



Weather Factors in Different Growing Periods Determine Inter-Annual Change in Growth of Four *Sphagnum* Species: Evidence from an Eight-Year Study

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Abstract

The growth of peat mosses is crucial for carbon uptake and storage in high latitude peatlands. Nevertheless, little is known on how variation in specific weather conditions affect *Sphagnum* functional traits and productivity. Using data from an eight-year study in a mire complex in the southern taiga of Western Siberia, we investigated how a suite of within-season weather conditions relates to *Sphagnum* growth. We collected weather data, and data on functional traits (length increment, increment biomass, capitulum numerical density and capitulum biomass) and net primary productivity of four *Sphagnum* species growing in raised bogs and poor fens. Overall, the most important factors were those related moisture conditions. Growing season averages of weather variables (e.g., precipitation and mean temperature) were often as good predictors of *Sphagnum* functional traits and productivity as early or late seasonal averages, but not necessarily for the same variables. The most sensitive traits to weather fluctuation were length increment (for *S. magellanicum* agg., *S. angustifolium*, *S. fallax*) and numerical density (for *S. fuscum*). Primary productivity of *S. fuscum* and *S. magellanicum* agg. were the highest under warm and wet conditions with *S. fuscum* being less sensitive to the weather; productivity of *S. angustifolium* increased under cool and wet conditions; and productivity of *S. fallax* was the highest under dry weather. Diversity in interspecific response to weather fluctuations may result in high peatland resistance towards environmental variability, and thereby maintaining a stable *Sphagnum* productivity in time across the mire complex.

Реферат

Прирост сфагновых мхов имеет решающее значение в процессах поглощения и депонирования углерода торфяниками северных широт. При этом влияние погодных флуктуаций на функциональные признаки и продукцию мхов мало изучены. На основе данных восьмилетнего эксперимента в болотном комплексе южной тайги Западной Сибири, мы выявили, как рост сфагновых мхов связан с внутрисезонными погодными колебаниями. Были собраны данные о погоде, функциональных признаках (линейный прирост, его биомасса, численность и биомасса капитул) и определена чистая первичная продукция четырёх видов *Sphagnum*, произрастающих в повышенных и пониженных болотных микроландшафтах. В целом, наиболее важными были погодные факторы, связанные с условиями увлажнения. Разные погодные переменные (например, количество осадков и средняя температура) были предикторами функциональных признаков и продуктивности мхов как в течение всего тёплого периода, так и в течение первой или второй его половины. Линейный прирост (для *S. magellanicum* agg., *S. angustifolium*, *S. fallax*) и численность капитул (для *S. fuscum*) были наиболее чувствительными к погодным колебаниям. Первичная продукция *S. fuscum* и *S. magellanicum* agg. была самой высокой в тёплых и влажных условиях, при этом *S. fuscum* менее чувствителен к погоде; продукция *S. angustifolium* повышалась в прохладных и влажных условиях; а продукция *S. fallax* – при засушливой погоде. Разнообразие видоспецифической реакции на колебания погоды может быть причиной высокой устойчивости торфяников к изменениям окружающей среды, что позволяет поддерживать стабильную во времени продукцию мхов во всём болотном комплексе.

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Introduction

Peat mosses (*Sphagnum*) species are the main peat formers in northern peatlands (Gorham 1991; Rydin and Jeglum 2013). *Sphagnum* biomass and growth reflect the local environmental conditions (Bengtsson et al. 2016), and therefore, their performance can serve as an indicator of regional climate change (Gignac and Vitt 1994). A deeper understanding of weather effects on moss productivity is essential for modelling plant growth and ultimately carbon sequestration in a changing climate. Examining primary productivity and growth of *Sphagnum* and their relationship to meteorological factors is especially important for Western Siberia, which is the largest peatland complex in the world (Gorham 1991). Here, *Sphagnum*-dominated peatlands cover 6×10^5 km² (Smith et al. 2004), including 1.4×10^5 km² in the southern taiga (Peregon et al. 2008). Earlier attempts of modelling *Sphagnum* growth using climatic data (reviewed in Bengtsson et al. 2021) have mostly focused on different spatial and temporal scales. However, detailed studies monitoring growth of many *Sphagnum* species over a long time period with varying weather are still lacking. Such data are particularly important to collect from a globally important peatland area like Western Siberia.

Climate directly affects peat moss distribution, abundance, and performance (Gignac and Vitt 1994; Oke and Hager 2017; Campbell et al. 2021). Peat moss growth varies considerably over years (Maksimov 1982; Beckéus 1988; Moore 1989; Lindholm and Vasander 1990; Grabovik and Nazarova 2013) and strongly depends on inter-annual weather variability in the same climate zone (Asada et al. 2003). Crucial factors affecting peat moss growth on a global scale are temperature, precipitation and photosynthetically active radiation (Bengtsson et al. 2021; Gunnarsson 2005; Loisel et al. 2012). *Sphagnum* growth begins at a temperature slightly above 0 °C (Asada et al. 2003; Moore et al. 2006), and rising temperature during the growing season causes increase in moss length growth and productivity (Breeuwer et al. 2008; Grabovik and Nazarova 2013; Krebs et al. 2016). On the other hand, if water availability is low, high temperature can lead to drying of the active apical part of the *Sphagnum* moss (i.e. the capitulum), which will reduce photosynthesis and productivity (Schipperges and Rydin 1998; Deane-Coe et al. 2015). Accordingly, experiments have demonstrated that elevated temperature do not necessarily increase *Sphagnum* growth (e.g. Bu et al. 2011).

For a specific moss patche, water availability is likely the most important factor for peat moss productivity (Maksimov 1982; Beckéus 1988; Lindholm 1990; Asada et al. 2003; Yurova et al. 2007; Waddington et al. 2015). Water to the

moss surface is provided from two main sources: drawn from the water table below and from above through precipitation. Laboratory experiments have revealed a negative correlation between water tables depth and photosynthesis, growth and moss productivity (Weltzin et al. 2001; Robroek et al. 2007, 2009; Nijp et al. 2014). In field experiments, the height above water table (HWT) appears to affect *Sphagnum* growth on certain mires (Maksimov 1982; Mulligan and Gignac 2001; Yazaki and Yabe 2012; Graham and Vitt 2016). However, HWT has been reported to be less significant in long-term multispecies investigations (Weltzin et al. 2001; Bengtsson et al. 2016, 2021). Instead, summer precipitation may be a stronger predictor of *Sphagnum* linear growth and productivity (Weltzin et al. 2001; Kosykh et al. 2017a). Furthermore, the temporal distribution of precipitation is important for peat moss growth. Frequent rains have a positive effect on growth because they maintain the active top-part of the moss wet, which makes a moss patch's growth independent of its HWT (Beckéus 1988; Robroek et al. 2009; Nijp et al. 2014; Krebs et al. 2016). Similarly, long rain free periods will reduce peat moss growth (Bengtsson et al. 2021), which further strengthens the need to besides annual sum, also include the precipitation pattern in moss growth studies.

In the boreal zone, *Sphagnum* growth fluctuates within the growing season. The growth pattern typically has a peak in the beginning of the growing season followed by decreased growth in the summer, and sometimes a second peak late in the season (Maksimov 1982; Kosykh et al. 2017a, b). However, the growth pattern likely shifts between years due to differences in weather. Depending on the year, the warmest months in the Western Siberia (Bakchar mire) is either June, July or August with a mean temperature between 18 and 20 °C, and monthly precipitation range from 20 to 160 mm during the growing season (Dyukarev and Golovatskaya 2013). Water table is close to the moss surface in May and June and subsequently drops and varies with weather conditions during the summer (Dyukarev and Golovatskaya 2013). The wet conditions observed early in the seasons is linked to snow melt in May and soil frost melt in May or June. Snow cover and frost depth, which determines the amount of melt water, are essential sources of water for bryophytes at high latitude early in the season (Küttim et al. 2020a).

