Arctoa (2025) **34**: *202–208*
doi: 10.15298/arctoa.34.17

STRUCTURAL TRAITS, CANOPY DENSITY AND PRIMARY PRODUCTIVITY OF *SPHAGNUM LENENSE* AND *S. FUSCUM* IN PEATLANDS OF THE FOREST-TUNDRA ZONE (WESTERN SIBERIA)

СТРУКТУРНЫЕ ПРИЗНАКИ, ПЛОТНОСТЬ КОВРА И ПЕРВИЧНАЯ ПРОДУКЦИЯ МХОВ *SPHAGNUM LENENSE* И *S. FUSCUM* НА БОЛОТАХ ЛЕСОТУНДРЫ (ЗАПАДНАЯ СИБИРЬ)

NATALIA G. KORONATOVA[1]

НАТАЛЬЯ Г. КОРОНАТОВА[1]

Abstract

The study of ecological characteristics of Arctic species and communities remains insufficient. In particular, knowledge is lacking about the growth and productivity of the Arctic species *Sphagnum lenense*, which occupies habitats similar to *S. fuscum* and replaces it in permafrost palsas in the forest-tundra zone. To address this gap, a seven-year investigation of the dynamics of structural traits, canopy variables and primary productivity of *S. lenense* and *S. fuscum*, which co-exist in the Pangody palsa complex, was carried out. Significant differences were revealed between these species in numerical density and capitulum weight, which can be attributed as species-specific features. In *S. fuscum*, the values of these parameters increased in permafrost peatlands compared to bogs of the southern taiga of Western Siberia, while the other traits decreased. The dynamics of length increment and net productivity of both species correlated significantly with weather factors affecting moisture during the growing season and, to the greatest extent, with the dry period duration. No relationship with air temperature was found. The effect of weather predictors on numerical density, increment weight or capitulum weight were detected. Net productivity of *S. lenense* and *S. fuscum* was similar, with long-term median of 134 and 177 g·m^{-2} year^{-1}, respectively. Productivity of *S. fuscum* in the forest tundra was 1.4 times lower than in the southern taiga of Western Siberia.

Резюме

Изучение экологических особенностей арктических видов и сообществ остается недостаточным. В частности, нет сведений об особенностях роста и продукции арктического вида *Sphagnum lenense*, который занимает сходные с *S. fuscum* местообитания и приходит ему на смену на мерзлотных бугристых болотах лесотундры. Чтобы восполнить этот пробел, в течение семи лет проводили исследование динамики структурных признаков, плотности ковра и первичной продукции *S. lenense* и *S. fuscum,* которые сосуществуют на мерзлотных буграх болота Пангоды. Выявлена значимая разница между видами для численной плотности и массы капитул, которые можно отнести к видоспецифическим особенностям. У *S. fuscum* количественные показатели этих признаков возросли на мерзлотных болотах по сравнению с болотами южной тайги Западной Сибири, а остальных – снизились. Динамика изменения линейного прироста и продукции обоих видов значимо коррелировала с погодными факторами увлажнения в вегетационный период и в наибольшей степени с длиной сухого периода. Зависимости от температуры воздуха не установлено. Связи плотности мохового ковра, массы прироста и капитул от погодных факторов не выявлено. Продукция *S. lenense* и *S. fuscum* была сходной, многолетнее медианное значение составило 134 и 177 г·м$^{-2}$ в год, соответственно, и у *S. fuscum* было в 1.4 раза ниже по сравнению с южной тайгой Западной Сибири.

KEYWORDS: palsa, functional traits, length increment, numerical density, capitula weight, increment weight, moss NPP, Arctic

INTRODUCTION

Sphagnum mosses are the dominant plant group in ombrotrophic mires of Western Siberia. In the forest-tundra zone, permafrost palsa-pool complexes are widespread. Here, *Sphagnum* mosses share a dominance with lichens on palsas and maintain dominance in low waterlogged habitats such as pools, poor fens and hollows (Lapshina *et al*., 2022; 2023). On palsas, there are typical for elevated boreal bogs *Sphagnum* species, such as *S. fuscum* (Schimp.) H.Klinggr., *S. capillifolium* (Ehrh.) Hedw., *S. divinum* Flatberg & K.Hassel. *Sphanum lenense* H.Lindb ex L.I.Savicz (subgen. Cuspidata) also ap-

[1] – Institute of Soil Science and Agrochemistry of Siberian Branch of RAS, Ak. Lavrent’ev ave., 8/2, Novosibirsk, 630090 Russia. E-mail: coronat@mail.ru; ORCID: 0000-0002-0557-0083

pears here replacing *S. fuscum* (subgen. Acutifolia). While *S. fuscum* is common in peatlands throughout Western Siberia, *S. lenense* is an Arctic species. Southern boundary of *S. lenense* distribution in Europe corresponds to the isotherm of annual mean temperature of "4°C and an annual precipitation amount of 500 mm (Popov, 2019). On palsas of the forest-tundra, these two species coexist occupying similar habitats on hummocks and flat surfaces in between (Alpert & Oechel, 1984; Luken & Billings, 1984; Vitt, 2014; Popov, 2019; Lapshina *et al*., 2023). In addition to the similarity of habitats, these two species are resembling each other both in coloration and in size.

