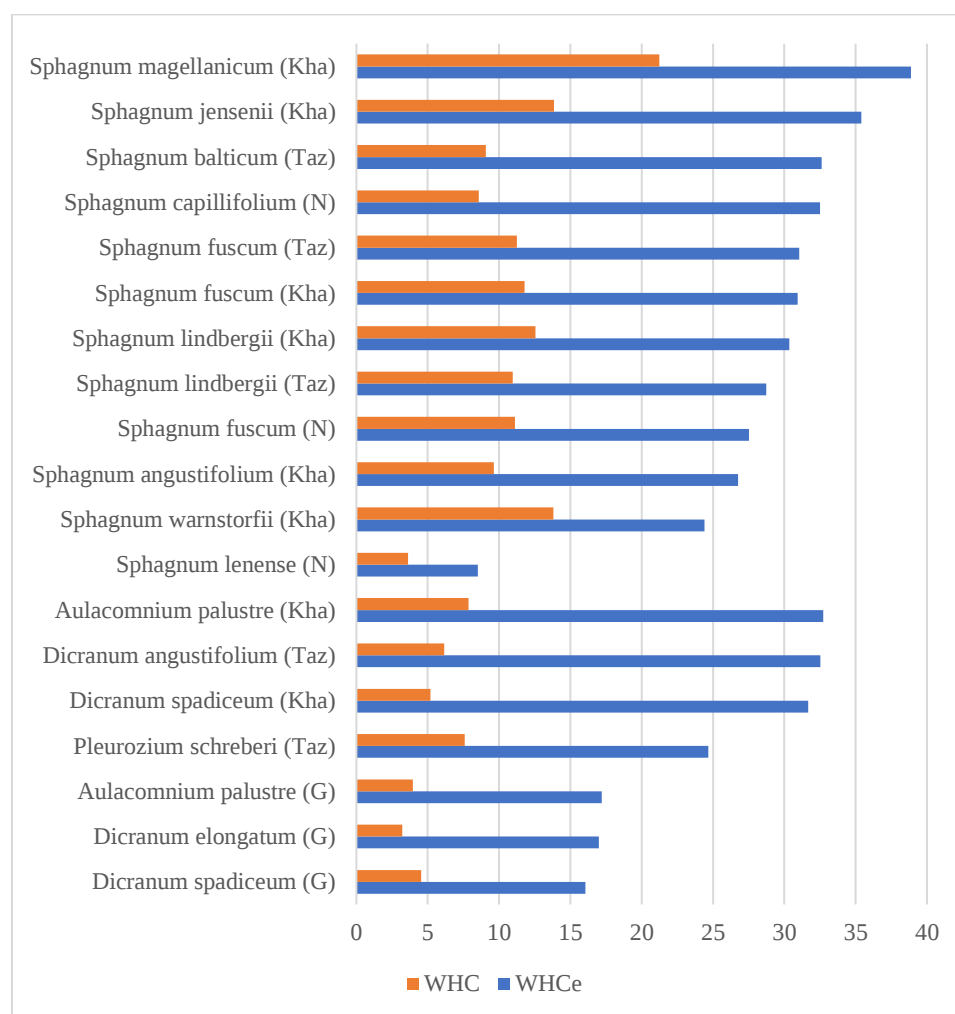


Figure 5. Bryophyta water holding capacity without (WHC) and with (WHCe) external water. *Sphagnum* and other mosses (Bryopsida) were ordered separately. Sample origin: G—Gyda, Taz—Taz, N—Noyabrsk, Kha—Khanymey.