How *Sphagnum* growth vary within and between years as a response to temperature, precipitation, and HWT differ among species and ecological groups. This can partly be explained by that *Sphagnum* species are adapted to different HWT, which has resulted in differences in functional trait values (Laing et al. 2014; Bengtsson et al. 2020). For example, stable length increment is typical for

hummock-dwelling species such as *S. fuscum* (Lindholm and Vasander 1990; Mulligan and Gignac 2001; Asada et al. 2003; Robroek et al. 2007; Granath et al. 2010) that are more resistant to environmental change (Bu et al. 2013). In contrast, species growing closer to the water table (i.e., lawns and hollows), e.g., *S. magellanicum* and *S. angustifolium*, can have higher growth rates under wet conditions but dry out easier, which strongly reduces growth (Mulligan and Gignac 2001; Robroek et al. 2007; Mazziotta et al. 2019). Thus, we need to improve our understanding of how traits related to growth and productivity, which differ between species, such as length increment, its weight and shoot density (Laing et al. 2014; Hájek 2009), respond to within- and between-year variation in weather.

It is clear that weather factors drive variation in *Sphagnum* productivity within and between growing seasons. To investigate within year variation, a separation between the early and the late period of the growing season is reasonable in our study area. High availability of soil melt water from snow and frozen peat observed in May and June is inherent for the early season. Intermittent availability of soil capillary water from varying HWT is an attribute of the late season and there is no clear “summer drought”. Furthermore, autumn *Sphagnum* growth is, in contrast to a more maritime climate, low in Siberia due to frequent frost (below 0°C) already in September (Kosykh et al. 2017a). Temperature, precipitation, number of days with rain (or length of dry period) are variables that vary during the growing season and between years. We predict that these variables affect *Sphagnum* growth over the growing season, possibly in opposite directions between the early and the late part of the season, depending on availability of soil moisture. For example, a high temperature should promote growth when peat is water saturated, while the same temperature can desiccate the moss and stops growth if water replenishment through rain or capillary water is low or absent. Precipitation promotes peat moss growth if peat moisture is low and acts contrarily, as a moss growth inhibitor, if water availability is high. In the latter case, reduction in light due to cloudiness can further decrease carbon uptake (Nijp et al. 2015).

Here, we tested the hypothesis that within-season weather variables (early or the late season) are stronger predictors of annual *Sphagnum* functional traits values and productivity compared to the growing season averages of the same weather variables. Firstly, we quantified inter-annual variability in functional traits (i.e., length increment, increment biomass, capitulum density and capitulum biomass) and productivity of the most common and functionally important peatland bryophytes (*Sphagnum fuscum*, *S. magellanicum*, *S. angustifolium*, and *S. fallax*) in two contrasting habitats that are typical for the investigated region, namely raised bogs and poor fens. Secondly, we examined the response of peat moss functional traits and productivity to weather variables

associated with the early and the late season as well as to the entire season. Thirdly, we investigated interspecies and habitat difference in moss responses to weather variables to test if *Sphagnum* species and habitats have different climate sensitivity (Robroek et al. 2017; Jasse and Signarbieux 2019; Küttim et al. 2020b; Bengtsson et al. 2021).

Materials and Methods

Study Sites

Our field study was carried out in the Bakchar mire, which is located in the southern taiga subzone of Western Siberia (56°51'N, 82°51'E). The mire complex occupies more than 1000 square kilometres and includes treed and open raised bogs and poor fens with a 2-m peat deposit on average. The water table varied from about 2 to 30 cm during the summer over the six growing seasons (Dyukarev and Golovatskaya 2013), with pH of 3.6–3.8 (portable pH-meter, Izmeritelnaya tekhnika, Russia) and total salinity of 34 ± 4 (portable salinity-meter, HANNA Instruments, USA). The climate is continental, between 1961 and 1990 mean monthly temperature was -17.7 °C in January and $+19.1$ °C in July, and mean annual precipitation was 539 mm (Hydrometeorological Center of Russia 2020). In the raised bogs the dominant plants are: trees, a sparse layer of *Pinus sylvestris* (height 1–3 m, age 40–60 years) that has a negligible shading effect of the ground; dwarf shrubs, *Rhododendron tomentosum* (syn. *Ledum palustre*) and *Chamaedaphne calyculata*; and mosses, *Sphagnum fuscum*, *S. angustifolium* and *S. magellanicum* aggregate (now divided into *S. medium* and *S. divinum* according to Hassel et al. 2018 but in this study we use *S. magellanicum* agg.), and rarely *S. balticum*. In the poor fens, the dominant plants are sedges, *Carex rostrata*; and mosses, *S. fallax*; other mosses are less common (*S. riparium*, *S. obtusum*, *S. angustifolium*) or found sporadically (*S. lindbergii*).

Measurements of Functional Traits and Annual Net Productivity Calculations

For functional traits we quantified *Sphagnum* length increment (or height increment, LI, $\text{mm}\cdot\text{yr}^{-1}$), length-specific stem biomass i.e. increment biomass (IB, $\text{g}\cdot\text{mm}^{-1}\cdot\text{dm}^{-2}$), numerical density i.e. capitula per unit area (ND, dm^{-2}) and capitulum biomass (CB, mg). We followed Laing et al. (2014) and considered *Sphagnum* LI, IB, ND as canopy traits, and CB as a shoot trait. According to Laing et al. (2014), LI of *Sphagnum* individuals signify stem elongation and it is controlled by water availability gradient with maximal elongation in wet habitats. CB controls photosynthesis and growth at

the individual shoot level. IB, ND and CB are attributed to habitat and water table gradient: shoot and capitulum mass decreases whereas numerical density increases with increasing height above water table (Laing et al. 2014). The plastic response of capitulum size and numerical density to water-table depth is a mechanism to maintain a moist moss canopy (Rydin 1993).

The method of peat moss LI measurement depended on carpet shoot density and direction of growth. Species with dense carpets and small vertical growth, in our study *S. fuscum* and *S. magellanicum*, were measured using the brush-wire method (Rydin and Jeglum 2013), which is a modification of the cranked wire method (Clymo 1970). To measure the LI of the more loose growing *S. fallax* and *S. angustifolium* we employed individual markings on shoots (Kosykh et al. 2008). The method was relevant for measuring the LI of species with high growth rate, not having an erect growth pattern and forming a loose carpet. The method is a modification of the tied thread method (Clymo 1970). We circled a thin stainless wire around moss shoots below the capitulum without tightening it so that the wire ring laid on moss branches. A foil label attached to the free end of the wire helped in finding the marked plants. In late September or early October, we sampled marked plants and measured the shoot increment above the place of the wire tie (Appendix Fig. S1). The synchronous use of both methods depending on *Sphagnum* features has been previously reported (Maksimov 1982; Bengtsson et al. 2016).

To measure IB, ND and CB, we sampled 3 to 4 cores of each *Sphagnum* species. We used a hard plastic cylinder with an area of 16.6 cm² and sampled at the same plots where the LI was measured. Both the capitula and 3-cm stem sections below the capitula were collected; the number of capitula were counted. To determine IB, a 3-cm stem section of each capitulum was measured and cut off. Here, IB is not necessarily identical to bulk density for a 3-cm section as a bulk density sample may include shoots longer than 3 cm if they are bend, as well as dead *Sphagnum* individuals. Capitula and stems were oven-dried to a constant weight at 60 °C and weighed.

Sphagnum net primary productivity (NPP, g·m⁻²·year⁻¹) was calculated as the annual LI (mm) multiplied by the IB (g·mm⁻¹·dm⁻²) and expressed per square meter.

Experimental Design

Species were chosen to represent the most common and functionally important bryophytes, *S. fuscum*, *S. magellanicum*, *S. angustifolium*, and *S. fallax*, in two contrasting habitats – namely raised bogs and poor fens – that are typical for this region. In addition to the four species, we also measured

traits in *S. balticum*, *S. riparium*, *S. obtusum*. However, they were not measured over many years and we therefore only present their raw data, which is available together with all other data at the Mendeley Data repository (<https://doi.org/10.17632/6d3sgzmdxp.2>).

In the raised bog, *S. fuscum* dominated the moss carpet and *S. magellanicum* and *S. angustifolium* were co-dominants. The surface of the bog had typical hummocks and hollows where *Sphagnum* species occupied different positions according to their microtopographical niche (Rydin and Jeglum 2013; Bengtsson et al. 2016). At our site, *S. fuscum* grows on the most elevated microtopographical position, while *S. magellanicum* and *S. angustifolium* occur in hollows and low hummocks. We established permanent monospecific 0.25 m² plots of *S. fuscum* on hummocks and *S. magellanicum* and *S. angustifolium* on low hummocks and hollows; four plots per species and separated by 100 m (random direction). Mean hummock height of the established plots was 32 ± 7 cm (mean ± SE) for *S. fuscum* and 13 ± 3 cm for *S. magellanicum* and *S. angustifolium*. We placed 3 to 5 brush-wires (*S. fuscum* and *S. magellanicum*) or markings on shoots (*S. angustifolium*) per plot and species. In the first years of the study, we observed that some markings disappeared when being buried deep by the growing moss carpet. Therefore, we doubled the number of markings on shoots after 2015. The total number of replicates per year were 12–14 for *S. fuscum*, 10–18 for *S. magellanicum*, and from 6 (2014) to 10–30 (2016–2020) for *S. angustifolium*.