Despite a large number of publications dedicated to *Sphagnum* mosses, mentions of the *S. lenense* are rare and pramirily relate to descriptions of Arctic phytocenoses, often accompanying research on various topics (Jorgenson *et al*., 2022; Kolesnichenko *et al*., 2019; Konstantinova *et al*., 2023; 2024; Paal *et al*., 2021; Raudina *et al*., 2023; Zarov *et al*., 2021). *Sphagnum lenense* is infrequently mentioned in analyses of the floristic composition of Arctic mire communities (Lapshina *et al*., 2023) and in the studies of peat botanical composition (Pastukhov *et al*., 2021; Preis *et al*., 2016). There is a lack of research on the functional traits, productivity, and species responses to abiotic factors in the Siberian Arctic. Previously, functional and structural traits of *Sphagnum,* such as length increment, increment mass, capitulum mass, and others, were found to influence its competitive strategy and fitness, playing a role in the carbon cycle (Laing et al., 2014; Mazziotta *et al*., 2018; Bengtsson *et al*., 2020).

The aim of this study was to assess the structural traits, canopy density and net primary productivity of *S. lenense* in comparison with the morphologically and ecologically similar species *S. fuscum* in a permafrost palsa within the forest-tundra of Western Siberia.

Materials and Methods

The study was carried out in palsas of the peat plateaus mire complex Pangody (65.8717° N, 74.9632° E) near the town of the same name in the forest-tundra of Western Siberia. The mire included permafrost palsas and waterlogged thawed depressed habitats of pools, poor fens and hollows. On the palsa, permafrost was located at a depth of 30–60 cm. Lichens predominated in the phytocenosis (*Cladonia stellaris* (Opiz) Pouzar et Vězda, *C. stygia* (Fr.) Ruoss, *C. amaurocraea* (Flörke) Schaer., *Flavocetraria cucullata* (Bellardi) Kärnefelt et A.Thell and others). *Sphagnum* mosses (*S. fuscum*, *S. capillifolium*, *S. divinum*, *S. lenense*) occurred in small patches among lichen and along the periphery of waterlogged thawed habitats. A sparse herbaceous - dwarf shrub layer with a coverage of 25% was represented by *Ledum palustre* L., *Vaccinium vitis-idaea* L., *Betula nana* L., *Rubus chamaemorus* L. Pools, poor fens and hollows were dominated by *Sphagnum*, such as *S. balticum* (Russow) C.E.O.Jensen, *S. jensenii* H.Lindb., *S. lindbergii* Schimp. and others with coverage of 100%. Here, the grass cover was sparse (covering 15%) and dominated by *Eriophorum russeolum* Fr. and *Carex rotundata* Wahlenb.

The technique of the field experiment was as the following. Permanent 0.25 m^2 plots were set up on the palsa in monospecific moss patches with *S. fuscum* and *S. lenense*. On the plots, length increment measurements were carried out using the brush-wire method (Rydin & Jeglum, 2013) in 2–4 replicates per plot. The length increment was measured for seven years, in 2013, 2015–2018, 2022 and 2023. The total number of replicates using brush-wire method was 6–12 for *S. lenense* and 6–14 for *S. fuscum* per year. In the monospecific moss patches adjacent to the permanent plots, cores with an area of 16.6 cm^2 were collected to determine the numerical density and the weight of capitula and increment. Number of core replicates were 3–7 per species a year. Capitula were calculated in cores, fractions of capitula and 30 mm stem below capitulum were dried at 60°C to a constant mass and weighed. Core sampling of such a technique had been carried out since 2016. Field work was carried out in the second decade of August.

The numerical density was expressed in number of capitula per dm^2; the increment weight was expressed in g of the absolutely dry weight of 1 mm of stem per m^2; the capitulum weight was expressed in mg per item. Net primary productivity of each species was equal to the weight of the length increment in the current year and was evaluated as multiplication of the increament weight by the length increment. Years 2013 and 2015 were not included in the productivity evaluation, as no cores were taken according to the technique described above.