Sphagnum magellanicum is followed by *Sphagnum jensenii* H.Lindb. ex L.I.Savicz and *Aulacomnium palustre* (Hedw.) Schwägr. (the sample that was collected from palsa mire in Khanymey). Like *S. magellanicum*, *S. jensenii* also can reach big heights. The turf is loose and high. The hyaloderm of the stem is 1–2- or 3–5-layered and usually ranges from unevenly developed to completely unbounded. The stem leaves are 0.9–1 mm long and 0.8–1 mm wide. The branch leaves are 2.3 mm long and 0.5–0.9 mm wide, broadly ovate-lanceolate. There are hyaline cells on the convex surface of the branch leaves with numerous small, rounded or oval-shaped thin- and thick-ringed pores, organized in 1–3 rows along commissures and in the middle of the cell walls. The plants are submerged in water sometimes reaching 40 cm deep.

Aulacomnium palustre has unbranched stems that are densely covered by rhizoids, which can hold water very well. The plants are in loose or dense tufts. The stems grow up to 12 cm in height and are simple or with sub-apical shoots that reach almost to the top with dense rhizoid felt.

Somewhat close to these species are *Sphagnum balticum* (Russow) C.E.O.Jensen and *Dicranum angustifolium* Kindb. *Sphagnum balticum* is a moderately-sized moss. The turf is mostly loose and soft. The stem hyaloderm has 2–3 (5) layers that are clearly limited, with relatively thick-walled irregular cells. The branch leaves are 1–1.7 mm long and 0.3–0.6 mm wide, with an ovate-lanceolate shape. The hyaline cells are narrow, with abundant fibers on the convex surface of branch leaves with small pores, turning downward into larger

pores on the concave (dorsal) one with large, rounded non-annular pores in the cell ends and angles.

Dicranum angustifolium is most often found in coniferous and deciduous forests on the ground and at the base of rotting trunks and stumps. This moss is clearly visible due to its size (which reaches up to 10–15 cm in height) and its shiny green, sometimes yellowish-green, tufts.

The specimen with the lowest water holding capacity with external water was *Sphagnum lenense* H.Lindb. ex L.I.Savicz. The turfs are usually dense. The stem reaches up to 10 cm tall. The hyaloderm of the stem is 2–4-layered. The stem leaves are not more than 1 mm long and are almost the same width. The branch leaves are small, up to 1–1.5 mm long and 0.3–0.4 mm wide, ovate-lanceolate and concave. There are hyaline cells on the convex surface of branch leaves with small apical pores, often bilateral, and with small annular pores in short rows along the commissures on the concave surface with numerous rounded non-annular pores.

The WHC comparison (Figure 5) shows that *S. magellanicum* and *S. jensenii* are in the leading positions again. This points to the great morphological and anatomical traits that support the WHC of these species, such as their shoot height, amount of hyaloderm layers, branching, hyaline cell structure and pore amount.

Sphagnum warnstorffii is very close to the *Sphagnum jensenii*'s WHC measurement, but in terms of holding external water, it took a place closer to the end of the list. Perhaps the leaf anatomy of *S. warnstorffii* is more capable of holding water than its shoot morphological features and colony structure. The turf is soft, loose, less often dense, low and up to 15 cm in height. Loose turf holds less water. The stem is thin and weak. The hyaloderm of the stem is 2–4 layers; its outer cells are always without pores. The stem leaves are 0.8–1.7 mm in length and 0.5–0.6 mm in width and lingual; the hyaline cells are usually without fibers and pores, with many folded membranes. The branch leaves are 5-row, sickle-bent, 0.9–1.5 mm long and 0.3–0.5 mm wide and ovate-lanceolate. There are hyaline cells on the convex surface of the branch leaves at the top with very small, thick-ringed, rounded pores in the lateral angles, moving downward with larger and thin-ringed, elliptical commissural pores on the concave side of the leaf with large, rounded, non-ringed pores. The changes in heights are minimal. Most often, the plants are medium in size or, in the shade, thin, slender and taller. The tundra is dominated by dense and short-branched plants; tussocks are usually dense. In such plants, the branch leaves are shorter and wider, with underdeveloped fibers in the hyaline cells and with somewhat compacted membranes.