In the poor fen, the even surface and absence of trees and dwarf shrubs forms a homogeneous environment and *S. fallax* is growing all over the mire. Here, we set one monodominant plot of *S. fallax* of 10 × 10 m size. The number of replicates were 3–18 per year after some markings were immersed in the moss carpet and lost.

Sphagnum growth measurements were carried out over eight growing seasons (2013–2020). In 2013, brush wires and markings on shoots were established in the spring after freezing–thawing had stopped (late May) and were re-established in late September. In the spring of the next year, we found out that the mosses did not grow during autumn and that the snowpack did not violate the marking position over the winter. In subsequent years, we visited study sites in late September or early October to sample and set new wires and markings. At the autumn visit, we also measured the heights of hummocks where wires and markings were applied in the raised bog, and the HWT in the poor fen. We also extracted 3 to 4 *Sphagnum* cores of each *Sphagnum* species per year. A few cores were lost between 2013 and 2015, which reduced the sample size, and we also lost some LI measurements for *S. angustifolium* in 2013 and 2015.

Weather Data

Weather data were extracted from the weather station “Bakchar”, which is situated 50 km from the study site (Raspisanie pogody 2019).

As *Sphagnum* growth starts slightly above 0 °C (Lindholm 1990; Asada et al. 2003; Moore et al. 2006; Küttim et al. 2020b), we defined the beginning of the growing season as three consecutive days with a minimum daily temperature above zero followed by a period with rising temperature. We considered the first three consecutive days with minimum daily temperature below zero in the autumn as the end of the growing season. Over the observed years, the growing season started from the middle of April to the end of May and ended from the early to the late September (Appendix Table S1). We used data on water table fluctuations and the period of frozen peat thawing reported for our study region by Dyukarev and Golovatskaya (2013) to separate the growing season weather data into two periods: i) the early growing season, from its beginning to the end of June; and ii) the late growing season from July to its end. The early season is characterized by a water table close to the bog surface and a wet upper peat layer due to water from snow and soil frost melt. Higher temperature followed by a dropping water table are inherent for the late season. This is a continuous transition and for simplicity we used the end of June as the division point for all years.

Seven weather variables were used in the analyses (Table 1). We included the standard variables *mean temperature* (T_m , °C) and *precipitation* (Pr, mm), but also *number of days with rain* (RD, days) to better capture the temporal distribution of rain. *Sphagnum* productivity has been shown to decrease after three days without rains (Krebs et al. 2016) and moss photosynthesis and respiration are induced during the 2 to 3 days following even small rain events (Strack and Price 2009). Therefore, *length of dry period* (DD, days) was calculated from the fourth consecutive day without precipitation, and then we added up the calculated days without rain over a period. We used the *climatic index* (CI_{As}) proposed by Asada et al. (2003) as it should reflect conditions

important for *Sphagnum* growth. We calculated the index value using a simplified formula:

$$CI_{As} = \sum_{i=1}^n p_i \cdot t_{maxi} / n,$$

where p is precipitation on the i th day, t_{maxi} is maximal daily temperature on the i th day, and n is the number of days. Finally, we used the parameter “*precipitation at mean daily temperature above 15 °C*” (Pr_{T15} , mm). This parameter was included because moisture is especially important for mosses in hot weather as it prevents the capitulum from drying, which could be particularly important given the continental climate of Western Siberia.

Statistical Analysis

Statistical models were examined for normality and as the residuals did not follow an approximate normal distribution, we ran non-parametric tests. To test differences between years and seasons, the Kruskal–Wallis non-parametric test was performed separately for each weather variable. Pairwise post-hoc differences within the season were tested by the Mann–Whitney test.

To test differences between years in peat moss functional traits, the Kruskal–Wallis test was performed followed by Mann–Whitney post-hoc pairwise test between study years. To quantify the strength of weather variables predictability of *Sphagnum* functional traits between growth periods, we applied Spearman’s rank correlations. Here we considered the whole data set, i.e. including intra-seasonal variation, as individual samples (n for length increment = 6–30 per year, 76–106 total; n for other functional traits = 1–5 per year, 22–28 total, for each of four species). We did not account for potential temporal correlation between samples in cases where growth was measured on the same patch. This can lead to slightly anti-conservative P-values for these analyses. To examine which trait had the largest impact on NPP we performed Pearson’s correlation analysis as they showed linear relationships. In this statistical testing, we pooled values from each year

Table 1 Values of weather variables (mean over 2013–2020 with the range given in parenthesis) during different periods of the growing season

Weather variables	Periods of the growing season		
	The early season	The late season	The entire season
Mean temperature (°C)	14.0 (12.7–17.4)	15.9 (14.2–17.1)	15.0 (14.0–15.7)
Sum of temperatures (°C-days)	738 (437–1027)	1182 (1054–1385)	1919 (1537–2352)
Precipitation (mm)	121 (59–197)	142 (81–192)	263 (140–347)
Precipitation at mean daily temperature above 15 °C (mm)	41 (1–116)	78 (39–163)	118 (51–215)
Climatic index	44.2 (21.1–116.5)	37.0 (25.5–51.0)	37.7 (24.7–61.5)
Number of days with rain (days)	24 (12–37)	30 (22–50)	54 (34–87)
Length of dry period (days)	10 (0–29)	16 (6–27)	26 (15–56)

and considered mean values as individual samples ($n=6-8$ depending on species).

We employed principal component analysis (PCA) to explore correlations among traits and multivariate trait differences between species. We employed two-block partial least squares analysis (PLS) to explore how meteorological variables can explain variation in *Sphagnum* trait values. In short, this method maximizes the covariation between two blocks (i.e., sets of variables) of data where each row has the same id (Rohlf and Corti 2000). Here, the first block included seven weather variables and the second block contained the *Sphagnum* functional traits.

Differences were considered significant at $P < 0.05$. Data analyses were performed using PAST software V. 2.17 (Hammer et al. 2001).

Results

Weather Variability

On average across the study period, the growing season lasted 129 days, and it was particularly long in 2015 (159 days), 2016 and 2020 (160 days). Weather variables showed significant variation between seasons (Table 1). Differences between years were detected for mean temperature ($\chi^2 = 10.02$, $P = 0.007$), precipitation ($\chi^2 = 12.54$, $P = 0.002$) and number of days with rain ($\chi^2 = 14.22$, $P = 0.001$). Number of days without rain ($\chi^2 = 7.91$, $P = 0.019$) and precipitation at mean daily temperature above 15 °C ($\chi^2 = 9.50$, $P = 0.009$) differed in the early season, and no difference was found for climatic index (Appendix Table S2). Correlations were detected for a few weather variables within a season (Appendix Table S3) as well as between seasons (Appendix Table S4).

Inter-year dynamics and interspecific difference of *Sphagnum* functional traits and productivity

Sphagnum fuscum had the most stable length increment (LI) over the observed period whereas LI of other species considerably varied from year to year (Fig. 1a, b, c, d; Appendix Table S5). Numerical density (ND) of *S. fuscum*, in contrast, significantly changed between growing seasons while this was not observed for the other species (Fig. 1e, f, g, h; Appendix Table S6). No differences were detected in inter-year IB values among all species (Fig. 1i, j, k, l; Appendix Table S7). *Sphagnum fallax* capitulum biomass (CB) significantly varied over the years with its lowest value in 2015 and highest in 2019, but no difference in CB was detected for other species (Fig. 1m, n, o, p; Appendix Table S8). Finally, we found that NPP substantially differed between growing seasons for all species (Fig. 1q, r, s, t;

Appendix Table S9). NPP of the fen species *S. fallax* was two-fold higher than that of bog species.

Species growing in the bog had lower LI and CB, with the lowest value being found for *S. fuscum*. Conversely, *S. fuscum* had the greatest IB and ND. The PCA revealed two principal components where the first axis defined a tradeoff between CB and ND (Fig. 2) that has previously been shown by Laing et al. (2014). The first axis was also associated with IB whereas the second axis was associated with LI. Significant interspecific differences were detected between all species for all traits, except for between *S. fallax* and *S. magellanicum* for ND and CB (Appendix Table S10).

