

# Controls of *Sphagnum* growth and the role of winter

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## Abstract

*Sphagnum* is the major genus in northern peatlands that contributes to peat formation and carbon sequestration. *Sphagnum* growth in summer has been fairly well studied but the information about growth in autumn and winter is limited. Therefore, we studied how the growth of *Sphagnum* is seasonally distributed with a particular interest on possible winter growth. The linear increment and biomass production of three *Sphagnum* species was measured in three Northern European bogs over a year. In all sites, our results indicate the highest annual linear increment in *S. angustifolium* (28 mm), followed by *S. magellanicum* (20 mm) and *S. fuscum* (13 mm), but the biomass production was fairly even among the species (189, 192 and 215 g m<sup>-2</sup>, respectively). Both linear increment and biomass production depended mostly on meteorological parameters rather than ecophysiological or microsite properties. The seasonal measurements revealed a significant linear increment and biomass production during the winter that accounted for ca. 10% and ca. 5% from the annual values, respectively. Moreover, the mean daily rates of linear increment in autumn often exceeded the increment in summer. Our results thus indicate the ability for year-around growth of *Sphagnum* if the conditions are favorable, including during boreal winter.

## KEYWORDS

biomass production, linear increment, peat moss, peatland, seasonality

## 1 | INTRODUCTION

Northern peatlands store vast quantities of carbon through the accumulation of peat, and thus play a significant role in the global carbon cycle. The accumulation of peat is a result of imbalance between the production and decay of plants. *Sphagnum* mosses play a major role in it: they cover 1.5 million km<sup>2</sup> of northern peatlands and hold over 150 Gt of carbon (Rydin & Jeglum, 2013)—more than any other terrestrial plant genus (Clymo & Hayward, 1982). *Sphagnum* mosses are ecosystem engineers of the majority of ombrotrophic peatlands, successful in growth, distribution and competition with other plants. If a *Sphagnum* population has established on a peatland, it starts to rapidly increase and modify the

habitat by making it wet, acid, nutrient-limited and anoxic (Van Breemen, 1995). These conditions are characteristic of ombrotrophic peatlands.

*Sphagnum* species cover a range of specific habitats along several environmental gradients, such as shade, nutrient status, microtopography and water table (Rydin & Jeglum, 2013; Vitt, 1990). Mean air temperature, photoperiod, precipitation and water table have generally been considered to primarily control the growth of *Sphagnum* (Gerdol, 1995; Grabovik & Nazarova, 2013). Correspondingly, temperature decreases northwards with a concomitant decrease in *Sphagnum* growth (Gunnarsson, 2005). Nevertheless, *Sphagnum* growth is positively correlated with a warmer temperature only if it is not compromised by low capitula water content (Asada, Warner, & Banner,

2003; Dorrepaal, Aerts, Cornelissen, Callaghan, & van Logtestijn, 2004; Grabovik & Nazarova, 2013).

The phenology of moss growth and photosynthesis differ from vascular plants (Glime, 2017). *Sphagnum* mosses have a poikilohydric water economy, and thus their active period for growth and photosynthesis is mainly restrained by the availability of water (Gaberščik & Martinčič, 1987; Robroek, Schouten, Limpens, Berendse, & Poorter, 2009). For example, Lindholm (1990) demonstrated that *S. fuscum* produces biomass when temperature exceeds 0°C. It is therefore likely that *Sphagnum* growth is not restricted to the traditional growing season of most vascular plants, and that their growth and other physiological processes do not cease in the late summer but can continue year-around (Krebs, Gaudig, & Joosten, 2016). While the studies targeting winter growth are limited, evidence for its existence have been found: Asada et al. (2003) proposed that in the maritime region at the West-Coast of Canada winter growth is likely. Their estimations were based on the linear relationships between the Climate Index and growth of several *Sphagnum* species. Hulme and Blyth (1982) have given a similar estimation for South-west Scotland. Krebs et al. (2016) have recorded winter growth (both linear increment and production) of *S. papillosum* and *S. palustre* in Georgia (Transcaucasus), affirming the possibility of continuous growth year-around if frost is absent. In addition to locations with mild oceanic climate, late-autumn and winter growth of *Sphagnum* has been measured at higher latitudes with more continental climate as well. In several types of peatlands in Southern Finland 1/4–1/3 of annual *Sphagnum* growth have been detected outside the classical growth period (from late September to May, when daily mean air temperature does not exceed 5°C) (Laine, Juurola, Hajek, & Tuittila, 2011; Maanavilja, Kangas, Mehtätalo, & Tuittila, 2015). Lütt (1992) has documented a late-autumn and winter growth of *Sphagnum* in Northern Germany as well. However, the focus of these papers has been elsewhere, and thus so far the winter growth of *Sphagna* have not been studied and discussed in detail. Therefore, the mechanisms behind and seasonality of *Sphagnum* growth are not entirely understood. Given that *Sphagnum* species differ in their climatic preferences (Breeuwer, Heijmans, Robroek, & Berendse, 2010), the seasonal and geographic variations in *Sphagnum* growth are likely species specific.

The majority of *Sphagnum*-dominated peatlands can be found at high latitudes (>45°N) where the rate of climate change is expected to be above the global average, and is particularly rapid in winter (Jylhä, Tuomenvirta, & Ruosteenoja, 2004; Lode, Küttim, & Kiiivit, 2017; Makoto et al., 2014). In addition to the warmer air temperatures in winter, precipitation will come more often as rain, and the snow cover will decrease both in thickness and

duration (Templer, 2012). Consequently, it will leave ground vegetation, including mosses, exposed to the rapid changes in temperature (Bombonato & Gerdol, 2012), and alter the functions of northern terrestrial, including carbon and nutrient cycling (Makoto et al., 2014). Although the responses are species specific, climate warming is generally expected to increase *Sphagnum* productivity (Zhaojun et al., 2011). However, the possible shifts in the seasonal distribution of cumulative *Sphagnum* growth due to changing climate have not gained much attention and thus are not well known. While the increased length of autumn, higher overall temperatures and rate of precipitation could favor *Sphagnum* growth, midsummer desiccation, lack of protecting snow cover and thus lower minimum temperatures in winter could reduce the *Sphagnum* growth (Gerdol, 1996; Hajek, 2014; Küttim et al., 2017; Yazaki & Yabe, 2012).