On the very bottom of the table are *Sphagnum lenense* and *Dicranum elongatum* once again. *Sphagnum lenense* has small leaves and smaller pores, which is probably the reason why it scores so low in WHC.

3.2. The Comparison of Average Water Holding Capacity Inside the Species

The comparison inside the species will help to establish if there is a clear difference between samples that grew in tundra and taiga habitats. The samples of one species share common anatomy and morphology, so in this comparison the habitat plays a major role in forming the right features to achieve the potential water holding capacity.

The WHC_e of the sample collected from the taiga is almost twice the WHC_e of the tundra sample. This difference follows the same pattern for WHC as well. This means that for *Aulacomnium palustre* (Table 2), the moister bog habitat made a huge difference in growing features for the water holding capacity both anatomically and morphologically. It can also be connected to *A. palustre*'s tendencies in height changes, and the moss shoots from the tundra sample were shorter than those from the taiga sample.

The sample of *Dicranum spadicum* taken from the taiga region showed the WHC_e almost two times higher than the sample from the tundra (Table 3). The WHC was more or less similar between the samples, with the taiga sample showing a result that is a little higher than the tundra one. Compared to the previous pair of samples, which showed both WHC_e and WHC being higher in the taiga sample, there must be no striking difference

between zones in *Dicranum spadicum* ability to keep water at the inner structures, but at the morphological level (leaf axils), they do differ in a favor of taiga sample. We assume that this may be due to the size and proportions of the plant body, which differ in the tundra and taiga. This could be a prospective research issue.

Table 2. Average WHC_e and WHC comparison in *Aulacomnium palustre*.

	Origin	Habitat	Average WHC _e	Average WHC
1	Khanymey	Wooded bog	32.72	7.87
2	Gyda	Herb-dwarf shrub-moss tundra	17.19	3.95

Table 3. Average WHC_e and WHC comparison in *Dicranum spadicum*.

	Origin	Habitat	Average WHC _e	Average WHC
1	Khanymey	Wooded bog	31.67	5.19
2	Gyda	Herb-dwarf shrub-moss tundra	16.06	4.54

The *Sphagnum fuscum* samples (Table 4) do not show a significant difference in water holding capacity with or without external water. The WHC difference is barely noticeable, which means that the habitat or colony structure were not key elements in the development of the *Sphagnum fuscum* body. Those species reach small heights. The tufts are cushion-shaped and dense. The stems are thin. The hyaloderms of the stems are 3–4 (5)-layered, usually without pores in the outer cells. The stem leaves are 0.8–1.2 mm long and 0.5–0.8 mm wide. The branch leaves have hyaline cells on the convex surface with small, thick-ringed, downwardly larger and thin-ringed pores on the concave side in the lateral parts of the leaf with large, rounded, non-ringed pores. In humid habitats, large plants with larger stem leaves are found; more often, they are of medium size with smaller stem leaves.

Table 4. Average WHC_e and WHC comparison in *Sphagnum fuscum*.

	Origin	Habitat	Average WHC _e	Average WHC
1	Taz	Shrub-dwarf shrub-moss tundra	31.05	11.24
2	Khanymey	Bog near its border	30.94	11.78
3	Noyabrsk	Dwarf shrub-moss-lichen community	27.53	11.11

The *Sphagnum lindbergii* sample collected from the taiga has little difference from tundra sample; yet, the WHC of the taiga sample is still a little higher than the sister sample (Table 5). As for the previous sample, it seems that habitat does not play a major role in developing water holding capacity in *Sphagnum lindbergii*.

Table 5. Average WHC_e and WHC comparison in *Sphagnum lindbergii*.

	Origin	Habitat	Average WHC _e	Average WHC
1	Khanymey	Wooded bog	30.34	12.55
2	Taz	Shrub-dwarf shrub-moss tundra	28.73	10.97

To conclude the comparison of the water holding capacity inside the species:

1. Overall, the taiga samples showed a higher water holding capacity both with and without external water, sometimes reaching a number almost twice the measurement of the sample taken from the tundra area. This does not come as a surprise—moss colonies tend to hold more water in moister habitats, and the taiga is moister than the tundra. The other reason is that shoots grow higher and bigger in moister habitats and, the size of the shoot is a trait that supports WHC.

