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ORIGINAL PAPER

Effects of both substrate and nitrogen and phosphorus fertilizer on *Sphagnum palustre* growth in subtropical high-mountain regions and implications for peatland recovery

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Abstract Human activities have recently caused severe destruction of *Sphagnum* wetlands in subtropical high-mountain regions, calling for urgent efforts to restore *Sphagnum* wetlands. Through a greenhouse experiment in western Hubei, China, we studied the effects of different substrate types (peat and mountain soil) and different levels of nitrogen (N) (0, 2, 4, 6, 10 g m^{-2} $year^{-1}$) and phosphorus (P) (0, 0.2, 0.5, 1, 2 g m^{-2} $year^{-1}$) on the growth of *Sphagnum palustre*, which was evaluated by four growth indicators: length growth, number of capitula, coverage change and biomass. We aimed to determine the optimal nutrient conditions for *S. palustre* growth, which would contribute to the rapid colonization and restoration of *Sphagnum* wetlands. The results showed that the different substrates significantly influenced *S. palustre* growth. Compared with those of peat, the acidic properties of the local yellow brown soil in the subtropical high-mountain regions were more favorable for *S. palustre* growth. As N addition increased, the four growth indicators responded inconsistently to the different substrates. While the number of capitula markedly increased, the other three indicators significantly decreased in the mountain soil or exhibited no definitive changes in the peat. The addition of P markedly promoted *S. palustre* growth in both substrates. However, a threshold for P fertilization existed; the highest productivity occurred at P additions of 0.2 and 0.5 g m^{-2} $year^{-1}$ in the peat and mountain soil, respectively. The N and P contents in the capitula increased in parallel as the N and P fertilization rates increased, suggesting that these nutrients were absorbed proportionately and were used during the growth of *S. palustre*.

Keywords Nitrogen · Phosphorus · Substrates · pH · Wetland restoration

Introduction

Peatlands are important carbon sinks and are estimated to contain one-third of the global soil organic matter; consequently, peatlands influence the global carbon cycle (Gorham 1991; Clymo et al. 1998; Yu et al. 2010). *Sphagnum* is the most important genus of peat-

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forming moss (Gunnarsson 2005; Warner and Asada 2006; Medvedeff et al. 2015; Limpens et al. 2017) and comprises approximately 250–400 species (Shaw et al. 2016). Of those species, *Sphagnum palustre* is common and is widely distributed throughout Europe and East Asia, as well as the Pacific and Atlantic coasts of North America as far south as Mexico (Daniels and Eddy 1990). In the subtropical regions of southern China, patchy distributions of high-mountain wetlands dominated by *S. palustre* are found in the high-altitude areas of the Huangshan Mountains, Yunnan-Kweichow Plateau and western Hubei Mountains (Ma et al. 2008). In addition to their important ecological functions concerning carbon accumulation, climate regulation and biodiversity protection, these subtropical high-mountain wetlands also play a significant role in water storage, acting as headstreams of important rivers. However, the abundance of *S. palustre* has diminished because of habitat destruction and excessive harvesting for horticultural purposes, necessitating efforts to restore *Sphagnum* wetlands.

Sphagnum wetlands are complex ecosystems influenced by various biotic and abiotic factors (Price et al. 2003), among which nutrient availability (such as nitrogen [N] and phosphorus [P]) is an important factor for *Sphagnum* wetland development. N is vital for plant growth. Its effects on *Sphagnum* have been widely studied, but the results have been somewhat contradictory. Quinty and Rochefort (2003) suggested that N fertilization is not needed because bare peat surfaces already contain enough N to ensure plant growth. Limpens and Berendse (2003) and Limpens et al. (2004) reported that N addition can lead to decreased productivity and length growth of *Sphagnum*, which is in agreement with the results of a series of studies (e.g., Berendse et al. 2001; Bubier et al. 2007; Wiedermann et al. 2007; Gerdol et al. 2010; Bu et al. 2011; Bragazza et al. 2012; Nishimura and Tsuyuzaki 2015). In contrast, Bonnett et al. (2010) reported that N fertilization can markedly increase *Sphagnum* biomass, which was observed also by other earlier studies (Paavilainen and Päivänen 1995; Williams and Silcock 1997; Vitt et al. 2003). The inconsistency of N effects may be influenced by various factors, including P availability, temperature, cultivation method, temporal differences in fertilization (Gunnarsson and Rydin 2000; Arroniz-Crespo et al. 2008; Breeuwer et al. 2009; Bu et al. 2011; Kim et al. 2014), and, most importantly, dissimilarity between study areas (Aerts et al. 1992; Gunnarsson and Rydin 2000) and species of interest (Nordin and Gunnarsson 2000; Limpens and Berendse 2003). Regional differences cause variation in background values of N deposition, and the diversity of *Sphagnum* species also contributes to differences in N demand. Therefore, the effects of N on *S. palustre* require careful investigation when no relevant studies have been carried out in particular regions, such as the subtropical high-mountain areas of southern China.