In this study, we measured the seasonal linear increment and biomass production of three widespread *Sphagnum* species in three ombrotrophic peatlands in Northern Europe. Climatic factors, especially winter conditions, including the continuity of snow cover, differ among the sites. This climatic gradient allows us to use the plants of our southern sites as sentinels of future behavior under a warmer climate at northern latitudes. We divide the annual growth period into three seasons, namely autumn, winter and late spring/summer. With these data we aim to (a) quantify interspecies differences in growth rate, (b) evaluate the impacts of latitudinal climatic gradient on *Sphagnum* growth and (c) quantify the contribution of growth per season to the annual growth rate. We use seasonal meteorological parameters, micro-site properties and the ecophysiological traits of *Sphagnum* in explaining the growth rates. The likely effects of a changing climate on the growth of *Sphagnum* during different seasons are discussed.

## 2 | MATERIALS AND METHODS

### 2.1 | Focal species

We chose three common and widespread *Sphagnum* species, typical of ombrotrophic bogs, as our focal species. *S. angustifolium* (Russ.) C. Jens. (section Cuspidata) is a medium-sized yellowish moss that grows most often in a loose form on the low hummocks and lawns of marginal wooded edges of peatlands and paludified forests. *S. fuscum* (Schimp.) Klinggr. (section Acutifolia) is a small brownish moss that forms tall compact hummocks in ombrotrophic peatlands, where it is the main contributor to peat formation. *S. magellanicum* Brid. (section Sphagnum) is a large red (in open habitats) or greenish (in the shade) moss. This

species forms low hummocks and extensive lawns in ombrotrophic and weakly minerotrophic peatlands.

## 2.2 | Study sites

We chose three ombrotrophic bogs along a circa 800-km latitudinal gradient as our study sites: two bogs in Estonia and one in Finland (Figure 1). The southernmost of them, the excentric Männikjärve bog, is located in Central Estonia, in the hemiboreal vegetation zone. Pääsküla bog is situated in Northern Estonia, close to the city of Tallinn. Due to its proximity to the Baltic Sea its climate is more maritime than at the other two sites. Most of this large bog (946 ha) has been drained, but our sampling location is situated in the nearly pristine part of the bog that accounts only for 10 ha. Likasuo bog is situated in Northwestern Finland ~ 30 km to northeast from the Bothnian Bay and the city of Oulu. It belongs to a boreal vegetation zone, and has a subarctic climate. Meteorological records of each study site were attained from the Estonian Weather Service and from the Finnish Meteorological Institute (Table 1).

In general, all study sites have similar conditions: low pH (ca 4), electrical conductivity (EC < 50  $\mu\text{S cm}^{-1}$ ) and the peat layer exceeding 2.5 m; however, the climatic

conditions between the Estonian and Finnish sites clearly differ (Table 1).

At the beginning of our study in early autumn 2014 the water table at the lawn surfaces was on average similar at all sites: -19 cm in Männikjärve, -22 cm in Pääsküla and -16 cm in Likasuo. The annual fluctuation of the water table generally remains within 10 cm in open and within 20 cm in wooded parts of our bog sites, being the deepest in August and the highest in April.

In all sites, the tree cover varies from a few dozen Scots pines (*Pinus sylvestris* L.) per 100 m<sup>2</sup> in the marginal wooded bog microsite, to few scarce pines around the wet hollows (see for more from Küttim, Küttim, Puusepp, & Sugita, 2016; Lode et al., 2017). The ground vegetation in the wooded part of the bogs is dominated by species like *Ledum palustre* L., *Empetrum nigrum* L. subsp. *nigrum*, *Rubus chamaemorus* L., *Calluna vulgaris* L., *Andromeda polifolia* L. and *Eriophorum vaginatum* L. The open parts of the bogs are rather poor in vascular plant species with the dominance of *Trichophorum cespitosum* (L.) Hartm., *Rhynchospora alba* (L.) Vahl., *Ledum palustre* L., *Scheuchzeria palustris* L. and *Vaccinium oxycoccus* (L.). The moss layer is dominated by *Sphagnum angustifolium*, *S. magellanicum*, *S. fuscum* and *Pleurozium schreberii* (Brid.) Mitt. and J. Linn. in the wooded bog, and *S. magellanicum*, *S. fuscum*, *S. balticum* (Russ.) C. Jens. and *S. rubellum* Wils. in the



**FIGURE 1** Locations of the study sites: Männikjärve (M), Pääsküla (P) and Likasuo (L) bogs

**TABLE 1** The prevailing annual mean environmental conditions at the study sites during the study period (2014/15) and preceding years (2007/08–2013/14)

	Männikjärve		Pääsküla		Likasuo	
Coordinates	N 58°52'; E 26°14'		N 59°21'; E 24°39'		N 65°07'; E 26°00'	
Elevation above the sea level (m)	78		36		60	
Area (ha)	320		10		78	
	Mean	2014/15	Mean	2014/15	Mean	2014/15
Air temperature (°C)	5.83	6.33	6.3	7.57	2.22	2.99
Winter air temperature (December–February; °C)	−5.24	−1.91	−3.45	−0.34	−9.33	−6.53
Sum of precipitation (mm)	736	613	734	589	571	735
Days with precipitation	194	180	182	184	151	183
Days with snow cover	121	106	109	76	170	188
Mean snow depth (cm)	28	6	15	4	33	34
Daylight time (June 24)	04:06–22:24 (18:17 hr)		04:04–22:42 (18:39 hr)		02:20–00:20 (22:00 hr)	
Daylight time (December 24)	09:01–15:23 (06:22 hr)		09:18–15:22 (06:03 hr)		10:29–14:05 (03:36 hr)	
Distance to the meteorological station (km)	0.8		6.5		52.8	

Note: Meteorological records are provided by the Estonian Weather Service and the Finnish Meteorological Institute. Daylight durations are downloaded from timeanddate.com. According to the timing of the study the annual data is from 1 October to 30 September of the following year.

open areas. In both of wooded and open bog, *Sphagnum* mosses have formed hummocks up to 40 cm. The hollows are inhabited by *S. cuspidatum* Ehrh. ex Hoffm. in Estonian sites, and by *S. majus* (Russ.) C. Jens. and *S. lindbergii* Schimp. in Likasuo.

### 2.3 | Study set-up and measurements

In each study site we established sample plots ( $\varnothing = 50$  cm) into monocultures of *Sphagnum angustifolium*, *S. fuscum* and *S. magellanicum*, five plots per species so that they covered the microtopographic and tree cover gradients as evenly as possible. As the variation in Scots pine cover was considerably higher in Männikjärve, we established 10 plots per species there. Therefore, we had 60 plots in total. Microforms were distinguished according to their relative height: hummock as a positive, hollow as a negative and lawn as a neutral microform. Their relative height was measured from the bottom of the nearby deepest hollow. For the temperatures at the moss surface ( $T_M$ ), hourly recording temperature data loggers (Lascar Electronics EL-1, UK; 12 loggers in total) were installed to the capitula level of the moss layer of certain plots so to cover the variation in shading and microforms of the plots.  $T_M$  data of the most similar logger-equipped plot in terms of shade and microform was applied to each plot. Freeze–thaw cycles were counted according to these  $T_M$  data: in case of negative  $T_M$  in the night and positive  $T_M$  value in the day-time, the cycle was counted to be present. The shade of the

vascular plants was evaluated by comparing the light intensity measured by the luxmeter (Li-Cor Li-189, USA) on top of the moss layer and 1.5 m above it. Around the sample plots, we measured tree height, shrub height and the distance of the sample plots from the trees, and estimated canopy closure.