To reveal the relationship between structural traits, numerical density and the weather, publicly available meteorological data were used (https://rp5.ru/ Accessed 01.VIII.2025). Since the vegetation season in the forest-tundra begins in June and ends in August, meteorological data over the period from June 1 to July 31 were taken in the analysis. The growth of *Sphagnum* depends primarily on water supply (Maksimov, 1982; Waddington *et al*., 2015; Bengtsson *et al*., 2016, 2021; Grabovik *et al*., 2024), including precipitation distribution (Nijp *et al*., 2014). Therefore, moisture-related predictors such as precipitation totals, number of rainy days, duration of the dry period and the climate index proposed by Asada *et al* (2003) were included in the analysis. The technique of calculating of the dry period duration proposed previously (Koronatova *et al*., 2022). Temperature may also be an effecting factor (Deane-Coe *et al*., 2015; Grabovik *et al*., 2024). Therefore, the average temperature of the warm period was included in the analysis.

Statistical data processing was performed using PAST v. 2.17 (Hammer *et al*., 2001). The obtained data hardly met the requirement of a normal distribution. Therefore, Spearman's rank correlation was used to search for rela-

Table 1. Meteorological parameters for the period 1.VI–31.VII over the study years (https://meteoinfo.ru Accessed 08.VIII.2025). T av – average temperature, Prec – total precipitation, RD – number of rainy days, DD – length of dry period, Ind – climatic coefficient proposed by Asada *et al*. (2003.).

Year	Parameters				
	T av, °C	Prec, mm	RD, days	DD, days	Ind
2013	14.5	93	26	11	17.4
2015	14.4	202	45	3	55.9
2016	18.0	44	20	23	11.9
2017	13.7	66	20	16	20.0
2018	14.1	100	28	12	25.8
2022	14.9	105	28	9	33.3
2023	14.2	133	38	2	38.8

tionship between traits, density and meteorological parameters. To compare data set of different years, Kruscal-Wallis test followed by Mann-Whitney pairwise comparison was used. The number of replicates of length increment and productivity varied between years. Therefore, to compare the two species over the entire observation period, the median values for each permanent plot were taken into consider. This ensured a similar number of replicates per year.

Results

The average long-term climatic properties in the Pangody town in June-July (averaging period 1991-2020) were as the follows: air temperature 13.3°C, precipitation totals 119 mm, number of rainy days 19 (Hydrometeorological…, 2025). The weather of the growing season (1.VI–31.VII) for the studied period of 2013-2023 had the following features (Table 1). During the seven years, the average air temperature varied from 13.7 to 14.9 °C. The exception was 2016, when the temperature reached 18.0 °C. Thus, during the observed period, the temperature always exceeded the long-term norm with the extreme increasing in 2016. The total precipitation was minimal in 2016, it was below the norm in 2017, and it was maximal in 2015. In 2013, 2018, 2022, and 2023, precipitations were close to the long-term average. The number of rainy days exceeded the long-term average in all years except 2016 and 2017, when it coincided with the norm. The number of rainy days and the duration of the dry period correlated with precipitation (Pearson correlation coefficient $k = 0.95$, $p = 0.00032$ and $k = -0.87$, p = 0.0047, respectively). The years 2015 and 2023 had the shortest dry period. The climate index (Asada *et al*., 2003) was also collinear with precipitation ($k = 0.95$, $p = 0.00025$). The index was highest in 2015, 2022 and 2023, which were characterized by high moisture and heat supply. Minimum index values were in 2013 and especially in 2016.

Structural traits of mosses varied widely from year to year. A similar pattern in the length increment dynamics was revealed for both species (Fig. 1). In 2016, the length increment was the lowest over the years of observation,

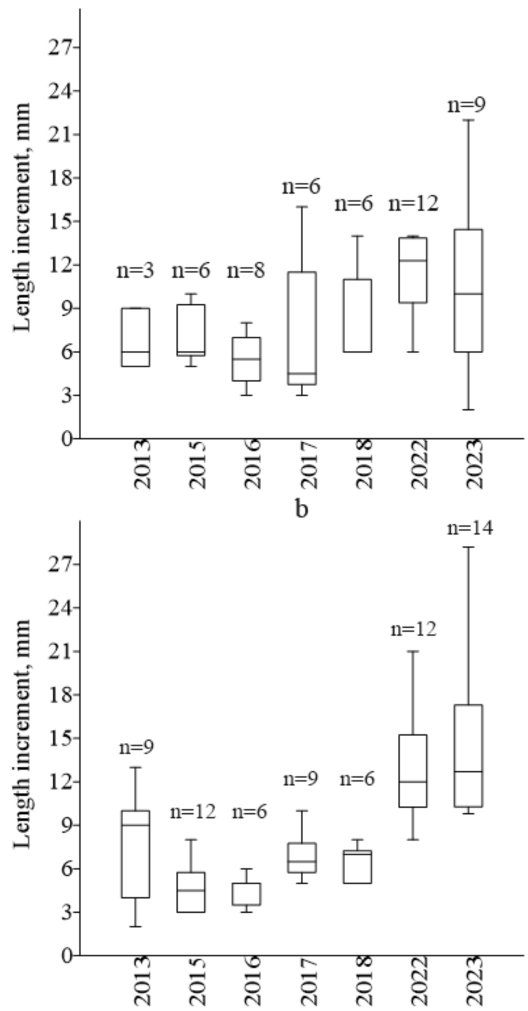

Fig. 1. Long-term dynamics of *S. lenense* (a) и *S. fuscum* (b) length increments. The 25–75 percent quartiles are drawn as boxes. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with whiskers, "n" means replicates per year.