Effects of weather variability on *Sphagnum* length increment

Correlations between LIs and weather factors were different between species (Fig. 3). The LI of *S. fuscum* was almost independent of weather factors. For *S. magellanicum*, LI was positively correlated with precipitation, especially at high temperature, and the climatic index during both seasonal periods (i.e., early and late season), and even stronger over the entire season. Length of dry period negatively affected *S. magellanicum* growth in the early season.

Unlike *S. magellanicum*, the LI of *S. angustifolium* positively responded to increasing temperature and total precipitation in the early season, as well as the number of days with rain in the late season. Contrary to the early season, increasing temperature in the late season inhibited *S. angustifolium* LI. Across the entire season, precipitation (both total and at mean temperature above 15°C) showed a strong positive correlation with LI, while temperature showed a negative effect.

The effects of weather on *S. fallax* LI were complex across the season. In the early season, higher temperature and number of rain days decreased LI, while precipitation at high temperature increased LI. Late in the season, higher temperature and length of dry period were correlated with increased LI. Similar to the early season, number of days with rain decreased LI and this was also true for the entire season. Like *S. angustifolium*, the correlation between *S. fallax* LI and temperature was different depending on the period of the growing season, but with opposite signs compared to *S. angustifolium*.

Generally, LI of all species except *S. fuscum* were sensitive to varying weather in different periods, i.e. there was an individual set of significant weather variables controlling LI of these *Sphagnum* species. For *S. angustifolium* and *S. fallax*, weather variables over the entire growing season were less pronounced predictors in contrast to the early or the late season.

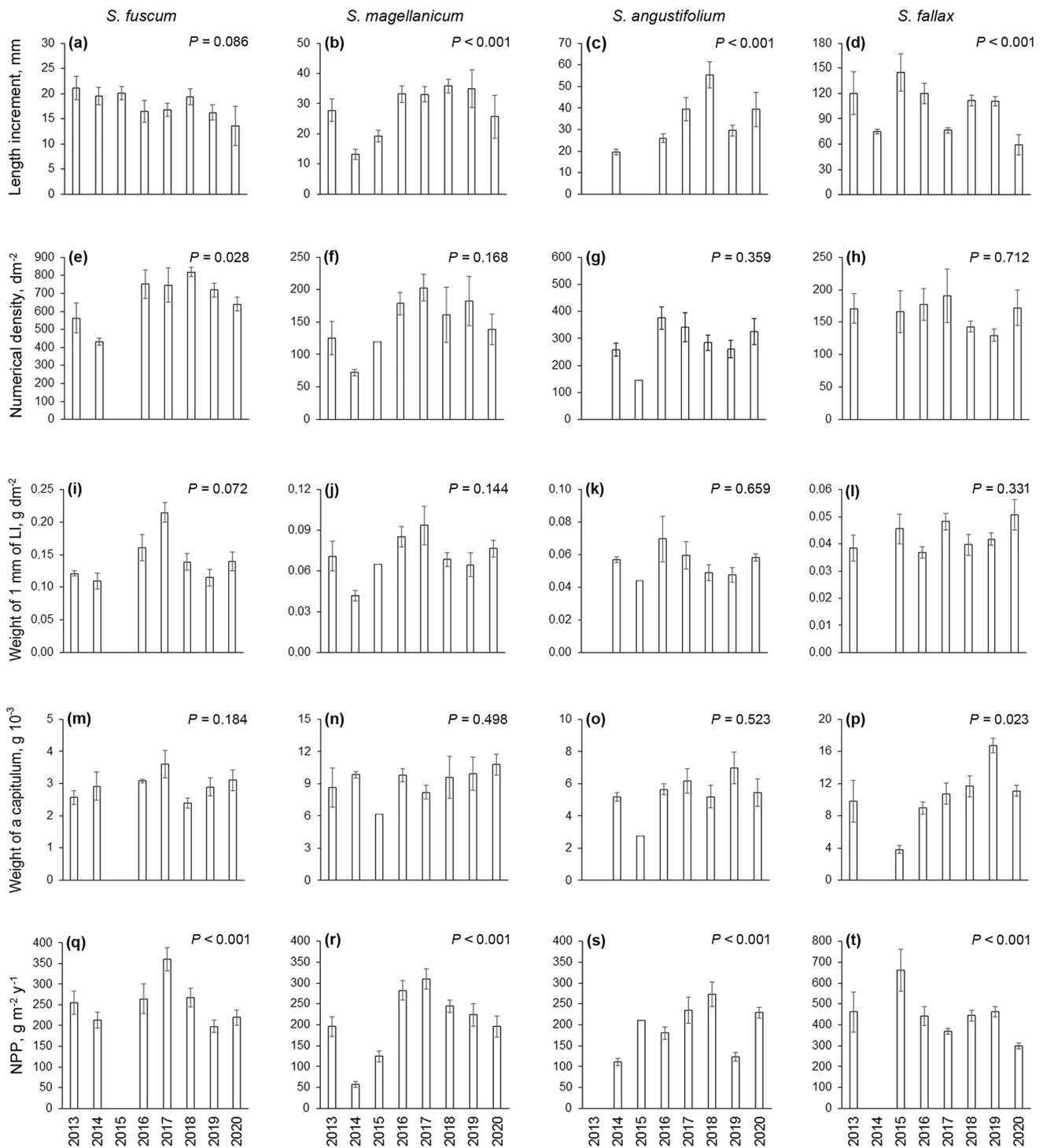
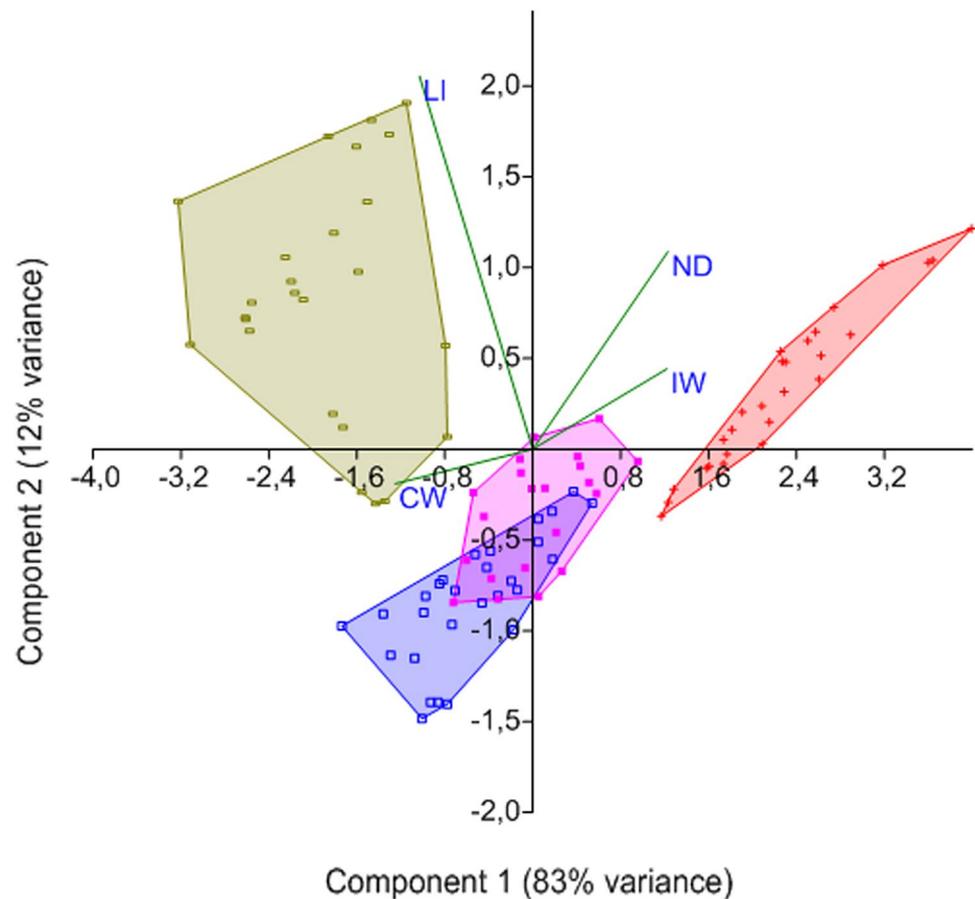