We used stainless steel cranked wires (Clymo, 1970) to measure the linear increment of mosses, as this is the only method enabling repeated growth measurements of the same *Sphagnum* shoots. Three wires per plot were installed in late September–early October 2014 to each sample plot. The height increment of *Sphagnum* was measured (a) in late November 2014 before the first snow (autumnal growth); (b) in April 2015 after the snowmelt and saturation of *Sphagnum* with melt water that indicated the recovery from the snowpack-caused compaction (winter growth); and finally (c) in late September–early October 2015 (summer growth during the classical growing season; Supporting Information 1). As some of the cranked wires heated up in the summer and caused damage to the nearest mosses, the measurements were implemented on the closest healthy looking shoots. At each visit, we took a 6 cm diameter moss sample from each plot using a plastic tube, trying to leave the surroundings of the wires intact. The sample was cut into two segments—capitulum (0–1 cm) and upper stem (1–3 cm). The shoots were counted and 30 shoots from both segments dried for 24 hr at 65°C for *Sphagnum* biomass, bulk density and water content estimations.

We used about half of these dry *Sphagnum* samples ( $n = 31$  per season,  $n = 93$  in total)—covering all sites, species and the microtopographic variation—to analyze their nutrient (N, P, K) concentration from the two segments of *Sphagnum* shoots in a laboratory. From Pääsküla and Likasuo, three samples per species from different microforms (hummock, lawn, hollow) were analyzed. In Männikjärve we had to consider higher variation in tree cover, and thus four samples of *S. angustifolium* and *S. fuscum*, and five samples of *S. magellanicum* were analyzed for nutrients. N concentration was analyzed according to Kjeldahl method (burning with  $H_2SO_4$ ), dilution with water and measured by Kjeltec Auto 1030 analyser. P concentration was measured photometrically (720 nm) after wet ashing the samples. Ammonium lactate extractable method with flame photometry was used to determine the K concentration of *Sphagnum* capitula and upper stem.

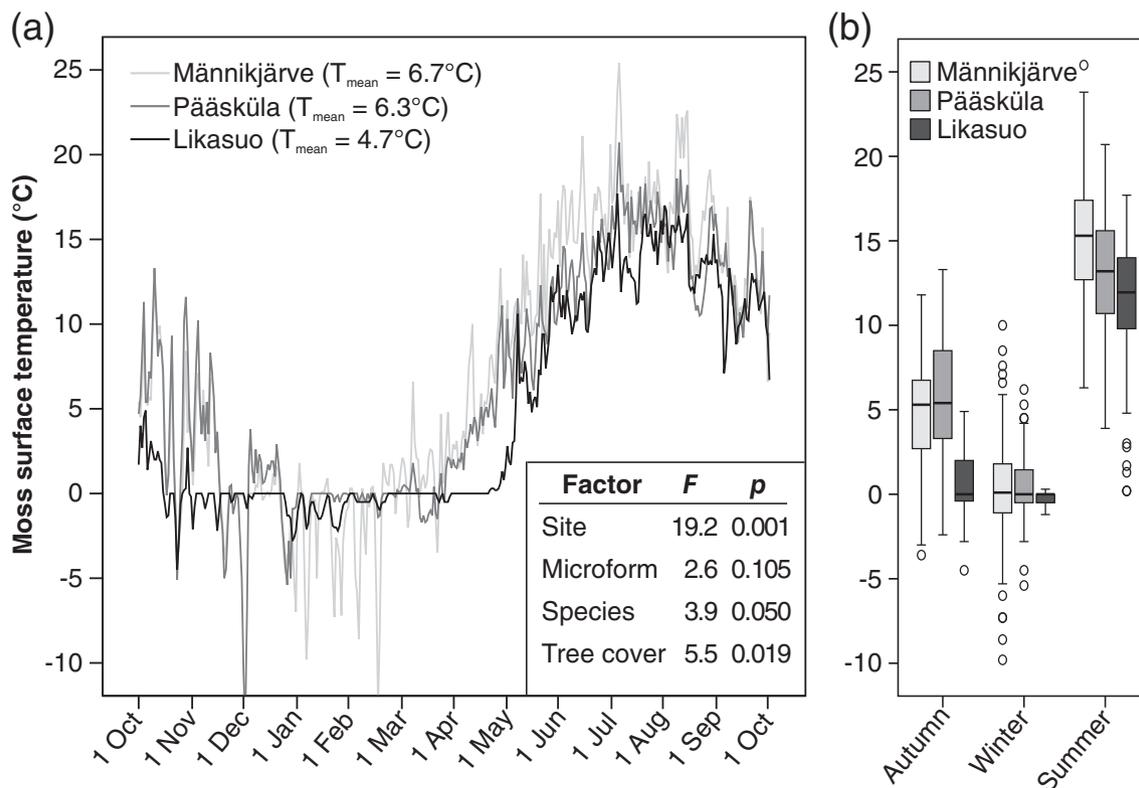
In addition, we collected randomly approximately 10 shoots of *Sphagnum* from each sample plot for the chlorophyll concentration analyses at the end of each season. The samples were deep frozen shortly after collection. Chlorophyll concentrations from the two segments of *Sphagnum* were analyzed using 80% acetone method (Porra, Thompson, & Kriedemann, 1989) by measuring

the absorbance at 470, 647, 664 and 750 nm by UV spectrophotometer Shimadzu UV-1800 (Japan).

## 2.4 | Data analyses

Before the analyses, three estimates of the linear increment per sample plot were pooled. The biomass production was calculated according to the linear increment, number of shoots per unit area, and the bulk density of the upper stem. Throughout this paper, data are given as mean values  $\pm 1$  SE. Ecophysiological traits (linear increment and production, concentrations of nutrients and *chlorophyll-a*) were analyzed with generalized linear mixed models (GLMM), with season, species and site as fixed factors. The same method was applied to test the dependence of daily mean temperature on the capitula layer ( $T_M$ ) on the study site, tree cover, microtopography and *Sphagnum* species. Post hoc differences were found by the Tukey test.