and in 2022 and 2023, it became the highest. The interannual growth dynamics of *S. lenense* ranged less than that of *S. fuscum*. Mann-Whitney pairwise comparison (with the Bonferroni correction) of the length increment over the years showed a weak significant difference for *S. lenense* in the pair "2016–2022" ($p = 0.014$). A significant interannual difference of *S. fuscum* increment was found out between 2022, 2023 and the other years ($p < 0.05$) with the exception of the pairs "2013–2022" and "2022–2023"; the differences between 2016 and 2022, 2023 were the strongest ($p < 0.003$).

The interannual *S. lenense* weight of 1 mm of the increment slightly varied ranging from 16.5 to 20.1 g·m^{-2} (Fig. 2 a, b). As for *S. fuscum*, this trait was minimal in 2016 (16.5 1 g·m^{-2}) and almost doubled in 2017 (27.8 1 g·m^{-2}). In other years, it varied a little (18.4–21.1 1 g·m^{-2}). The weight of *S. lenense* capitulum was higher than that of *S. fuscum* (Fig. 2 c, d). The weight of *S. lenense* capitulum varied from 5.5 to 7.1 mg while *S. fuscum* ca-

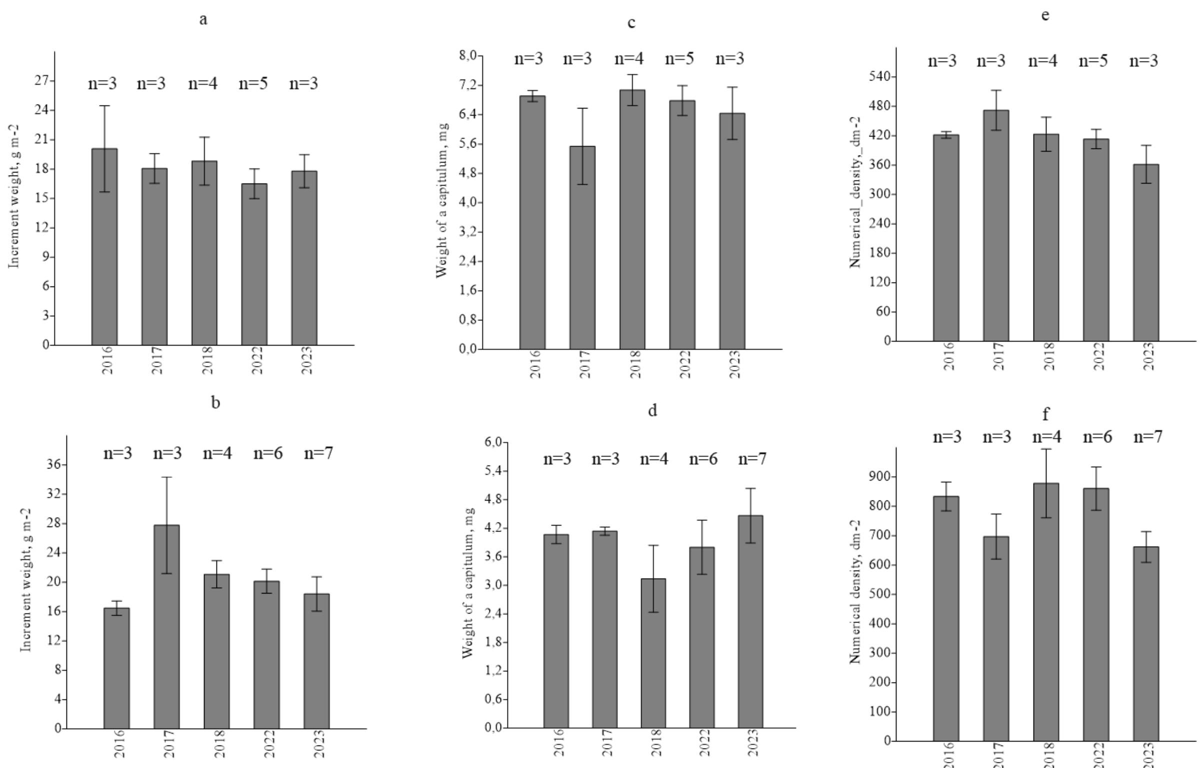

Figure 2. Long-term dynamics of structural traits and canopy density in *S. lenense* (a, c, e) and *S. fuscum* (b, d, f). The whisker interval represents the standard error, "n" means replicates per year.

pitulum varied from 3.1 to 4.5 mg. The numerical density of *S. lenense* ranged from 361 to 472 pcs·dm^{-2} in different years, and it was twice as high in *S. fuscum*, varying from 662 to 878 pcs·dm^{-2} (Fig. 2 e, f). The Kruscal-Wallis test revealed no significant differences among years in these traits or in density.