Fig. 1 Mean yearly values of length increment (a-d; $n=12-14$, 10-18, 6-30 and 3-23, respectively), numerical density (e-h; $n=3-5$, 1-5, 1-4 and 3-5, respectively), increment biomass (i-l; $n=3-5$, 1-5, 1-4 and 3-5, respectively), capitulum biomass (m-p; $n=3-5$, 1-5, 1-4 and 3-5, respectively), and primary productivity (q-t; $n=12-14$,

10-18, 1-30 and 3-23, respectively) in four *Sphagnum* species. Bars show means \pm SE. No bars indicates absence of replicates. Results of non-parametric Kruskal-Wallis test on inter-year differences are shown as P values

Fig. 2 Ordination of weather variables – *Sphagnum* traits over the entire season based on principal components analysis. The species are shown with convex hulls: red – *Sphagnum fuscum*, blue – *S. magellanicum*, pink – *S. angustifolium* and greeny grey – *S. fallax*. The abbreviations of weather variables: T_m – mean temperature, Pr – precipitation, Pr_{T15} – precipitation at mean daily temperature above 15 °C, CI – climatic index, RD – number of days with rain, DD – length of dry period. The abbreviations of trait variables: LI – linear increment, IB – increment biomass, ND – numerical density and CB – capitulum biomass



Effects of weather variability on *Sphagnum* increment biomass, numerical density and capitulum biomass

In contrast to the LI, the ND of *S. fuscum* depended on many weather factors, but mainly precipitation (Pr and Pr15) and climatic index, with the early and the entire seasons being equally good predictors for ND (Fig. 4). IB was affected by moisture conditions over the growing season, specifically with precipitation in the early season and number of days with rain in the late season. Rising mean summer temperature decreased both *S. fuscum* ND and IB. Number of days with rain and precipitation at high temperature were predictors increasing *S. fuscum* CB.

The ND of *S. magellanicum* was also to a similar degree controlled by the weather of the entire season as by a specific period. The precipitation, including those at high temperature and the number of days with rain, affected both ND and IB at similar magnitudes.

IB of *S. fallax* was positively affected by the number of rainy days, and negatively by the length of dry period in the late season. Its CB was negatively correlated with the precipitation and the length of dry period. However, the strongest weather factor affecting CB was mean temperature

in the entire season, which correlated positively with *S. fallax* CB.

We did not detect significant effects of weather variables on the CB of *S. magellanicum*, ND of *S. fallax* nor ND, IB and CB of *S. angustifolium*.

Results of the 2-block PLS were similar for the early and the entire season, and the amount of covariance explained by the Axis 1 was 82% and 83%, respectively (Fig. 5a, d). In the late season, the amount of covariance explained by the Axis 1 and the Axis 2 were 50% and 46%, respectively. In the first case, *S. fuscum* distinguished from other species (Fig. 5b), and in the second case, species were distributed according to the water table gradient (Fig. 5c).

Weather factors controlling *Sphagnum* NPP

The net primary productivity (NPP) of peat moss is a function of LI, IB and ND. Using yearly averages for each species as individual samples in our statistical analyses, the contributions of these functional traits to NPP were species-specific (Table 2). Productivity of *S. fuscum* was mainly determined by IB, while the productivity of *S. angustifolium* and *S. fallax* was mostly influenced by LI. *Sphagnum magellanicum* NPP was almost equally determined by all these traits.

Fig. 3 Spearman’s correlation between *Sphagnum* length increment (LI) and weather variables over the early season, the late season and the entire growing season. Arrows of different colours indicate significance. For positive correlations, red means $P < 0.001$, yellow means $P < 0.01$ and white means $P < 0.05$. For negative correlations dark blue means $P < 0.001$, blue means $P < 0.01$ and grey means $P < 0.05$. Absence of arrow means that the correlation is not significant ($P > 0.05$). The abbreviations of weather variables: T_m – mean temperature, Pr – precipitation, Pr_{T15} – precipitation at mean daily temperature above 15 °C, CI_{As} – climatic index, RD – number of days with rain, DD – length of dry period. Details on correlations are given in Supplementary materials (Appendix Table S11)

Correlations between NPP and weather variables illustrated how productivity depends on the weather through changes in growth traits (Fig. 6). NPP of *S. magellanicum*, *S. angustifolium* and *S. fallax* had the same strongest weather predictors as for LI of these species. NPP of *S. fallax* was also affected by weather variables, such as the climatic index, which was not linked to changes in its functional traits. Contrarily, *S. fuscum* NPP depended less on weather variables. The significant factors affecting *S. fuscum* NPP were also significant for its ND, but to a lesser degree for IB.

Mean growing seasonal temperature was not a significant predictor for *S. fuscum* and *S. magellanicum* productivity (NPP) whereas it was a strong predictor for *S. angustifolium* (correlation $r = -0.47$) and intermediate predictor for *S. fallax* ($r = 0.27$). Precipitation was one of the strongest predictors, where higher precipitation was associated with greater NPP, either per season or over the entire growing season. However, the fen-dwelling *S. fallax* showed a different pattern. Higher precipitation in the spring increased NPP while higher precipitation in the autumn decreased NPP. As a result, precipitation over the entire season had no effect on NPP for this species. Climatic index (CI_{As}) was of similar importance as Pr15 for *S. fuscum* and *S. magellanicum*, while it was a weak or negligible predictor for the other species. The strength of the positive association between the number of rainy days (RD) and NPP increased in the sequence of bog species *S. fuscum* (no impact) – *S. magellanicum* – *S. angustifolium*, which is accordance with their moisture sensitivity (i.e., water loss rate). In contrast, RD decreased NPP for *S. fallax*. Finally, length of dry period (DD) over the entire season decreased NPP for *S. magellanicum* ($r = -0.29$), which likely was related to DD early in the season ($r = -0.20$). For *S. fallax*, DD increased NPP, and did so strongest in the late season ($r = 0.44$). Overall, in the early season, *Sphagnum* productivity of all species intensified with moisture factors (Pr, Pr15 and/or CI_{As}). In the late season, the impact of these factors decreased for the species except *S. magellanicum*. Drier and warmer conditions in the late season especially affected *S. angustifolium*, which reduced NPP under higher mean temperature, likely causing capitulum desiccation, and enhanced it under increasing number of rainy days.