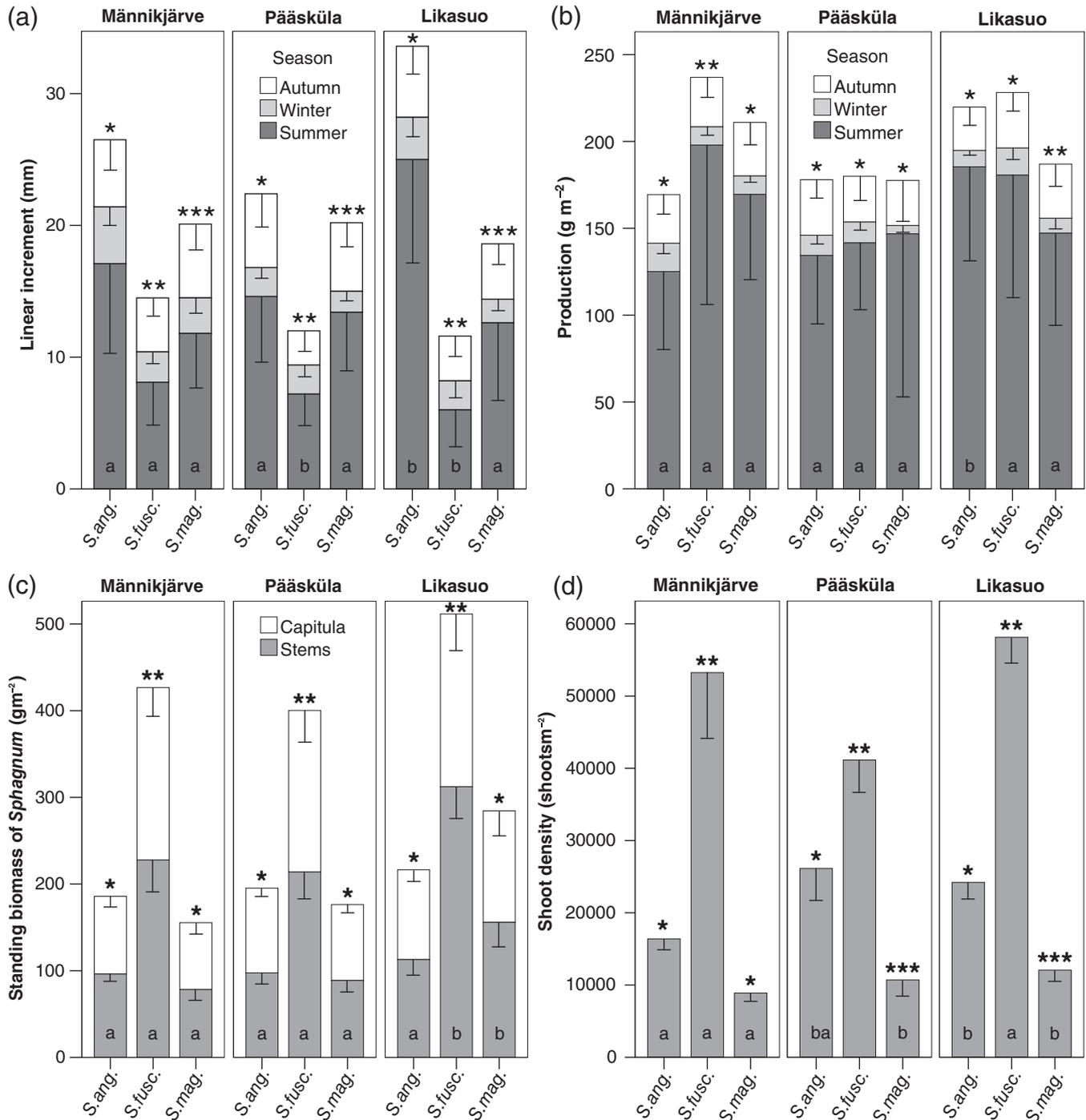
To assess the effect of environmental and ecophysiological parameters on annual *Sphagnum* growth in linear increment and biomass production we applied a two-step linear regression models (Backeus, 1988). This approach was chosen due to a large amount of possible parameters



**FIGURE 2** The average daily temperatures on the capitula level of the moss layer ( $T_M$ ) at the study sites during the annual study period (October 2014–October 2015) by its (a) daily dynamics and (b) among its seasonal ranges. The ANOVA results of the generalized linear mixed models (GLMM) on the effect of the study site, microform, *Sphagnum* species and tree cover on the daily  $T_M$  according to the temperature loggers ( $n = 12$ ) are added

explaining the growth. Models were built separately for the linear increment and biomass production of each species and season but combining all the sites. In the first analysis, each environmental and ecophysiological parameter was treated separately as a single predictor of

*Sphagnum* growth in a simple linear regression. As a second step, significant predictors at  $p \leq .05$  level were entered to a multiple stepwise linear regression with a forward selection. Separate models were performed for the linear increment and biomass production of each species



**FIGURE 3** The growth in (a) length and (b) biomass of *Sphagnum angustifolium*, *S. fuscum* and *S. magellanicum* during 1 year: during the autumn, winter and summer (exact periods given in Supporting Information 1). (c) Standing biomass and (d) shoot density of the focal species are given for the end of the measuring period. Statistical difference between the species is indicated by asterisks, and between the sites by letters ( $p < .05$ ). Different number of asterisks or different letter indicates statistical difference between the species and between the sites. Data are mean values  $\pm 1 SE$