Unlike N, P seems to exert universal positive effects on *Sphagnum* growth (Rochefort et al. 2003; Limpens et al. 2003, 2004; Gerdol et al. 2010; Bu et al. 2011). However, the amount of P fertilization in previous studies has been limited to a small range (e.g., 0–1 g m^{-2} $year^{-1}$) (Limpens et al. 2004; Limpens and Heijmans 2008; Bu et al. 2011; Gerdol and Brancaleoni 2015); therefore, whether *Sphagnum* growth increases continuously as P addition increases is unknown. However, excess amounts of any element, no matter how beneficial it is, can cause detrimental effects on plant physiological processes (Pan et al. 2008). In this study, we hypothesize that a threshold of P demand exists for *S. palustre* and that negative effects will occur once the P content exceeds that threshold. Thus, several treatment levels encompassing a relatively broad range are needed to test the effects of P addition on *S. palustre*.

The type of substrate in which *Sphagnum* is cultivated represents another factor influencing plant growth. In natural bogs, the hummock species *S. palustre* is separated from the underlying peat and feeds on only atmospheric deposition (Damman 1978; Clymo 1983). However, during the process of restoration, transplanted *Sphagnum* plants are in full contact with the substrate. Properties such as nutrient contents, pH, and water retention capacity are likely to differ among different types of substrates and thus likely affect *Sphagnum* growth. Traditional restoration of *Sphagnum* is mainly conducted on original or abandoned peatland, in which local peat is the only substrate. However, in subtropical high-mountain regions, *Sphagnum* mires are intermittently distributed in small patches. Peat use is limited by complicated topographic conditions and mire ranges. To ease the process of restoration, we used local yellow–brown soil (which is classified into Alfisols order, Moist Warm Alfisol suborder in accordance with the classification system of Chinese soil; Zhu et al. 2010) from subtropical mountain regions ("mountain soil" hereafter) as an innovative substrate for *S. palustre*.

We studied N, P and substrate type as factoring influencing the growth of *S. palustre* in subtropical high-mountain regions and possible mechanisms underlying these effects. We propose the following hypotheses: (1) different substrates will affect *S. palustre* growth, (2) *S. palustre* will show maximum growth at medium levels of N and P addition, and (3) the effects on *S. palustre* growth may be attributable to associated changes in the N and P contents in the capitula.

Materials and methods

Study site and species

The Qizimei Mountain National Nature Reserve (N29°39′30″–30°05′15″, E109°38′30″–109°47′00″) in southwestern Hubei, China, lies in the subtropical zone and encompasses an area of 34,550 ha; the altitude of the area ranges from 650 to 2015 m (Liu et al. 2006). The region is characterized as having a subtropical humid monsoon climate with definitive vertical differentiation (i.e., the temperature lapse rate is $-$ 0.6 °C 100 m^{-1}). The study site is within the reserve in a high-mountain area: the altitude is 1800 m, the annual average temperature is 8.9 °C, the annual precipitation is 1876 mm, and the sunshine duration is 1520 h.