2. *Sphagnum fuscum* showed a striking consistency between both WHC measurements of all samples. This species is expected to vary in height, but the researched samples did not demonstrate any variety.
3. The difference in WHC_e tends to manifest in numbers equal or proportional to WHC.

3.3. The Standard Deviation

The standard deviation is calculated if the obtained values are close to or far from the mean. It provides insight on the stability, consistency and credibility of the collected measurements [28]. The small standard deviation shows that the data are stable and not very variable, which points to credible research.

The standard deviation measurements obtained (Figure 6) show that WHC has a lower volatility than WHC_e. This might be explained by the irregular amounts of water drops brought with the samples while measuring the wet moss weight with external water. Some shoots may have held more water in between, and some may have held less, and this added to the volatility of the results. Overall, the standard deviation comes in relatively small numbers, which may be used as the reaffirmation of the research being conveyed properly and the results being reliable.

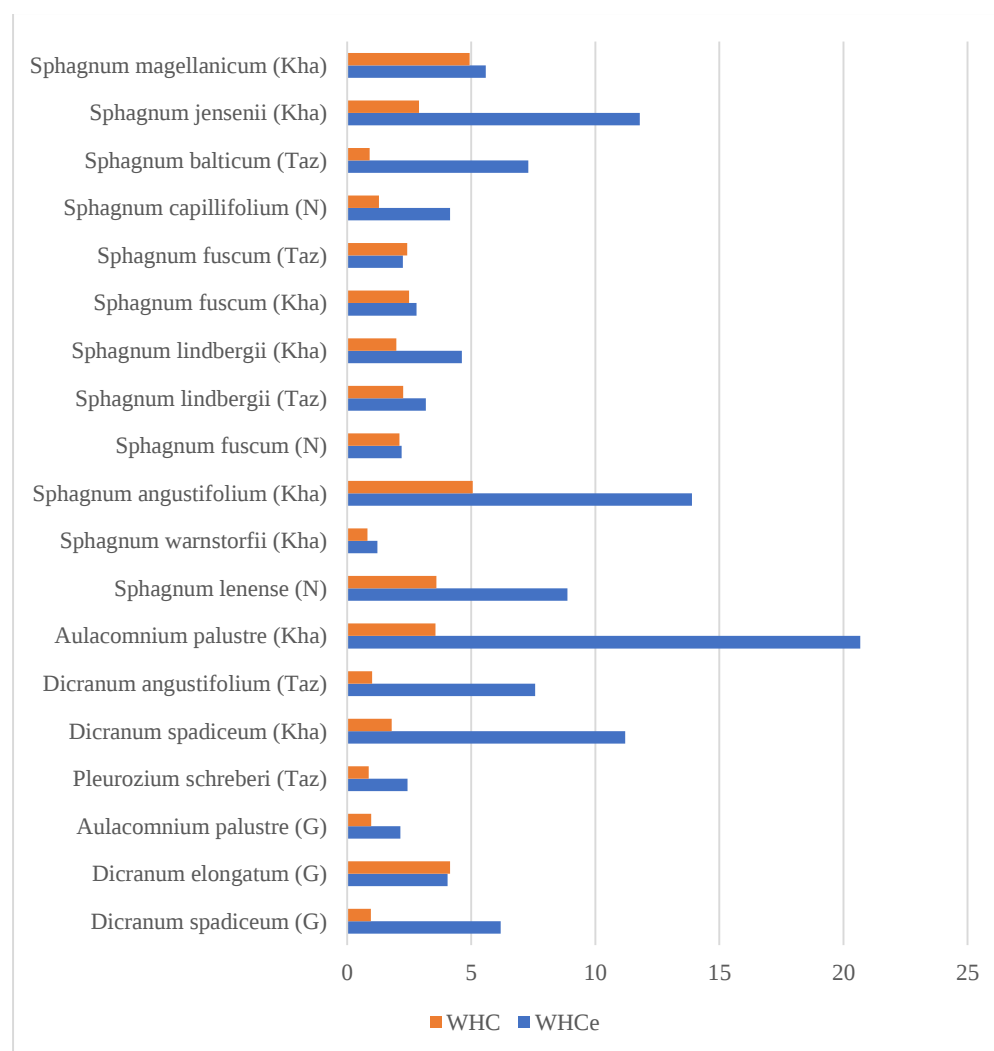


Figure 6. Standard deviation calculations for Bryophyta water holding capacity without (WHC) and with (WHCe) external water. *Sphagnum* and other mosses (Bryopsida) are ordered separately (the same order as for WHC/WHCe data at Figure 5). Sample origin: G—Gyda, Taz—Taz, N—Noyabrsk, Kha—Khanymey.

4. Conclusions

1. On average, the northern taiga samples showed slightly higher WHC than tundra samples, probably due to environmental specifics of the habitat—taiga habitats were moister, while the tundra was drier.
2. In regard to comparisons inside the species, overall, the northern taiga samples showed higher water holding capacity both with and without water, sometimes reaching a number almost twice the measurement of the sample taken from the tundra area. The difference in WHC_e tends to manifest in numbers equal or proportional to WHC.
3. The variability of WHC_e within moss samples is significantly higher than WHC in the majority of species, with the standard deviation of WHC_e rising up to 18.27, while the WHC standard deviation is 5.06 at maximum. Such high variability in WHC_e may be explained by the morphological features of each individual considerably shifting between the samples of the same species while the anatomical features retain more stable results. The worldwide level of WHC is lower, but the final comparison remains unsure.