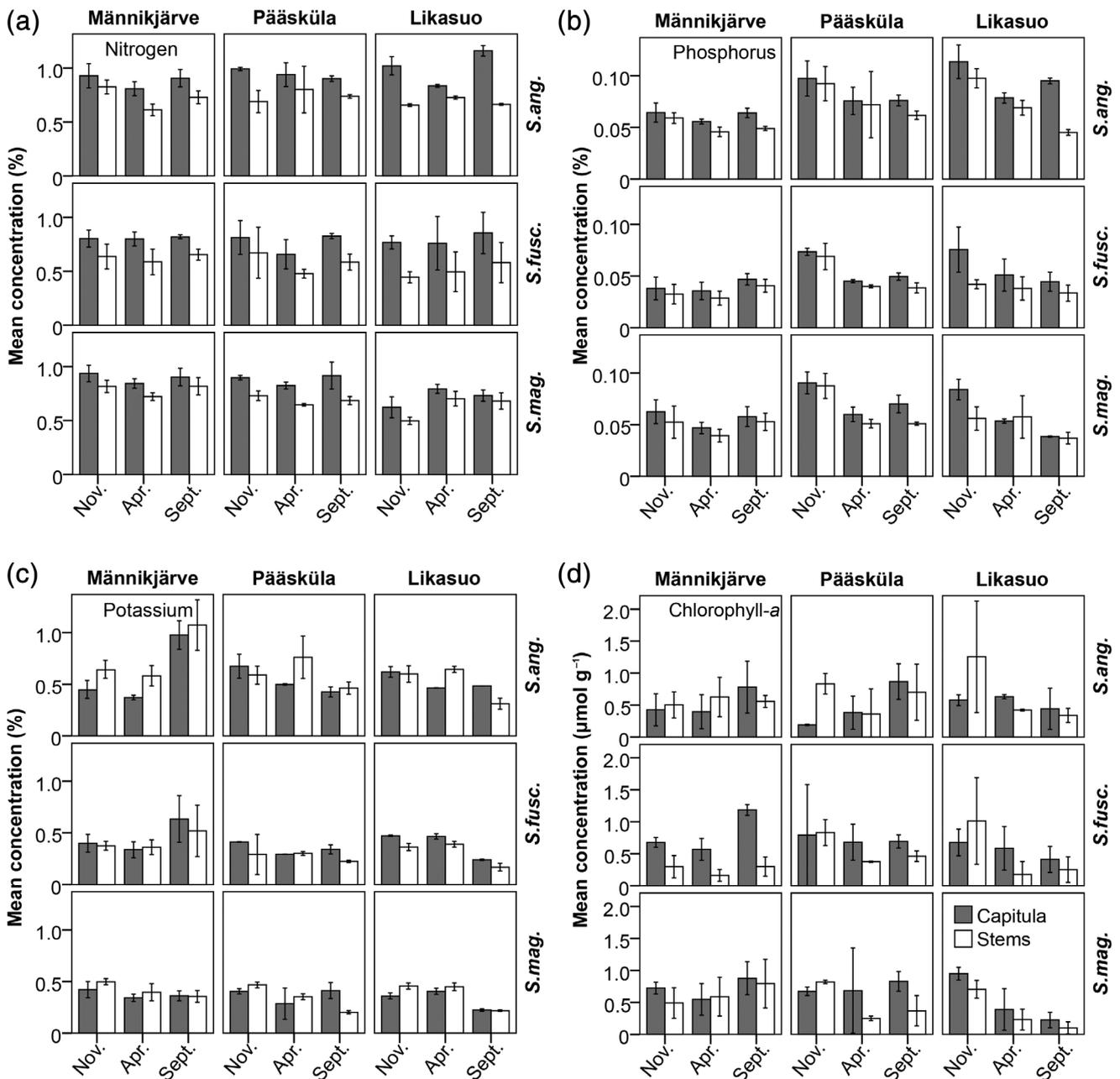
and season. All data analyses were performed by IBM SPSS 20. The schematic map of the study sites was created by R 3.2.3 (R Core Team, 2015), using the package *maps*.

### 3 | RESULTS

#### 3.1 | Microclimate of the habitats

The temperature regime of moss layer differed between sites, between microsites with contrasting tree cover, and somewhat between the *Sphagnum* species covering the

ground, but not between the microforms (Figure 2). In general, mean annual moss temperature at the capitulum level ( $T_M$ ) decreases along the south–north gradient (Figure 2). While the mean summer temperatures followed the same latitudinal pattern, winter temperatures fluctuated evenly around subzero temperatures at all sites. However, while the permanent snow cover maintained steady microclimate in Likasuo, numerous freeze–thaw cycles occurred at Männikjärve ( $n = 91$ ) and Pääsküla ( $n = 35$ ) due to intermittent snow melts. In autumn, ground temperatures at the northernmost site were significantly lower ( $F_{2,147} = 24.8; p \leq .001$ ) than at the other sites.



**FIGURE 4** The concentrations of (a) nitrogen, (b) phosphorus, (c) potassium and (d) *chlorophyll-a* in the capitula and stem of *Sphagnum angustifolium*, *S. fuscum* and *S. magellanicum* in our study sites. Concentrations were measured at the end of each season. Data are mean values  $\pm 1$  SE

**TABLE 2** The ANOVA results of the generalized linear mixed models (GLMM) on the effect of season, species and study site on the (a) *Sphagnum* growth and on the (b) N, P, K and *chlorophyll-a* concentration in the *Sphagnum* capitula (apical 0–1 cm) and stem (1–3 cm from the top)

<b>(a) <i>Sphagnum</i> growth</b>									
Factor	df	Linear growth			Production				
		F	p	P-hoc	F	p	P-hoc		
Season	2	121.1	<b>.001</b>	All differ	146.5	<b>.001</b>	All differ		
Species	2	31.4	<b>.001</b>	All differ	0.7	.511	None differ		
Site	2	2.1	.126	None differ	1.5	.229	None differ		
Season × species	4	8.0	<b>.001</b>		0.5	.731			
Season × site	4	1.6	.290		0.4	.775			
Species × site	4	1.9	.110		0.6	.640			
Season × species × site	8	1.6	.128		1.0	.425			
R <sup>2</sup>			.718			.698			
<b>(b) Nutrients and <i>chlorophyll-a</i></b>									
Factor	df	N		P		K		Chlorophyll a	
		F	p	F	p	F	p	F	p
Capitula									
Season	2	6.3	<b>.004</b>	19.7	<b>.001</b>	1.3	.274	0.8	.434
Species	5	15.4	<b>.001</b>	24.2	<b>.001</b>	12.8	<b>.001</b>	3.1	<b>.016</b>
Site	2	16.3	<b>.001</b>	30.9	<b>.001</b>	1.1	.330	3.4	<b>.039</b>
Season × species	7	1.2	.309	4.2	<b>.001</b>	2.1	.063	1.5	.163
Season × site	4	1.4	.237	14.4	<b>.001</b>	17.1	<b>.001</b>	7.7	<b>.001</b>
Species × site	5	18.2	<b>.001</b>	5.0	<b>.001</b>	1.7	.149	1.1	.373
Season × species × site	10	1.9	.061	2.1	<b>.045</b>	4.3	<b>.001</b>	1.0	.477
R <sup>2</sup>			<b>.798</b>		<b>.885</b>		<b>.830</b>		<b>.594</b>
Stem									
Season	2	34.5	<b>.001</b>	14.4	<b>.001</b>	10.9	<b>.001</b>	0.5	.601
Species	5	25.6	<b>.001</b>	16.9	<b>.001</b>	40.6	<b>.001</b>	3.4	<b>.041</b>
Site	2	1.3	.273	10.4	<b>.001</b>	3.5	<b>.038</b>	14.2	<b>.001</b>
Season × species	7	13.5	<b>.001</b>	1.5	.202	1.5	.230	2.9	<b>.030</b>
Season × site	4	3.5	<b>.013</b>	7.6	<b>.001</b>	11.9	<b>.001</b>	7.8	<b>.001</b>
Species × site	5	1.2	.315	3.6	<b>.002</b>	1.7	.166	0.2	.938
Season × species × site	10	1.4	.196	0.9	.554	2.7	<b>.015</b>	0.5	.855
R <sup>2</sup>			.816		.832		.804		.590

Note: Statistical significance at  $p < 0.05$  level is given in bold.