The patches of *Sphagnum* wetlands range in altitude from 1650 to 1950 m and cover a total of approximately 940 ha. The results of the most recent survey indicate that 197 species of higher plants, consisting of 8 ferns, 4 gymnosperms, 182 angiosperms and 3 bryophytes exist in the area (Wang et al. 2013; Zhao et al. 2013). *Sphagnum palustre* L. is the only *Sphagnum* species in the area and is the dominant species in wetlands that contains definitive hummocks. In addition, trees such as *Enkianthus chinensis* and *Rhododendron auriculatum*; shrubs such as *Sinarundinaria nitida* and *Malus hupehensis*; and herbs such as *Juncus setchuensis*, *Lycopus coreanus*, *Carex taliensis*, *Hosta ventricosa*, *Pteridium aquilinum* var. *latiusculum*, *Acorus calamus*, *Oenanthe dielsii* var. *stenophylla*, *Polygonum thunbergii*, and *Luzula effusa* also exhibit relatively high coverage.

Experimental design

A 20 × 15-m experimental greenhouse was constructed on a wasteland in the core zone of the reserve; the greenhouse was covered overhead with transparent plastic film and shade nets, and to keep the structure ventilated, only shade nets were applied around the sides of the greenhouse. The wasteland was historically covered with shrubs dominated by *Corylus heterophylla* var. *sutchuenensis*. However, these shrubs were removed several years prior to the experiment, and thereafter, the site had been overgrown with weeds, of which *Erigeron annuus*, *Inula japonica*, and several species within the genus *Polygonum* dominated before our greenhouse was constructed. All experiments were conducted in the greenhouse, in which the average temperature was 0.5 °C higher than the ambient temperature (measured 3–4 times per month during the whole experimental period). A three-factor design consisting of two types of substrates (peat and mountain soil), five levels of N (N0, N2, N4, N6, N10) and five levels of P (P0, P0.2, P0.5, P1, P2) was applied to potted *S. palustre* plants. Each combination of treatments has five replicates, and there were 250 samples in total.

In February 2016, an abundant amount of soil was excavated from the natural *Sphagnum* wetlands and nearby wasteland, after which the soil was air-dried for 72 h in the sun and then sifted through a 3-mm mesh screen. Since *Sphagnum* is easily propagated via cuttings, we collected the top 8-cm part of individuals from several *S. palustre* populations in the local natural *Sphagnum* wetlands. Shoot bundles composed of six shoots of similar size without side shoots or multiple capitula were transplanted in plastic pots filled with equal amounts of peat or mountain soil; each substrate was present in 125 pots. The bottom 3 cm of every shoot bundle was inserted into the substrate, leaving an initial aboveground length of 5 cm. Fertilization was applied bimonthly during the growing season (from April to October 2016); NH_4NO_3 (N) or $NaH_2PO_4 \cdot 2H_2O$ (P) was dissolved in 20 ml of local mountain spring water (pH 6.2; conductivity = 532 μS cm^{-1}). The chemicals added were equivalent to 0, 2, 4, 6, and 10 and 0, 0.2, 0.5, 1, and 2 g m^{-2} $year^{-1}$ of N and P, respectively. Water was sprayed evenly above the *S. palustre* plants to ensure sufficient soil and air humidity.

Measurements of growth indicators and elements

The peat and mountain soil used in the experiment were subsampled and subjected to physical and chemical analyses. Among the physical properties, the volume weight was measured by the cutting ring method, specific gravity was measured by the pycnometer method, and porosity was calculated by the formula $P = 1 - VW/SG$ (where P is the porosity, VW is the volume weight, and SG is the specific gravity). The pH of both substrates was measured by the potentiometric method. Fifteen samples of 0.5 g substrates were weighed and digested in accordance with the H_2SO_4–$HClO_4$ method, after which the total N and total P contents were analyzed by the indophenol blue method and molybdenum-antimony anti-spectrophotometric method, respectively. All measurement analyses were in accordance with the methods of Lao (1988).

From March until November 2016, the number of capitula and average shoot length of *S. palustre* were measured monthly for each pot on fixed dates, and images were collected at the same time for calculating coverage by Arc Map (version 10.2, developed by ESRI, America).

In November 2016, all tissues of *S. palustre* were collected and put into plastic bags, which were subsequently sealed. Moreover, the substrate in each pot was collected to measure the pH. To estimate the biomass, all tissues were first dried at ambient temperature and then at 70 °C for 48 h. Afterward, all dried *Sphagnum* capitula were removed and ground to fine powder to measure the total N and total P contents (dry mass). The methodology was identical to that used for the substrate.