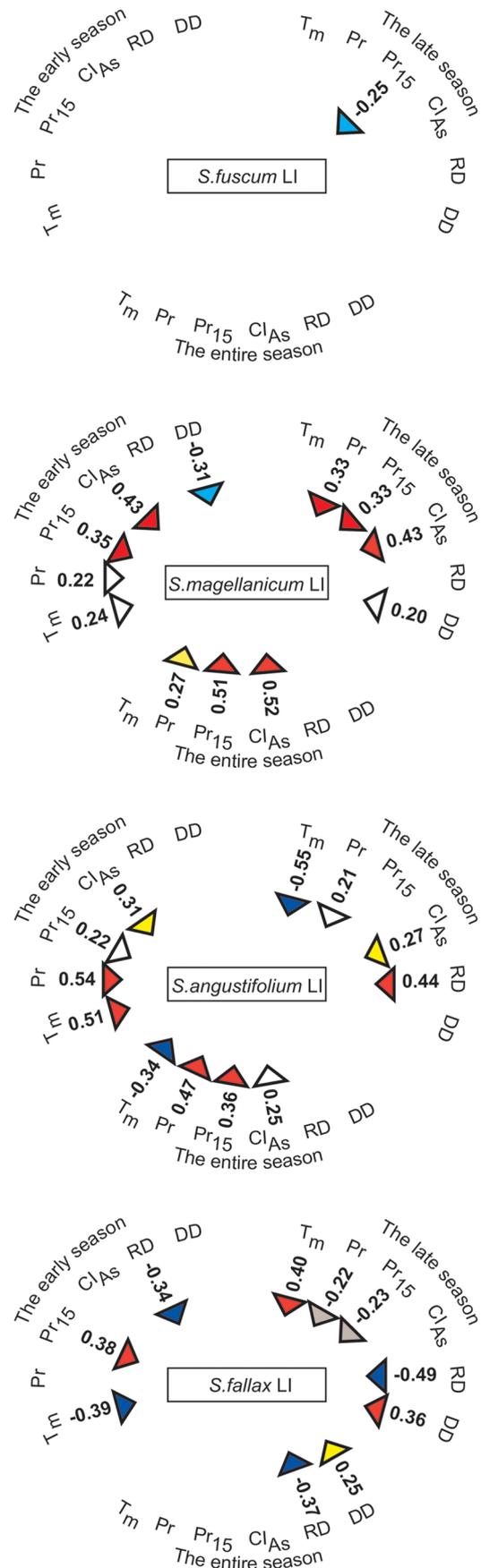
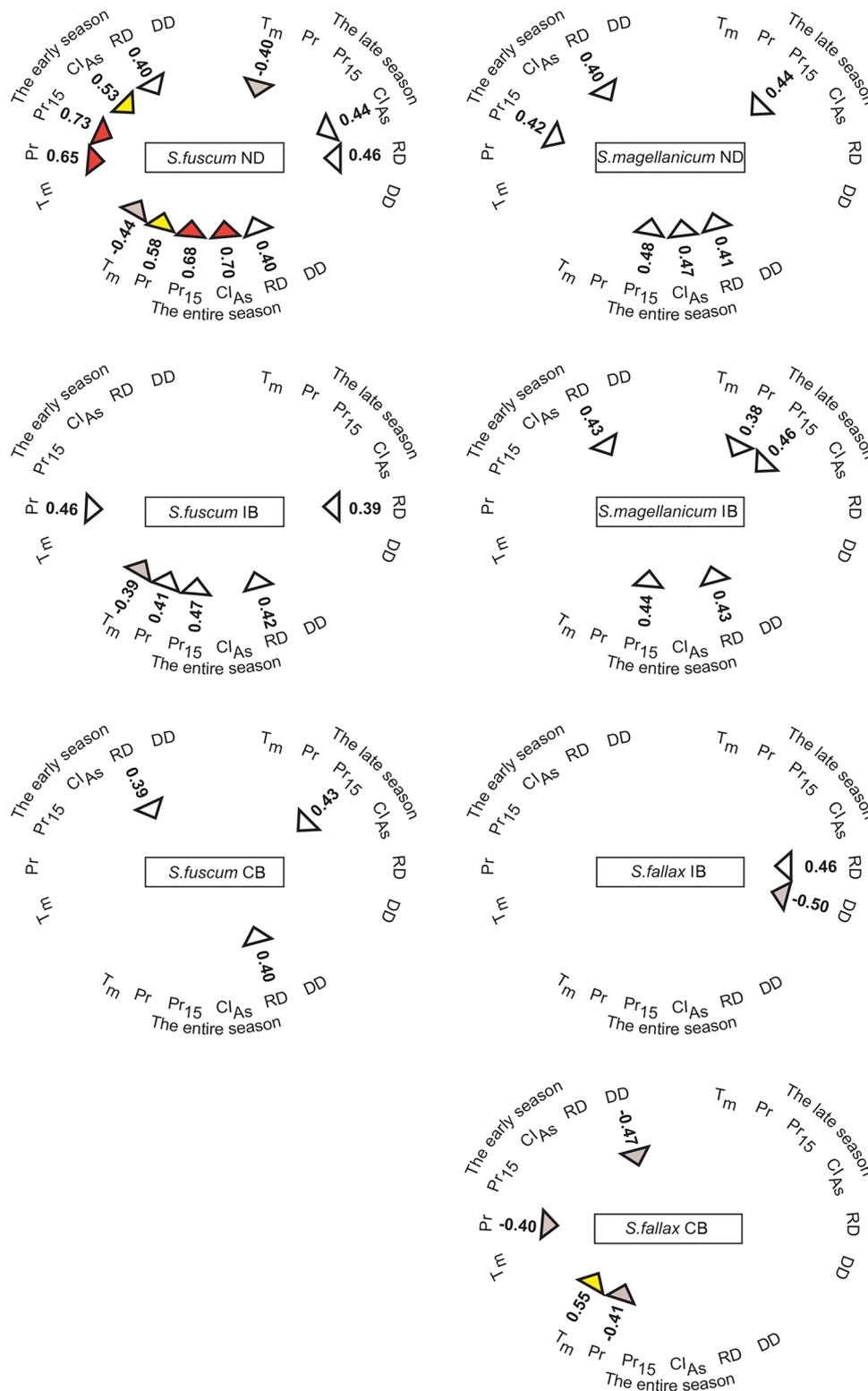


Fig. 4 Spearman’s correlations between *Sphagnum* numerical density (ND), increment biomass (IB), capitulum biomass (CB) and weather variables over the early season, the late season and the entire growing season. Arrows of different colours indicate significance. For positive correlations, red means $P < 0.001$, yellow means $P < 0.01$ and white means $P < 0.05$. For negative correlations dark blue means $P < 0.001$, blue means $P < 0.01$ and grey means $P < 0.05$. Absence of arrow means that the correlation is not significant ($P > 0.05$). No significant correlations were found for *S. magellanicum* CB, *S. fallax* ND and functional traits of *S. angustifolium*. The abbreviations of weather variables: T_m – mean temperature, Pr – precipitation, Pr_{T15} – precipitation at mean daily temperature above 15 °C, CI_{As} – climatic index, RD – number of days with rain, DD – length of dry period. Details on correlations are given in Supplementary materials (Appendix Table S12, S13, S14)



Discussion

This study tests the hypothesis that weather variables of the early or the late season are stronger predictors of the values of annual *Sphagnum* functional traits and productivity

compared to the growing season average. Weather variables show different correlations with *Sphagnum* growth depending on the period of the growing season and species. Within-season changes in weather are as important for *Sphagnum* growth as changes over the entire season, and