### 3.2 | *Sphagnum* biomass and growth

The standing biomass of all species generally increased northwards (Figure 3). *S. fuscum* had overwhelmingly the highest standing biomass—a twofold of the other species—and the highest shoot density as well. The

biomass of *S. angustifolium* was of the same magnitude as *S. magellanicum*.

Considering all study sites and species, *Sphagna* grew on average  $19.5 \pm 8.9$  mm in length, and  $200.4 \pm 74.4$  g m<sup>-2</sup> in biomass during the study period (Figure 3). Both linear increment and production varied greatly

**TABLE 3** The results of the simple linear regression models on the environmental control over *Sphagnum* growth in length (Lin.) and biomass production (Prod.)

Factor	Seasonally						Species-wise							
	All		Autumn		Winter		Summer		<i>S. ang.</i>		<i>S. fusc.</i>		<i>S. mag.</i>	
	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.
<b>Meteorology</b>														
Air temperature ( $T_{AIR}$ )	↑		↑		↑		↑		↑		↑		↑	
Moss temperature ( $T_M$ )	↑		↑		↑		↑		↑		↑		↑	
Sum of precipitation (Psum)	↑		↑		↑		↑		↑		↑		↑	
Days with precipitation (Pdays)	↑		↑		↑		↑		↑		↑		↑	
Freeze-thaw cycles (FTC)	↓		↓		↓		↓		↓		↓		↓	
Photoperiod (PP)	↑		↑		↑		↑		↑		↑		↑	
Mean snow depth (MSD)														
Days with snow cover (Sdays)														
<b>Ecophysiology</b>														
<b>Capitulum</b>														
Water content (WCc)	↑		↑		↑		↑		↑		↑		↑	
Standing biomass	↑		↑		↑		↑		↑		↑		↑	
N concentration (Nc)	↑		↑		↑		↑		↑		↑		↑	
P concentration (Pc)	↑		↑		↑		↑		↑		↑		↑	
K concentration (Kc)	↑		↑		↑		↑		↑		↑		↑	
N:P ratio	↓		↓		↓		↓		↓		↓		↓	
K:P ratio														
Chlorophyll $a$ concentration														
<b>Stem</b>														
Water content (WCs)	↑		↑		↑		↑		↑		↑		↑	
Standing biomass	↑		↑		↑		↑		↑		↑		↑	
N concentration (Ns)	↑		↑		↑		↑		↑		↑		↑	
P concentration (Ps)	↑		↑		↑		↑		↑		↑		↑	
K concentration (Ks)	↑		↑		↑		↑		↑		↑		↑	
N:P ratio	↓		↓		↓		↓		↓		↓		↓	
K:P ratio														
Chlorophyll $a$ concentration	↑		↑		↑		↑		↑		↑		↑	
Shoot density	↑		↑		↑		↑		↑		↑		↑	

(Continues)

TABLE 3 (Continued)

Factor	Seasonally						Species-wise							
	All		Autumn		Winter		Summer		<i>S. ang.</i>		<i>S. fusc.</i>		<i>S. mag.</i>	
	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.	Lin.	Prod.
<b>Meteorology</b>														
Microsite														
Relative height of microform	↑		↑		↓		↓		↓		↓		↓	
Shade	↑		↑		↑		↑		↑		↑		↑	
Tree canopy closure														
Tree height														
Shrub height (SH)														
Distance from trees														

Note: At first, tests are carried out for full data set over the annual study period (October 2014–September 2015). Second, the study period is divided into Autumn (October–November), Winter (December–April) and Summer (May–September). Third, the tests are performed separately for the three species: *Sphagnum angustifolium*, *S. fuscum* and *S. magellanicum*. ↑ indicates positive and ↓ negative regression; dark gray indicates significance at .001 level and light gray at .05 level; relations with white background are not statistically significant ( $p > .05$ ).

among the replicates. The interspecies differences in linear increment were significant and greater than between the site differences: *S. angustifolium* grew the most and *S. fuscum* the least at all sites ( $p \leq .05$ ). The production, in contrast, showed almost no significant differences between the species and sites ( $p > .05$ ) (Figure 3). Although its linear increment was low, *S. fuscum* exhibited the greatest annual production. The linear increment and production were the greatest in summer in all cases, but considerable growth was measured also in autumn and in winter at all species and sites. Winter growth accounted for  $12 \pm 6\%$  from the annual linear increment and  $7 \pm 4\%$  from the production of *S. angustifolium*,  $10 \pm 5\%$  and  $4 \pm 3\%$  of *S. magellanicum*, and  $18 \pm 13\%$  and  $6 \pm 5\%$  of *S. fuscum*, respectively. The mean daily rates of linear increment in autumn often exceeded the increment in summer, depending on the site and species (Supporting Information 2). The daily production, however, was always higher in summer than in autumn. Considering all species, the mean daily production in the autumn was in average 61% of the production rate in the summer.

We found species to differ in their seasonal growth rates as a response to differing site conditions: linear increment and production of *S. angustifolium* were annually the greatest in the northernmost site Likasuo, while both linear increment and production in the winter were greater at the Estonian sites (Figure 3). In contrast, both annual growth rates of *S. fuscum* were the greatest in the southernmost site Männikjärve, but the winter production was the greatest in Likasuo. The growth rates of *S. magellanicum* did not differ significantly between the sites ( $p > .05$ ), being however slightly higher at the southernmost site.

### 3.3 | Nutrient and *chlorophyll-a* concentrations

The nutrients and *chlorophyll-a* concentrations in *Sphagnum* capitula and stems were clearly species-specific ( $p \leq .05$ ; Figure 4; Table 2). The average concentrations of N and P were the highest in *S. angustifolium* and the lowest in *S. fuscum*, whereas the K concentration was the highest in *S. angustifolium* and the lowest in *S. magellanicum*. The mean *chlorophyll-a* concentration, in contrast, was the highest in *S. fuscum* and the lowest in *S. angustifolium*. Altogether, *chlorophyll-a* concentration varied greatly between species and sites ( $p \leq .05$ ), but not so much between the seasons ( $p \geq .05$ ; Figure 4; Table 2). The lowest nutrient concentrations in our *Sphagnum* samples were generally measured in April, and the highest in September (Figure 4). The N:P ratios were relatively large in Männikjärve (14–23) compared to those at the other sites

**TABLE 4** The results of the final multiple stepwise linear regression models on the environmental control over *Sphagnum* growth in length (Lin.) and biomass (Prod.) over the annual study period (October 2014–September 2015)