4. The highest WHC_e and WHC were demonstrated by *Sphagnum magellanicum*, while the lowest WHC_e and WHC were split between *Sphagnum lenense* and *Dicranum elongatum*. *Sphagnum fuscum* showed a striking consistency between both WHC measurements of all samples. This can be explained by shoot morphology: topping samples species tend to grow higher and form dense turf, while the leaf anatomy supports the WHC with curved leaf forms and big amounts of hyaline cells and many pores. The samples that showed those with lesser WHC tend to be species with lesser growth size, plainer leaf forms and lesser pores in concave and convex cells.
5. Based on the ratio of external and internal water, two groups of mosses can be distinguished: 1—mosses in which the amount of internal water is equal to or greater than external water (*Sphagnum magellanicum* and *Sphagnum warnstorffii*), and 2—mosses in which the amount of internal water is less than external. Mosses of the first group are able to hold the water better and theoretically will gain a certain stability and competitive advantage in the conditions of habitats' wetness reduction under climate change. At the same time, this advantage is likely to be less applicable in the tundra, where the thawing of permafrost at first is likely to compensate for the increased evaporation and the aridization of the climate. On the contrary, in the conditions of the taiga zone, where permafrost is absent or sporadic and lies more deeply, a change in the water balance can give a sharp advantage to these species. This is especially important in relation to raised bogs, which occupy a larger area of Western Siberia and in which *Sphagnum magellanicum* is one of the main edificators and engineering species. Therefore, the ability of this species to hold internal water may play a key role in the stability of the peatlands as one of the main carbon sinks in the context of global climate change.
6. The collected WHC measurements of Bryophyta may serve as an environmental change indication tool and contribute to worldwide WHC research. Our results confirm that the water holding capacity, being the key bryophyte functional trait, shows the potential for the identification and clarification of bryophyte functional groups (as was demonstrated by Lett et al. [27]), and the quantitative data on the WHC in areas with a high abundance of mosses can be used to assess the ecosystem water economy [29] and to predict the ecosystem dynamics in the tundra and north taiga under various climate change scenarios.

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