Statistical analysis

In this paper, we considered "length growth" a longitudinal elongation (or longitudinal growth) indicator and "number of capitula" a lateral expansion (or lateral growth) indicator. While "coverage change" and "biomass" are integrated growth indicators, the former represents growth potential, and the latter emphasizes productivity. The pairwise relationships among the four growth indicators were estimated by Pearson's correlation coefficients (r values).

One-way ANOVA was used to test for differences in the physical and chemical properties and *S. palustre* growth (the response variables included the length growth, number of capitula, coverage change and biomass) between peat and mountain soil. Within each substrate type, two-way ANOVA was used to analyze the effects of N and P as well as their interactive effects on *S. palustre* growth. Moreover, a MANOVA approach was used to evaluate the effects of N and P as well as their interactive effects on overall *S. palustre* growth (four indicators combined). Lastly, one-way ANOVA was used to analyze the effects of N and P fertilization on the N and P contents in the capitula, respectively, and regression analysis was used to test the relationships between the N and P contents in the capitula and biomass.

Prior to analysis, the data were checked for normality of errors and homogeneity. Any variables generating unequal variance were log or square root transformed. All statistical analyses were performed using IBM SPSS Statistics (version 19.0).

Results

Effects of substrate type on the growth of *S. palustre*

The peat had higher nutrient contents and pH than did the mountain soil (Table 1). The substrates significantly influenced *Sphagnum* growth. The number of capitula, coverage change and biomass of *S. palustre* grown in mountain soil were markedly higher than those grown in peat (number of capitula: 16.31 ± 9.16 and 9.46 ± 8.28, $F_{(1,231)} = 35.79$, $P < 0.001$; coverage change: 34.65 ± 18.82 and 26.94 ± 12.69, $F_{(1,231)} = 13.24$, $P < 0.001$; biomass: 1.43 ± 0.25 and 1.01 ± 0.16, $F_{(1,231)} = 226.63$, $P < 0.001$ in the mountain soil and peat, respectively). The length growth was greater in the mountain soil than in the peat, but the differences were not significant (mountain soil: 4.00 ± 1.50, peat: 3.78 ± 1.02, $F_{(1,231)} = 1.65$, $P = 0.20$). Overall, the mountain soil was a better substrate for the restoration of *S. palustre*.

Effects of N on the growth of *S. palustre*

No interactive effects occurred between N and P in the peat or in the mountain soil (Table 2). N significantly affected *Sphagnum* growth, but the effects varied between the two substrates. In the mountain soil, the

Table 1 Comparison of the baseline physical and chemical properties of two substrate types (n = 30 for each property)

Substrate	VW (g cm^{-3})	SG (%)	Porosity (%)	pH	TN (mg g^{-1})	TP (mg g^{-1})	OM (mg g^{-1})
Mountain soil	0.85 ± 0.07^a	2.51 ± 0.05^a	66.04 ± 2.79^a	5.58 ± 0.05^a	2.72 ± 0.29^a	0.87 ± 0.01^a	72.93 ± 6.63^a
Peat	0.40 ± 0.03^b	1.45 ± 0.03^b	72.45 ± 2.36^b	6.44 ± 0.06^b	6.78 ± 0.46^b	1.25 ± 0.04^b	222.04 ± 11.18^b

VW stands for volume weight; SG stands for specific gravity; TN stands for total nitrogen content; TP stands for total phosphorus content; OM stands for organic matter content

Different letters next to values indicate significant differences ($P < 0.05$) according to one-way ANOVA

Table 2 Effects of N and P and their interaction on each of four indicators of *Sphagnum palustre* according to two-way ANOVA (upper table) and on the overall growth (four indicators combined) of *S. palustre* according to two-way MANOVA (lower table)