	Growth	R <sup>2</sup>	p	F	df	Predictors with p-values
Species						
<i>S. angustifolium</i>	Lin.	.820	.001	28.88	3.19	Pdays (.001), PP (.001), T <sub>M</sub> (.016)
	Prod.	.823	.001	30.97	3.20	Psum (.001), PP (.001), T <sub>M</sub> (.039)
<i>S. fuscum</i>	Lin.	.707	.001	15.29	3.19	WCc (.005), T <sub>Air</sub> (.009), Pdays (.029)
	Prod.	.622	.001	95.30	1.58	T <sub>M</sub> (.001)
<i>S. magellanicum</i>	Lin.	.651	.001	53.16	2.57	Pdays (.001), PP (.001)
	Prod.	.718	.001	28.06	3.56	Psum (.004), PP (.041), T <sub>M</sub> (.048)
Season						
Autumn	Lin.	.429	.009	6.39	2.17	Kc (.020), Shade (.039)
	Prod.	.469	.001	13.25	2.30	Shade (.001), WCc (.014)
Winter	Lin.	.359	.001	10.09	1.18	MSD (.005)
	Prod.	.295	.001	8.77	2.42	Shade (.002), SH (.004)
Summer	Lin.	.286	.001	7.21	1.18	Pc (.015)
	Prod.	.347	.001	9.25	1.31	WCc (.005)
All	Lin.	.670	.001	31.98	4.63	Pdays (.001), PP (.001), Pc (.001), FTC (.020)
	Prod.	.573	.001	47.7	2.71	T <sub>M</sub> (.001), Shade (.012)

Note: Regression models are calculated both on species-wise and seasonal basis. The abbreviations for predictors are the same as in Table 3.

(8–19), and exhibited a major variation (Supporting Information 3). *S. fuscum* had relatively higher N:P ratios in capitula compared to other species. In the stem the interspecies differences in N:P ratios did not differ that clearly between the species and sites.

### 3.4 | Controls of site conditions and ecophysiological properties on growth rates

Both linear increment and production of *Sphagnum* depended more on meteorological parameters than ecophysiological or microsite properties (Tables 3 and 4). When considering annual growth rates, air temperature and a number of freeze–thaw cycles altered the linear increment and production of all species. Number of days with precipitation and capitula P concentration were common predictors for all linear increment models, and moss temperature, photoperiod and sum of precipitation for all production models. Capitula water content and shade were often important as well. Moreover, some factors affected *Sphagnum* growth only during certain seasons. For example, the shrub height and the depth and duration of snow, which were not significant for annual growth, became more important than temperature parameters in winter. The species differed in their response to some factors as well. For instance, while N concentration was

related to the growth of *S. angustifolium*, *S. fuscum* was more dependent on K.

## 4 | DISCUSSION

### 4.1 | Annual *Sphagnum* growth

This study shows that the annual mean linear increment of *S. angustifolium*, *S. fuscum* and *S. magellanicum* was within the range of values previously measured in the Northern Europe (e.g., Ilomets, 1982; Laiho, Ojanen, Ilomets, Hajek, & Tuittila, 2011; Laine et al., 2011; Lindholm & Vasander, 1990) but somewhat greater than the average values (Supporting Information 4). The higher linear increment compared to earlier studies is most likely related to the greater air temperatures and in the northernmost site, Likasuo, stimulated by the greater amount of precipitation in 2013/14 than in the previous years. Moreover, in our study, the annual production of *S. angustifolium* and *S. fuscum*—the species with a northern distribution (Robroek, Limpens, Breeuwer, & Schouten, 2007)—was above the global average, while the production of *S. magellanicum*, a cosmopolitan species, was below the global average (Gunnarsson, 2005). Our study sites lie in the hemiboreal and boreal vegetation zones of Northern Europe, and thus were expected to be more favorable habitats for *S. angustifolium* and *S. fuscum* than for *S. magellanicum*.

Similarly to Breeuwer et al. (2010), we found the differences in growth to be species-specific so that only the growth of *S. angustifolium* increased northwards along the latitudinal climate gradient. The higher temperatures southwards may restrict the availability of water through increased evaporation (Breeuwer, Heijmans, Robroek, & Berendse, 2008), and thus might not always facilitate *Sphagnum* growth. Indeed, as the growth rates were greater in the northernmost site only in the summer, the differences between the sites can be explained by the severe desiccation of *S. angustifolium* already in mid-May at the southern sites, where the evaporation is higher and the precipitation less abundant than in Likasuo. *S. angustifolium* has much lower water holding capacity than *S. magellanicum* and especially *S. fuscum* (Elumeeva, Soudzilovskaia, Doring, & Cornelissen, 2011; Robroek et al., 2009), making it more prone to desiccate and consequently less stressed in the northernmost site. Also, it is possible that *S. angustifolium* took advantage on longer daylight in Likasuo, which according to Li and Glime (1991) can increase the growth speed of *Sphagnum* at the northern areas. While the longer photoperiod appeared to enhance linear increment and production of *Sphagnum* in our study, our data gives also some support to Dorrepaal et al. (2004) that the increased snow cover can facilitate the production of *Sphagnum*. Some previous studies (e.g., Genet, Oberbauer, Colby, Staudhammer, & Starr, 2013) suggest that declines in winter snow cover can reduce the *Sphagnum* growth in summer, and relate it to increased number of freeze–thaw cycles and prolonged frost. While the depth of snow cover increased the linear increment, and the number of snow covered days increased the biomass productivity during the winter in our study, the impact of snow was, however, not significant for the annual growth rates. Nevertheless, the number of freeze–thaw cycles decreased both annual linear increment and production in our study. Thus, the results of this study confirm our earlier conclusion (Küttim, Laine, Küttim, Ilomets, & Robroek, 2019) that the negative effect of freeze–thaw cycles on moss physiology in winter and spring may cascade to the rest of the growing season. The physiological stress can be relieved by abundant precipitation (Küttim et al., 2019; Nijp et al., 2014), but if input of snowmelt water is minor due to reductions in snow cover, *Sphagnum* desiccates and its growth is likely to be suppressed.

## 4.2 | Winter growth

During the winter, the metabolic rates of plants are reduced by the cold. Some plants, such as *Fragaria vesca* L. and *Vaccinium vitis-idaea* L. continue physiological processes and development under snow, however (Åström,

Metsovuori, Saarinen, Lundell, & Hänninen, 2015; Crawford, 2014; Halfpenny & Ozanne, 1989; Lundell, Saarinen, Åström, & Hänninen, 2008). Our study confirmed that *Sphagnum* mosses have the ability for year-around growth. The average winter growth in our sites was ~10% and ~5% from the annual linear increment and production, respectively.