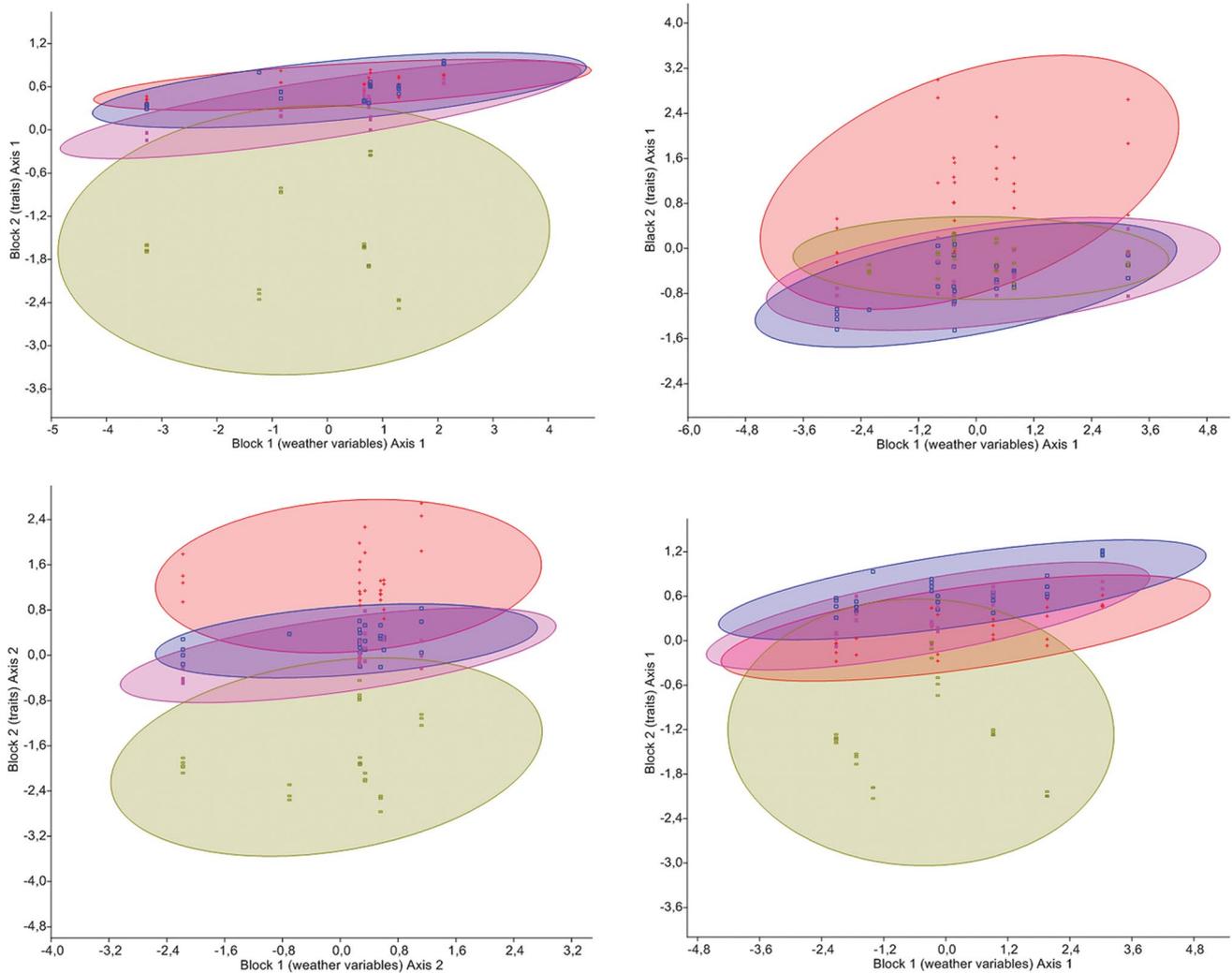


Fig. 5 Plots of the two-block partial least squares (PLS) analysis with weather variables (block 1) against traits (block 2): a) The early season: the amount of covariance explained by the Axis 1 (the first block) is 83% with the most component loadings of precipitation (-0.67), precipitation at mean daily temperature above 15°C (-0.57) and climatic index (-0.42); b) The late season: the amount of covariance explained by the Axis 1 (the first block) is 50% with the most component loadings of climatic index (0.73), precipitation (0.49) and precipitation at mean daily temperature above 15°C (0.42); c) The late season: the amount of covariance explained by the Axis 2

(the first block) is 46% with the most component loadings of length of dry period (-0.63), mean temperature (0.56) and precipitation at mean daily temperature above 15°C (0.42); d) The entire season: the amount of covariance explained by the Axis 1 (the first block) is 82% with the most component loadings of precipitation (-0.67), climatic index (-0.42), mean temperature (0.42) and precipitation at mean daily temperature above 15°C (-0.39). Species are marked with coloured 95% confidence interval ellipses: red – *Sphagnum fuscum*, blue – *S. magellanicum*, pink – *S. angustifolium* and greenish grey – *S. fallax*

Table 2 Pearson’s correlation between annual NPP and functional traits

Species	Linear increment, LI	Increment biomass, IB	Numerical density, ND
<i>S. fuscum</i>	0.08 ($P=0.865$)	0.92 ($P=0.004$)	0.43 ($P=0.332$)
<i>S. magellanicum</i> agg	0.89 ($P=0.003$)	0.91 ($P=0.004$)	0.95 ($P=0.001$)
<i>S. angustifolium</i>	0.93 ($P=0.007$)	-0.08 ($P=0.887$)	0.28 ($P=0.592$)
<i>S. fallax</i>	0.92 ($P=0.003$)	-0.29 ($P=0.528$)	-0.24 ($P=0.609$)

Mean annual value of NPP and functional traits for each species were considered as individual samples and n ranged from 6 to 8. Significant correlations are given in bold

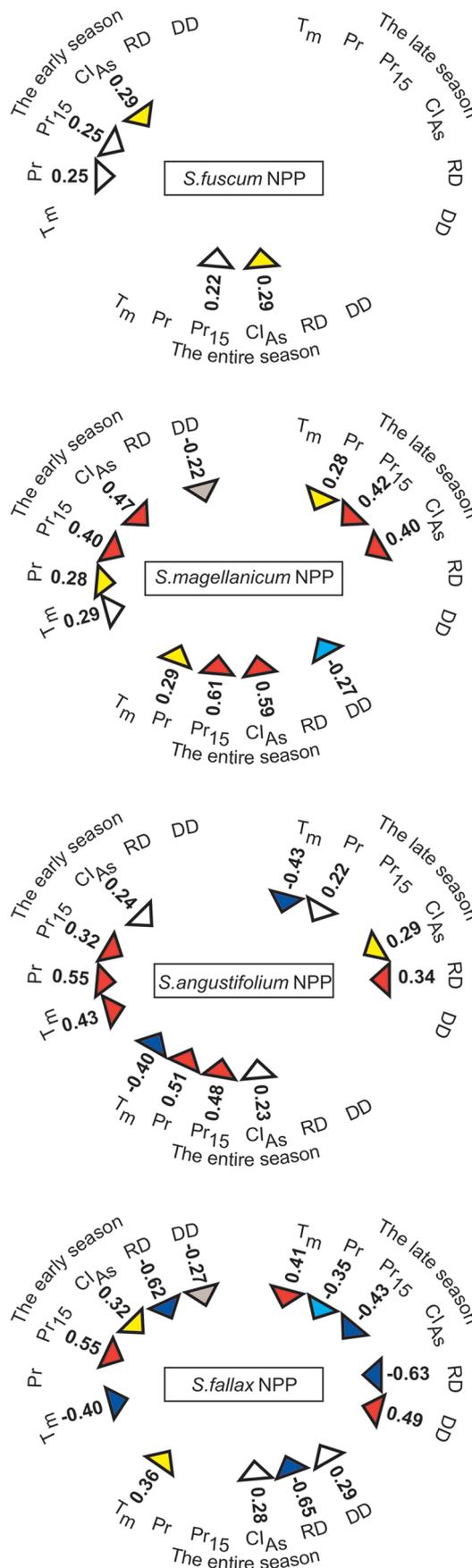
Fig. 6 Spearman's correlations between *Sphagnum* NPP and weather variables over the early season, the late season and the entire growing season. Arrows of different colours indicate significance. For positive correlations, red means $P < 0.001$, yellow means $P < 0.01$ and white means $P < 0.05$. For negative correlations dark blue means $P < 0.001$, blue means $P < 0.01$ and grey means $P < 0.05$. Absence of arrow means that the correlation is not significant ($P > 0.05$). The abbreviations of weather variables: T_m – mean temperature, Pr – precipitation, Pr_{T15} – precipitation at mean daily temperature above 15 °C, CI_{As} – climatic index, RD – number of days with rain, DD – length of dry period. Details on correlations are given in Supplementary materials (Appendix Table S15)

species differ widely in their responses to such changes. Growing season averages of weather variables are often as good predictors of the functional traits as late or early seasonal means, but not necessarily for the same variables. This indicates the complexity in identifying causal relationships between weather and plant performance.

Trait- and species-specific response of *Sphagnum* to weather factors

Numerous studies have shown how *Sphagnum* length increment changes between growing seasons (e.g. Moore 1989, Lindholm 1990, Graham and Vitt 2016). In our 8-year study, large inter-year variation of length increment (LI) of a lawn-hollow species (*S. fallax*) and species with a wide ecological niche (*S. angustifolium*, *S. magellanicum*) was linked to weather fluctuations. *Sphagnum angustifolium* and *S. magellanicum* are sensitive to low water availability (Schipperges and Rydin 1998; Mulligan and Gignac 2001; Robroek et al. 2007; Strack and Price 2009) and our study shows that for these species, weather factors associated with water availability are especially important in the late season. Interestingly, these factors differ between species: *S. magellanicum* LI correlates positively with precipitation, while *S. angustifolium* LI is positively correlated with number of days with rain, i.e. rain frequency. Unlike *S. magellanicum*, *S. angustifolium* LI decreases when temperature rises in the late season, which suggests higher susceptibility to desiccation of this species. In previous field studies, *Sphagnum* LI has increased with higher rain frequency (Beckéus 1988; Robroek et al. 2009; Nijp et al. 2014; Krebs et al. 2016) and decreased with longer rain free periods (Bengtsson et al. 2021). Our study show how weather factors simultaneously can have opposite effects on *Sphagnum* LI depending on species identity.

The dynamics of many functional traits of *Sphagnum* have mostly been studied across space in connection to the water table gradient (Laing et al. 2014; Bengtsson et al. 2016; Mazziotta et al. 2019), and these traits are often assumed to be constant on a temporal scale. Recent studies, nevertheless, have successfully attempted to find inter-year difference in moss carpet density



(Graham and Vitt 2016; Bengtsson et al. 2021). We find significant inter-year dynamics in numerical density (ND) of hummock species *S. fuscum* while *S. magellanicum*, *S. angustifolium* and *S. fallax* vary much less. Our interpretation is that while other species mainly govern stem growth, *S. fuscum* more actively controls carpet density depending on weather conditions. *Sphagnum fuscum* ND increases under the conditions of high moisture, and maybe stronger when combined with high temperature in the early season. In contrast, Bengtsson et al. (2021) reported a negative effect of seasonal precipitation on ND across the Northern Hemisphere, but similar to our study they found a negative effect of mean temperature on ND. Dense carpet (i.e. high bulk density) maintains a high water retention in the late season when capillary moisture content is dropping in peat. High bulk density is crucial to maintaining a high water content (Bengtsson et al. 2021; Nijp et al. 2014), and active branching of *S. fuscum* under favorable weather conditions will help to avoid future desiccation. In fact, branching instead of elongation can be a way in which *S. fuscum* becomes dominant in peatlands, but this needs further research.