Source	Mountain soil			Peat		
	df	*F*	*P*	*df*	*F*	*P*
Length growth						
N	4.96	37.86	< 0.01	4.87	1.35	0.26
P	4.96	14.96	< 0.01	4.87	8.25	< 0.01
N × P	16.96	1.10	0.36	16.87	1.45	0.14
Number of capitula						
N	4.96	13.17	< 0.01	4.87	29.05	< 0.01
P	4.96	52.26	< 0.01	4.87	9.95	< 0.01
N × P	16.96	1.48	0.12	16.87	1.58	0.09
Coverage change						
N	4.96	61.05	< 0.01	4.87	1.94	0.11
P	4.96	7.99	< 0.01	4.87	7.40	< 0.01
N × P	16.96	0.95	0.51	16.87	1.48	0.13
Biomass						
N	4.96	12.82	< 0.01	4.87	0.84	0.50
P	4.96	24.60	< 0.01	4.87	3.39	0.013
N × P	16.96	1.13	0.34	16..87	0.75	0.73

Source	Mountain soil				Peat			
	df	Wilks' lambda	*F*	*P*	df	Wilks' lambda	*F*	*P*
N	16,284.76	0.12	17.75	< 0.01	16,257.26	0.30	7.72	< 0.01
P	16,284.76	0.14	16.07	< 0.01	16,257.26	0.41	5.52	< 0.01
N × P	64,366.35	0.48	1.17	0.19	64,331.12	0.42	1.27	0.095

four growth indicators responded differently to N addition (Table 2, Fig. 1). As the N addition increased, the number of capitula increased gradually, but the effect was substantial only when N was at the highest rate (N10). At the same time, length growth, coverage change and biomass decreased significantly as N increased, suggesting that N addition can negatively impact *S. palustre* (Table 2).

In the peat, the four growth indicators responded differently to N addition (Table 2, Fig. 1). As the N addition increased, the number of capitula also tended to increase, while the length growth, coverage change and biomass remained unchanged. Taken together, N addition positively affected *S. palustre* growth, but with respect to biomass (an estimator of productivity), N addition had no significant impact (Table 2, Fig. 1).