The conditions during the winter, which allow growth and most strongly affect it, are the occurrence of above-zero temperatures, liquid water and the availability of light adequate for photosynthesis; all these factors are linked to the existence of snow cover. Bryophytes are evolutionally regarded as shade plants (Marschall & Proctor, 2004) that are most abundant and species-rich in cold and humid environments. Accordingly, they cope well in low-light environments (Glime, 2017). The snowpack provides dark and cool, but stable and moist conditions that are suitable for the growth of *Sphagnum*. Likewise for some vascular plants (Lundell et al., 2008), the thick snow cover enables increased winter activity. Our result that the shrubs enhance the linear increment and production of nearby *Sphagnum* in the winter points to the ability of these shrubs to trap snow and increase the height of the insulating snow cover. Although we have not enough evidence to prove it, probably these mosses are able to photosynthesize under snow as well. Gaberščik and Martinčič (1987) have reported *Sphagnum* photosynthesis to last until February, when it ceased completely. Indeed, the late winter is most likely the time when the frost has penetrated the snow, and consequently *Sphagnum* activity halts.

Despite the difference in snow cover, the winter growth was apparent and rather similar at all sites. We found that the snow cover had a unimodal effect on moss layer temperature: during the winter the snow maintained steady subzero temperature at our northernmost site, but during autumn and spring, compared to the two southern sites, snow cover suppressed the moss surface warm-up. The peat layer has a high thermal capacity and accumulates energy during the warm period, while snow cover is a fine thermal isolation (Federer, 1965). Consequently, heat flow from the peat layer initiates the long-lasting slow thaw rate at the snow–soil interface (Federer, 1965; Nagare, Schincariol, Quinton, & Hayashi, 2012) with ground temperatures at our northernmost site typically around the freezing point from November until late-April (but yet with some periods of frost; Figure 2).

At the two southern sites, the impersistent snow cover exposed the ground to the freeze–thaw cycles, but also enabled the ground to warm up a month earlier than in the northern site. There are indications that freeze–thaw cycles are harmful for plants (e.g., Min, Chen, & Arora, 2014; Schmitt, Schramm, Pfanz,

Coughlan, & Heber, 1985). In the current study, the winter growth of *Sphagnum* was, however, only to some extent compromised by the regular freeze–thaw cycles. Although the linear increment and production of all species were significantly decreased by freeze–thaw cycles, the growth rates in the southern sites were similar to those measured at northern site with continuous snow cover. This is probably due to the ability of bryophytes to take advantage on the intermittent warm periods of winter, and use it for active growth after relatively rapid recovery. Although the photosynthetic capacity and chlorophyll concentration of *Sphagnum* declines due to freeze–thaw cycles (Küttim et al., 2017), the recovery seems to be faster than in case of vascular plants. Indeed, with relatively high concentrations of fatty acid derivatives and phenylpropanoids, soluble sugars and abscisic acid, bryophytes are usually more freezing tolerant than vascular plants (Glime, 2017). Moreover, bryophytes have no roots (Rydin & Jeglum, 2013) and therefore are not so dependent on the ground frost that postpones the metabolic activity of most of the vascular plants (Glime, 2017).

### 4.3 | Environmental and ecophysiological controls over *Sphagnum* growth

The present investigation has demonstrated the paramount importance of meteorological parameters on *Sphagnum* growth rather than ecophysiological or microsite properties. Our study confirms the comprehension that the precipitation and temperatures exceeding the melting point are the prerequisites and best explanators of *Sphagnum* growth (Breeuwer, Heijmans, Gleichman, Robroek, & Berendse, 2009; Grabovik & Nazarova, 2013; Krebs et al., 2016; Nijp et al., 2014), while low quantities of nutrients are tolerated by the *Sphagnum* species of ombrotrophic peatlands (Wang, Larmola, Murphy, Moore, & Bubier, 2016). The impact of temperature seems to be subordinate to moisture conditions as also Dorrepaal et al. (2004) showed that higher mean air temperature will not increase *Sphagnum* growth if low capitula water content is limiting growth. Indeed, our results also point to the importance of indirect factors that alter the moisture balance of Sphagna, such as shading and snow depth.

## 5 | CONCLUSIONS

We detected significant linear increment and production of all our focal species in winter. The growth rate

in winter was related to several factors, particularly to sum of precipitation, the presence of snow and the number of freeze–thaw cycles. While the predicted decline in snow cover in Northern Europe is likely to increase the number of freeze–thaw cycles—a major stress for mosses—the results of modeling (Jylhä et al., 2004) predict an increase in sums of precipitation—particularly in winter—that relieve the stress and facilitate *Sphagnum* performance (Krebs et al., 2016; Nijp et al., 2014). Although there is much uncertainty in precipitation predictions, its increase is likely to balance the increased evaporation, leaving the possible water level drawdown rather minor (Laine et al., 2019). Higher precipitation frequency that shifts from summer to winter (Jylhä et al., 2004) is likely to change the annual *Sphagnum* growth pattern as well (Nijp et al., 2014), thus increasing the *Sphagnum* growth and its overall share from the annual growth rates in winter.

In addition to changes in winter, climate change has prolonged the autumn, as the air temperatures have increased the most in the cold season, and the increased amounts of precipitation come more often as rain, not snow (Jylhä et al., 2004; Lode et al., 2017). The cool, wet and cloudy weather is inherent to the autumn in Northern Europe and is at the same time favorable for *Sphagnum* mosses. Our results demonstrate the high growth rates of Northern European *Sphagnum* species during the autumn. Moreover, we observed often higher mean daily growth rates in the autumn than in the summer, indicating more suitable conditions for growth during autumn. Longer autumns induced by climate change are seen negative for carbon sequestration capacity of most ecosystems as most vascular plants cannot respond to longer autumns by increased photosynthesis (Halfpenny & Ozanne, 1989; Korrensalo, Hájek, Vesala, Mehtätalo, & Tuittila, 2016; Zhaojun et al., 2011), but at the same time the warmer soil enhances the respiration rates (Dorrepaal et al., 2009; Zhaojun et al., 2011). Taken together, carbon storage would decrease under those scenarios. In *Sphagnum*-dominated peatlands the situation is somewhat different as Sphagna can be active whenever conditions are suitable for them. Thus, even though *Sphagnum* production in autumn and winter may not balance soil carbon emissions, the overall active period and rate of growth are more stable than in plant communities dominated by vascular plants; therefore, the effects of climate change on the carbon sink of *Sphagnum*-dominated peatlands are likely to appear modest. Still, our assumption holds as long as hydrological conditions allow *Sphagnum* to stay the major component of the vegetation.

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## CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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