The link between increment biomass (IB) and capitulum biomass (CB) to weather variables are weak in our study. Slowly changing weight traits (IW and CB) respond to integrated conditions of the growing season, which is in line with the finding of Laine et al. (2011) that weight increases after linear growth stops at the end of summer. However, we do not observe that late season variables are better predictors, with the exception of *S. fallax* CB.

Habitat- and season-specific response of *Sphagnum* to weather factors

The impact of the weather on *Sphagnum* growth depends on the local mire conditions, such as the current water table position. For example, high temperature promotes the growth as long as peat moisture is high (Jassey and Signarbieux 2019). We found that temperature, precipitation and number of days with rain have the opposite effect on *Sphagnum* functional traits synchronously depending on the habitat, which is likely due to varying peat water availability. The water table drop often observed during the summer leads to a subsidence of peat in ecosystems with a water-surplus such as flarks and hollows (Nijp et al. 2019), while hummock height almost does not change with HWT fluctuation (Yazaki and Yabe 2012). In the study site of Bakchar mire, the HWT during the late growing season does not fall below 20 cm in the poor fen, but it noticeably drops in the raised bog (Dyukarev et al. 2015). Our results support the idea that warmer and drier weather conditions promote moss desiccation and ceased growth in bogs, while it can promote moss growth in poor fens.

For bog species, mean temperature positively correlates with functional traits and NPP or it is insignificant in the early season, and it becomes indifferent or an inhibiting factor for growth in the late season. For the fen species *S. fallax*, the opposite pattern is observed.

Precipitation, number of days with rain and length of the dry period are factors of water availability. “Number of days with rain” is a complex factor that includes temporal distribution of moisture, higher cloudiness and lower photosynthetically active radiation. There is evidence that the precipitation dependence of *Sphagnum* growth is high when the water table is deep (Nijp et al. 2014), but frequent daytime rain events reduce light and, consequently, may decrease carbon uptake in peatlands (Nijp et al. 2015). Assuming that photosynthesis is more limited by water availability than light, the effect of clouds on growth is more substantial when water table is closer to the moss surface like at our poor fen site. As a result, days with rain contribute to moss growth in bogs but potentially not in poor fens. “Length of the dry period” includes both moisture deficit and light availability. In the bog, this factor has a weak negative effect early in the season, and has no effect later in the season. In the poor fen, this factor is the driver of *S. fallax* LI and NPP augmentation as well as IB dropping.

Climatic index and precipitations at daily mean temperature above 15 °C combine heat and moisture conditions. Such indices have previously been used to understand *Sphagnum* growth (e.g. Beckéus 1988; Asada et al. 2003). The higher their value the more moisture is available at high temperature. In this study, climatic index is always positively correlated with growth in the bog but not in the poor fen. In the bog, precipitation at high temperature is always positive factor for *Sphagnum* growth with varying strength in different seasons. The only exception is found for *S. fuscum* LI, which decreases with this factor. In the poor fen, moss growth is stimulated by this factor in the early season and it is inhibited in the late season. Combined climatic factors were the strongest predictors and showed higher importance early in the season or over the entire season.

Overall, thermal and moisture factors accelerate or inhibit *Sphagnum* growth depending on the period of the growing season, species and habitat. A switch from a positive correlation with a factor (e.g. mean temperature or length of the dry period) to a negative one during the growing season is the reason of weak or no relationship average for the entire season. This complexity has to be taken into account in peatland-climate modelling of *Sphagnum* productivity.

Weather-induced inter-year difference in *Sphagnum* NPP and resistance of peat moss community

There is evidence of similar productivity of *Sphagnum* across species over time due to a trade-off between maximizing

Table 3 NPP ($\text{g m}^{-2} \text{y}^{-1}$) of the dominant species in bogs (*S. fuscum*) and poor fens (*S. fallax*) and the total productivity of the both species

Year	<i>S. fuscum</i>	<i>S. fallax</i>	Total
2013	128 ± 14	231 ± 49	359
2016	132 ± 18	221 ± 23	353
2017	180 ± 14	184 ± 8	364
2018	134 ± 11	222 ± 13	356
2019	99 ± 8	231 ± 12	330
2020	110 ± 10	150 ± 8	260

Mean ± SD, $n = 12\text{--}14$ for *S. fuscum* and $4\text{--}23$ for *S. fallax*

length growth and maintaining high water content (Laing et al. 2014; Mazziotta et al. 2019; Bengtsson et al. 2021; Jassey and Signarbieux 2019). In our study, inter-year range in NPP values is higher than in functional traits values for all studied species and this depended on changes in weather. Over the entire season, *S. fuscum* and *S. magellanicum* were the most productive under warm and wet conditions with *S. fuscum* being less sensitive to weather fluctuations; *S. angustifolium* had highest productivity under cool and wet conditions, while *S. fallax* was the most productive under dry weather. What are the consequences of such contrasting species- and habitat-dependent (bog versus poor fen) weather effects on *Sphagnum* productivity for a mire complex? Total productivity of the dominant species in different habitats, *S. fuscum* and *S. fallax*, was stable over several growing seasons ($337 \pm 6 \text{ g m}^{-2} \text{ y}^{-1}$). This stability is a result of the asynchrony between *S. fuscum* NPP and *S. fallax* NPP (Table 3), which is illustrated by a strong negative linear correlation between productivity of these species ($r = -0.93$, $P = 0.022$) over the period of 2013–2019. Recently, a study found high *Sphagnum* functional diversity and intraspecific variability in late successional peatlands, and suggested that these factors together promote peatland resistance towards environmental perturbations (Laine et al. 2021). Here, on a contemporary temporal scale, we show intraspecific variability in peat moss responses to weather varying that also indicates peatland resistance towards environmental inconstancy. Our finding is in accordance with the findings of Jassey and Signarbieux (2019), who showed stable ecosystem productivity with temperature changes due to the differential responses of *Sphagnum* species. Such complementary feedback between *Sphagnum* and weather fluctuations stabilises functioning of mire complexes regardless of meteorological conditions. Nevertheless, combinations of weather variables can cause a drop in the total productivity as observed in 2020 where a likely a combination of high frequency of rainy days (crucial for *S. fallax*) and moderate precipitation and low value of climatic index (crucial for *S. fuscum*) limited productivity (Table 3). To establish if

such weather tipping points for mire productivity exists is an urgent task for future research.

Mutual replacement of *Sphagnum* productivity depending on weather can be found both within a mire ecosystem and between different mire types due to various dominant species. Our study indicates that the predicted increase in temperature and drought periods (Moore 2002) are favourable for water-surplus mire microforms in Western Siberia, such as pools and lawns, in contrast to raised bogs and ridges in patterned mires. This is in contrast to the general idea that hummock species will be favoured over hollow/lawn species under climate change (e.g., Breeuwer et al. 2008; Robroek et al. 2009). Thus, there are still gaps in our understanding of which weather factors and of which magnitude cause shifts in peat mosses productivity, and subsequently, peat moss composition. Identifying critical ranges in climatic factors governing *Sphagnum* performance across climate zones is essential for predicting ecosystem change in a changing climate.

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Author's Contributions Natalia P. Kosykh and Gustaf Granath outlined the study; Natalia G. Koronotova, Ekaterina A. Saib, Vera A. Stepanova, Evgenia K. Vishnyakova and Natalia P. Kosykh collected the data; Natalia G. Koronotova proposed the hypothesis, performed the data analysis and wrote the first draft of the manuscript; Gustaf Granath contributed with text and edited the manuscript; all authors reviewed and approved the manuscript.

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Data Availability The raw data are available via Mendeley Data repository [<https://doi.org/10.17632/6d3sgzmdxp.2>].

Declarations

Competing Interests The authors have no conflicts of interest to declare that are relevant to the content of this article. The authors have no relevant financial or non-financial interests to disclose.

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