The primary productivity of both species showed a pattern similar to that of length increment dynamics. It was at its minimum in 2016 and at its maximum in 2022 and 2023 (Fig. 3 a, b). The median NPP of *S. lenense* varied within the range of 81–198 g·m^{-2} year^{-1}, while in *S. fuscum* it ranged from 82 to 242 g·m^{-2} year^{-1}, indicating greater variation. Significant interannual difference in productivity in *S. lenense* was found between 2022 and 2016 (Table 2). In *S. fuscum*, significant differences were also found between 2016, 2018 and other years with the exception of the pair "2017–2018".

To understand how weather conditions affect the traits, density and productivity of the mosses, a correlation analysis was performed. Length increment and productivity showed a significant relationship with moisture-related predictors but not with temperature (Table 3). The duration of the dry period was the strongest predictor of length increment of both species, shoeing a negative correlation. Productivity of both species responded primarily to precipitation, dry period, and the index. Interestingly, these relationships were stronger for *S. fuscum* than for *S. lenense*. No relationships with meteorological parameters were found for other structural traits or density.

Discussion

Over the seven-year study period, 2016 was characterized by extremely hot and dry weather conditions in June and August, which triggered major fires in the region. This year, the dry period in late July and August lasted for two consecutive two-week periods. Schipperges & Rydin (1998) showed that in the absence of capillary rise, photosynthesis ceases within four days in various *Sphagnum* species, while in the presence of capillary rise, it recovers more quickly in *S. fuscum*. In 2016, the median productivity of *S. fuscum* was 82 g·m^{-2} year^{-1}, which is 1.8–3.0 times lower than in other years. In contrast to *S. fuscum*, the median productivity of *S. lenense* in 2016 was higher than in 2017 and 1.9 times lower than in the most productive year, 2023. This indicates that under drought conditions, the productive capacity of *S. lenense* was higher and more stable. The most favorable moisture and temperature conditions occurred in 2015, and to a lesser extent in 2023 and 2022. Accordingly, the length increment and productivity of both species were maximal in 2022 and 2023, as confirmed by correlation analysis. Nevertheless, both length increment and productivity of these species were low in wet and warm 2015, which could be explained by excess precipitation, as excessively high humidity in capitula also reduces photosynthetic intensity (Schipperges & Rydin, 1998).

Numerical density, increment weight and capitula weight of both species did not differ between years and did not depend on the weather conditions. For *S. fuscum*, this result is inconsistent with the previously established

Table 2. Bonferroni corrected Mann-Whitney pairwise comparisons of *Sphagnum* NPP: *p* values for *S. lenense* (below diagonal) and *S. fuscum* (above diagonal).

	2016	2017	2018	2022	2023
2016		0.016	0.015	0.0013	0.00079
2017	1		0.62	0.54	0.35
2018	1	1		0.031	0.0061
2022	0.022	0.82	1		0.98
2023	0.92	1	1	1	

dependence of the density on weather conditions in the south of Western Siberia (Koronatova *et al*., 2022). This may be due to the fact that *S. fuscum* achieves maximum canopy density under forest-tundra conditions, which limits its density dynamics. For example, in the southern taiga of Western Siberia, the average annual density of the species ranged from 431 to 819 pcs·dm^{-2}, varying almost twofold (Koronatova *et al*., 2022). In this study, density renged from 662 to 878 pcs·dm^{-2}, varying only 1.3-fold.

To reveal differences in traits, density and productivity between *S. lenense* and *S. fuscum*, averaged and median parameters were assessed over all observation years, and the statistical tests of differences were performed (Table 4). Overall, the median and average values were close. However, the median value was often smaller than the average one, indicating a shift in the peak of the sample distribution toward lower values. Length increment and increment weight of both species were similar, with no significant differences between them. Compared to the southern boreal zone of Western Siberia (Koronatova *et al*., 2022), the length increment of *S. fuscum* was 2.5 times lower, while the increment weight was 1.5 times higher. This suggests that in the Arctic, annual increment decreases and moss canopy density increases, which smooths out the difference in productivity between the south and the north of the region. *Sphagnum fuscum* net productivity was only 1.4 times higher in the south of the region. In the forest-tundra, the difference in productivity between two species was not convincing. Significant differences were observed between them in numerical density and capitulum weight, which can be attributed to species-specific features. Additionally, these parameters of *S. fuscum* were higher than those in the southern taiga of Western Siberia.