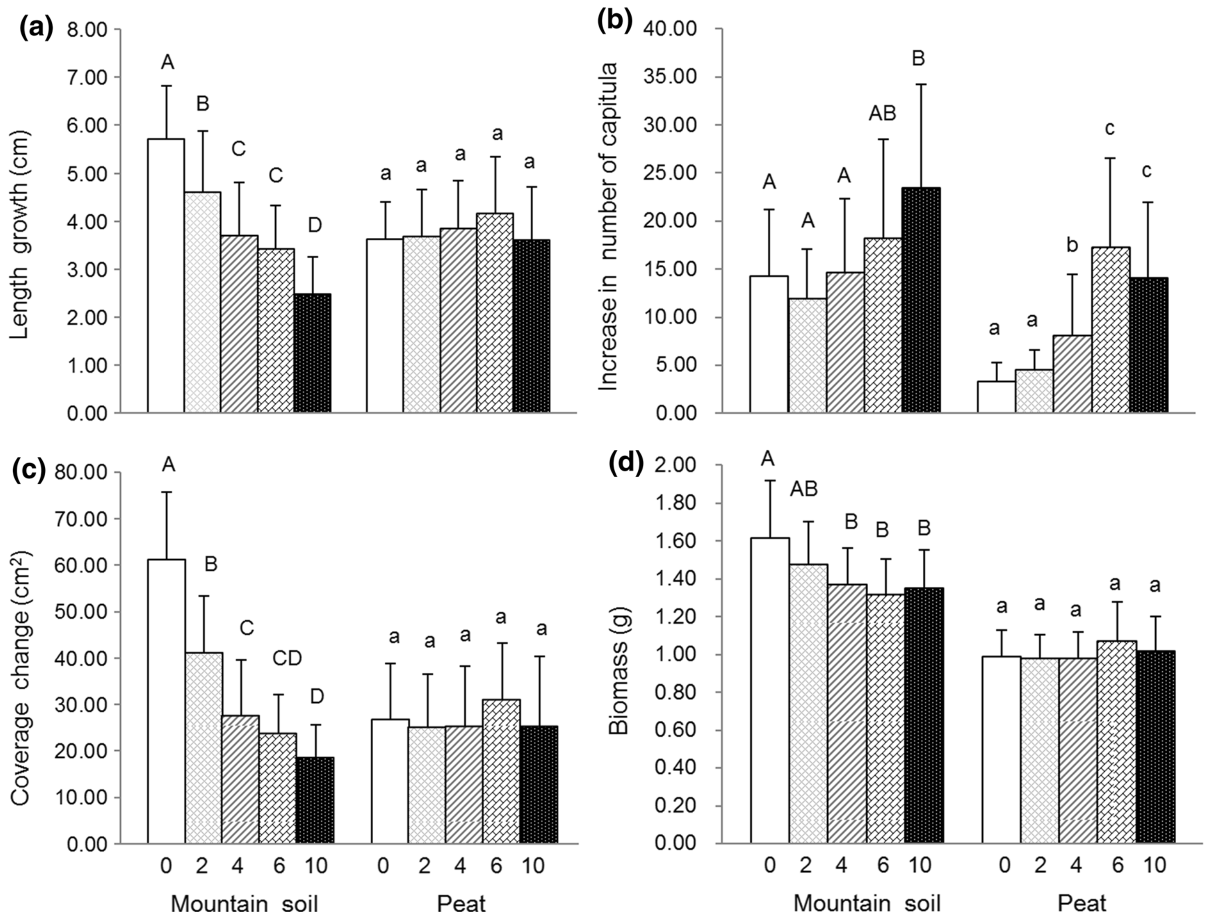

Fig. 1 Effects of N addition (0, 2, 4, 6, and 10 g m^{-2} $year^{-1}$ from the leftmost bars to the rightmost bars) on the **a** length growth, **b** number of capitula, **c** coverage change and **d** biomass (means ± SDs) of *Sphagnum palustre* in mountain soil (n = 121) and peat (n = 112). (Different letters above the bars indicate significant differences at $P < 0.05$ according to one-way ANOVA)

Effects of P on the growth of *S. palustre*

P markedly influenced *S. palustre* in both substrates (Table 2). In the mountain soil, within a certain range, P fertilization positively affected *S. palustre* growth. The length growth and coverage change tended to increase as the P addition increased but quickly stabilized beginning with P0.5. The number of capitula and biomass first increased as P addition increased but then decreased afterward, implying that the number of capitula and biomass were negatively impacted when the P addition exceeded 0.5 g m^{-2} $year^{-1}$. The results of the four indicators combined indicated that *S. palustre* performed best at P0.5 in the mountain soil (Table 2, Fig. 2).

In the peat substrate, within a certain range, P fertilization positively affected *S. palustre* growth. Length growth tended to increase as P addition increased but quickly stabilized beginning with P0.2. The number of capitula, coverage change and biomass first increased as P addition increased but then decreased when the P addition surpassed 0.2 g m^{-2} $year^{-1}$. The results of the four indicators combined indicated that *S. palustre* performed best at P0.2 in the peat (Table 2, Fig. 2).

Relationships among the four growth indicators

In the mountain soil, positive correlations existed between any two of the four growth indicators except