Table 3. Spearman's correlation between the length increment and productivity of two species and meteorological predictors of growing seasons. *P*–values: * p <0.05, ** p <0.01, *** p <0.001. Absence of * indicates no significant difference. LI – length increment, NPP – net primary productivity of the species. Abbreviations for meteorological predictors are given in Table 1.

Predictors	*S. lenense*		*S. fuscum*	
	LI	NPP	LI	NPP
T av	0.02	0.02	–0.13	–0.22
Prec	0.33*	0.42**	0.44***	0.74***
RD	0.29*	0.38*	0.39**	0.62***
DD	–0.37**	–0.42**	–0.61***	–0.74***
Ind	0.33*	0.42**	0.43***	0.74***

This study assessed structural traits and canopy density of *S. lenense* and *S. fuscum* in the forest-tundra zone of Western Siberia. It revealed significant differences between the species in numerical density and capitulum weight. For *S. fuscum*, these parameters increased in permafrost peatlands compared to bogs in the southern taiga of Western Siberia, while other traits were lower. The dynamics of length increment and productivity showed significant correlations with weather factors, including moisture during the growing season and, to the greatest extent, dry period duration. No dependence on air temperature was found. No relationships were found between numerical density, increment weight, capitula weight and weather.

ACKNOWLEDGEMENTS

The author is grateful to her colleagues Natalia Kosykh and Vera Stepanova who accompanied and assisted in the fieldwork. The work was carried out under the state assignment from the Institute of Soil Science and Agrochemistry SB RAS.

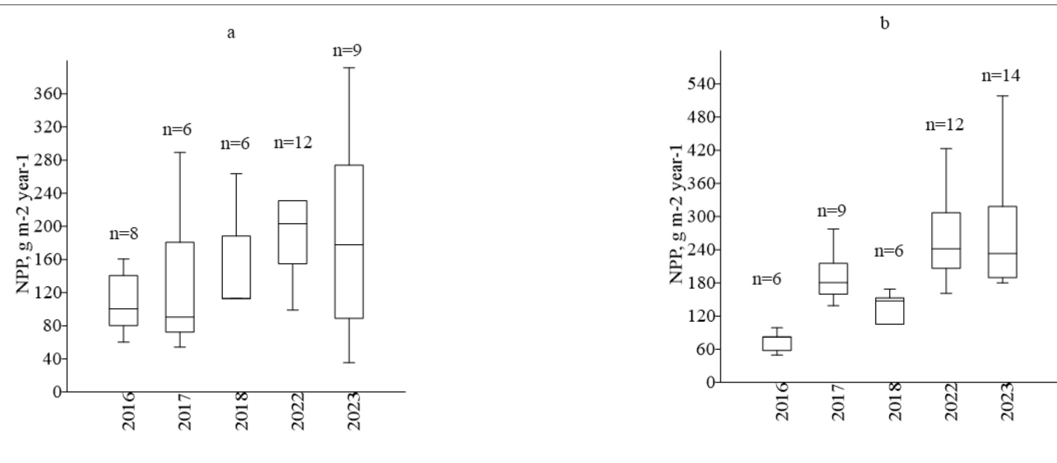

Figure 3. Long-term dynamics of *S. lenense* (a) and *S. fuscum* (b) productivity. The 25–75 percent quartiles are drawn as boxes. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with whiskers, "n" means replicates per year.

Table 4. Comparison of structural traits, canopy density and productivity of *S. lenense* and *S. fuscum* over the entire observation period from 2013 to 2023. The reliability of differences were assessed using Mann-Whitney test.

Parameters	*S. lenense*	*S. fuscum*	*p*-value
length increment, mm: sample size	50	68	
average ± standard error	8.0 ± 0.6	8.2 ± 0.4	0.69
median	7.1	8.1	
Weight of 1 mm length increment, g·m–2: sample size	18	23	
average ± standard error	18.1 ± 1.0	20.3 ± 0.9	0.25
median	17.4	18.7	
Weight of a capitulum, mg: sample size	18	23	
average ± standard error	6.6 ± 0.3	4.0 ± 0.3	$2.41 \cdot 10^{-6}$
median	6.7	4.1	
Numerical density, pcs·dm–2: sample size	18	23	
average ± standard error	418 ± 14	778 ± 36	$6.16 \cdot 10^{-8}$
median	425	771	
Productivity, g·m–2 year–1: sample size	41	47	
average ± standard error	151 ± 11	186 ± 9	0.045
median	134	177	

Literature cited

ALPERT, P. & W.C. OECHEL. 1984. Microdisrtibution and water loss resistances of selected bryophytes in an Alalskan *Eriophorum* tussock tundra. – *Holarctic Ecology* **7**: *111–118*.