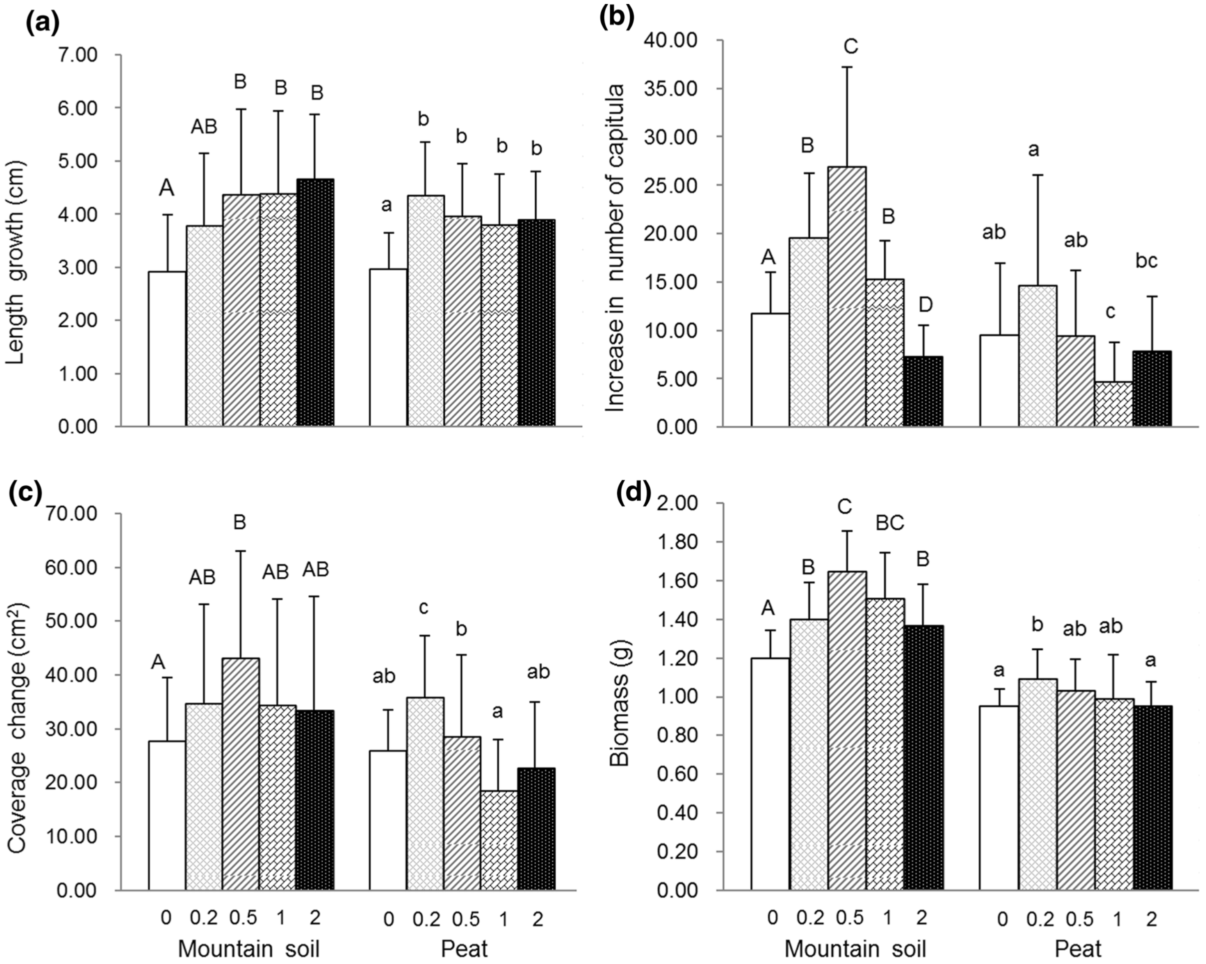

Fig. 2 Effects of P addition (0, 0.2, 0.5, 1, and 2 g m^{-2} $year^{-1}$ from the leftmost bars to the rightmost bars) on the **a** length growth, **b** number of capitula, **c** coverage change and **d** biomass (means ± SDs) of *Sphagnum palustre* in mountain soil (n = 121) and peat (n = 112). (Different letters above the bars indicate significant differences at $P < 0.05$ according to one-way ANOVA)

Table 3 Pairwise Pearson correlation coefficients among length growth, number of capitula, coverage change and biomass (n = 121 for mountain soil, n = 112 for peat; mountain soil is below the diagonal, and peat is above the diagonal)

	Length growth	Number of capitula	Coverage change	Biomass
Length growth		0.29**	0.49***	0.44***
Number of capitula	− 0.13		0.52***	0.48***
Coverage change	0.73***	0.10		0.64***
Biomass	0.60***	0.40***	0.68***	

**$P < 0.01$; ***$P < 0.001$

for that between the number of capitula and length growth and that between the number of capitula and coverage change. In the peat, all pairwise correlations were significantly positive (Table 3).

Effects of fertilization on the N and P contents in the capitula

In both substrates, N and P addition significantly affected the N and P contents, respectively, in the