ASADA, T., B.G. WARNER, A. BANNER. 2003. Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. – The Bryologist **106(4)**: *516–527*. http://doi.org/10.1639/0007-2745(2003)106[516: GOMIRT] 2.0.CO;2

BENGTSSON, F., G. GRANATH, H. RYDIN. 2016. Photosynthesis, growth, and decay traits in *Sphagnum* – a multispecies comparison. – *Ecology and Evolution* **6(10)**: *3325–3341*. https://doi.org/10.1002/ece3.2119

BENGTSSON, F, G. GRANATH, N. CRONBERG, H. RYDIN. 2020. Mechanisms behind species-specific water economy responses to water level drawdown in peat mosses. – *Annals of Botany* **20**:1–12. https://doi.org/10.1093/aob/mcaa033

BENGTSSON, F, H. RYDIN, J.L. BALTZER, L. BRAGAZZA, ZH.-J. BU, S.J.M. CAPORN, E. DORREPAAL et al. 2021. Environmental drivers of *Sphagnum* growth in mires across the Holarctic region. – *Journal of Ecology* **109**(1): *417–431*. https://doi.org/10.1111/1365-2745.13499

DEANE-COE, K.K., M. MAURITZ, G. CELIS, V. SALMON, K.G. CRUMMER, S.M. NATALI & E.A.G. SCHUUR. 2015. Experimental warming alters productivity and isotopic signatures of tundra mosses. – *Ecosystems* **18(6)**: *1070–1082*. https://doi.org/10.1007/s10021-015-9884-7

[GRABOVIK, S.I., L.V. KANTSEROVA & S.R. ZNAMENSKIY] ГРАБОВИК, С.И., Л.В. КАНЦЕРОВА, С.Р. ЗНАМЕНСКИЙ. 2024. Результаты многолетних исследований годичного прироста мхов рода *Sphagnum* L. В среднетаежной Карелии. – [Results of long-term studies of the annual growth of mosses of the genus Sphagnum L. in the central taiga of Karelia] *Экология* [*Russian Journal of Ecology*] **4**: *256–272*. http://doi.org/10.31857/S0367059724040021

HAMMER, O., D.A.T. HARPER & P.D. RYAN. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. – *Palaeontologia Electronica* **4**(1): *9pp*.

JORGENSON, M.T., M. KANEVSKIY, C. ROLAND, K. HILL, D. SCHIROKAUER, S. STEHN, B. SCHROEDER & Y. SHUR. 2022. Repeated permafrost formation and degradation in boreal peatland ecosystems in relation to climate extremes, fire, ecological shifts, and a geomorphic legacy. – *Atmosphere* **13**: *1170*. http://doi.org/10.3390/atmos13081170

KOLESNICHENKO, L.G., S.N. VOROBYOV, S.N. KIRPOTIN, IU.Y. KOLESNICHENKO, R.M. MANASYPOV, I.I. VOLKOVA, V.I. SUSLYAEV, K.V. DOROZHKIN, A.V. SOROTCHINSKY & O.S. POKROVSKY. 2019. Changes in the palsa landscapes' components in the West Siberian northern taiga 10 years after wildfires. – *IOP Conference Series: Earth and Environmental Science* **232**: *012021*. http://doi.org/10.1088/1755-1315/232/1/012021

KONSTANTINOVA, N.A., E.D. LAPSHINA & G.N. GANASEVICH. 2023. The liverworts of the Avam tundra (southern Taimyr). – *Arctoa* **32**: *34–47*. http://doi.org/10.15298/arctoa.32.04

KONSTANTINOVA, N.A., E.D. LAPSHINA & I.V. FILIPPOV. 2024. Liverworts of the southern part of "Kytalyk" national park (tundra zone of republic of Sakha (Yakutia), Russia) – *Arctoa* **33**: *172–183*. http://doi.org/10.15298/arctoa.33.18

KORONATOVA, N.G., N.P. KOSYKH, E.A. SAIB, V.A. STEPANOVA, E.K. VISHNYAKOVA & G. GRANATH. 2022. Weather factors in different growing periods determine inter-annual change in growth of four *Sphagnum* species: evidence from an eight-year study. – *Wetlands* **42(8)**: *118*. https://doi.org/10.1007/s13157-022-01636-5

LAING, C.G., G. GRANATH, L.R. BELYEA, K.E. ALLTON & H. RYDIN. 2014. Tradeoffs and scaling of functional traits in *Sphagnum* as drivers of carbon cycling in peatlands. – *Oikos* **123**: *817–828*. https://doi.org/10.1111/oik.01061

[LAPSHINA, E.D., I.V. FILIPPOV & G.N. GANASEVICH] ЛАПШИНА, Е.Д., И.В. ФИЛИППОВ, Г.Н. ГАНАСЕВИЧ. 2023. Растительность торфяных бугров болотных комплексов севера Западной Сибири и полуострова Таймыр. – [The vegetation of frozen peat palsa of mire complexes in the north of Western Siberia and Taimyr peninsula] *Растительность России* [*Vegetation of Russia*] **47**: *72–111*. http://doi.org/10.31111/vegrus/2023.47.72

LUKEN, J.O. & W.D. BILLINGs. 1984. Succession and biomass allocation as controlled by *Sphagnum* in an Alaskan peatland. – *Canadian Journal of Botany* **63**: *1500–1507*.

[MAKSIMOV, A.I.] МАКСИМОВ А.И. 1982. К вопросу о приросте сфагновых мхов. – [To the question of *Sphagnum* growth]. *В кн.: Комплексные исследования растительности болот Карелии (ред. Лопатин, В.Д. и Юдина, В.Ф.) Петрозаводск: Кар. отд-ние АН СССР [In: Lopatin, V.D., Yudina, V.F. (eds) Kompleksnye issledovaniya rastitelnosti bolot Karelii. Petrozavodsk: KB AS USSA]: 170–179*.

MAZZIOTTA, A., G. GRANATH, H. RYDIN, F. BENGTSSON & J. NORBERG. 2019. Scaling functional traits to ecosystem processes: towards a mechanistic understanding in peat mosses. – *Journal of Ecology* **107**: *843–859*. http://doi.org/10.1111/1365-2745.13110

NIJP, J.J., J. LIMPENS, K. METSELAAR, S.E.A.T.M.VAN DER ZEE, F. BERENDSE & B.J.M. ROBROEK. 2014. Can frequent precipitation moderate the impact of drought on peatmoss carbon uptake in northern peatlands? – *New Phytologist* **203**: *70–80*. http://doi.org/10.1111/nph.12792

PAAL, J., A. PESTEROV & V. NESHATAEVA. 2021. Diversity of *Pinus pumila*-dominated communities of the Kamchatka Peninsula. – *Forestry Studies | Metsanduslikud Uurimused* **74**: *26–57*.

PASTUKHOV, A., T. MARCHENKO-VAGAPOVA, S. LOIKO & D. KAVERIN. 2021. Vulnerability of the Ancient Peat Plateaus in Western Siberia. – *Plants* **10**: *2813*. http://doi.org/10.3390/ plants10122813

POPOV, YU.S. 2019. Species distribution patterns in subgenus Cuspidata (genus Sphagnum L.) on the East European Plain and Eastern Fennoscandia. *In*: *M.S. Sabovljevic and A.D. Sabovljevic (eds.). Bryophytes. IntechOpen.* http://doi.org/10.5772/intechopen.84648

PREIS, YU.I., G.V. SIMONOVA & E.A. SLAGODA. 2016. Detailed reconstruction of the functional state of the Central Yamal khasyrey as a response to local conditions and regional climate changes in the late Holocene. – *IOP Conference Series: Earth and Environmental Science* **48**: 012010. http://doi.org/10.1088/1755-1315/48/1/012010

RAUDINA, T.V., G.I. ISTIGECHEV & S.V. LOIKO. 2023. Soil-ecological conditions of the north taiga flat-mound bog, Western Siberia. – *Acta Biologica Sibirica* **9**: *195–208*. http://doi.org/10.5281/zenodo.78548<u>16</u>

RYDIN, H. & J.K. JEGLUM. 2013. *The biology of peatlands, 2nd edn. Oxford: Oxford University Press: 432 p*.

SCHIPPERGES, B. & H. RYDIN. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation – *New Phytologist* **140**: *677–684*.

VITT, D.H. 2014. A key and review of bryophytes common in North American peatlands. – *Evansia* **31(4)**: *121–158*. http://dx.doi.org/10.1639/079.031.0402

WADDINGTON, J.M., P.J. MORRIS, N. KETTRIDGE, G. GRANATH, D.K. THOMPSON & P.A. MOORE. 2015. Hydrological feedbacks in northern peatlands. – *Ecohydrology* **8**: *113–127*. https://doi.org/10.1002/eco.1493

ZAROV, E.A., L.L. GOLUBYATNIKOV, E.D. LAPSHINA & S.V. LOYKO. 2021. Vegetation and soils of tundra landscapes in the Pur–Taz interfluvial region. – *Biology Bulletin* **48**, Suppl. 3: *S118–S127*. http://doi.org/10.1134/S1062359022010186

Received 12 October 2025 *Accepted 15 December 2025*