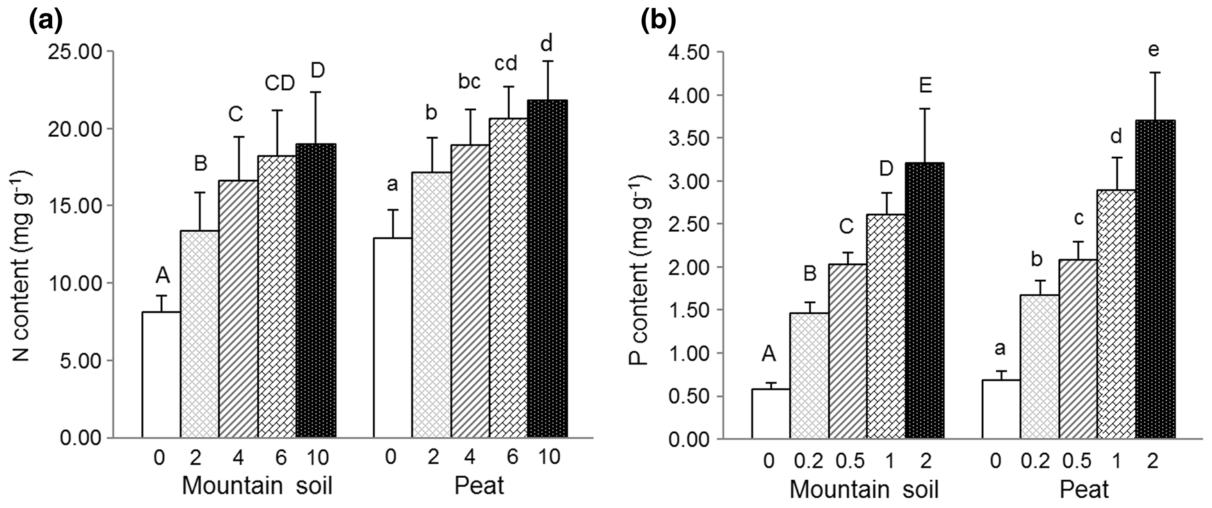

Fig. 3 Effects of N addition (0, 2, 4, 6, and 10 g m^{-2} $year^{-1}$ from the leftmost bars to the rightmost bars) on (**a**) the N content (means ± SDs) and the effects of P addition (0, 0.2, 0.5, 1, and 2 g m^{-2} $year^{-1}$ from the leftmost bars to the rightmost bars) on (**b**) the P content (means ± SDs) in the capitula of *Sphagnum palustre* in mountain soil (n = 125) and peat (n = 121). (Different letters above the bars indicate significant differences at $P < 0.05$ according to one-way ANOVA)

capitula. As N addition increased, the N content in the capitula continued to markedly increase (mountain soil: $F_{(4,120)} = 69.25$, $P < 0.001$; peat: $F_{(4,116)} = 60.30$, $P < 0.001$; Fig. 3a). Likewise, the P content in the capitula showed a continuous significant increase as the P addition increased (mountain soil: $F_{(4,120)} = 258.07$, $P < 0.001$; peat: $F_{(4,116)} = 306.66$, $P < 0.001$; Fig. 3b). Furthermore, the N content in the capitula was negatively correlated with the *S. palustre* biomass in the mountain soil (biomass = − 0.26 ln(N) + 2.12; $r^2 = 0.20$, $P = 0.025$), which is an estimator of productivity, but was not significantly correlated with biomass in the peat substrate. The P content, however, exhibited optimal values in maximizing biomass in both substrates (mountain soil: biomass = − 0.148 N^2 + 0.644 N + 0.865, $r^2 = 0.63$, $P < 0.001$; peat: biomass = − 0.043 N^2 + 0.17 N + 0.87, $r^2 = 0.34$, $P = 0.011$).

Discussion

Growth rate

Sphagnum palustre exhibits very rapid growth. Zaccone et al. (2017) recently reported very high growth rates of *S. palustre* in central Italy; 2 m of *Sphagnum* peat accumulated in less than 100 years. Investigating the growth of four different *Sphagnum* species under laboratory conditions, Harpenslager et al. (2015) reported that the initial biomass of *S. palustre* increased by 600% during a 12-week experiment. Joe (2015) reported that *S. palustre* increased more than 43-fold during a 16-year period in Hawaii, where it is considered an invasive moss species. In terms of growth length, our control group data, with values of 4.21 ± 0.98 cm in mountain soil and 3.01 ± 0.46 cm in peat recorded over 8 months, were similar to those in Hawaii (4 cm $year^{-1}$; Beilman et al. 2014), but the coverage change and biomass were much lower at our site than in Hawaii. One important factor may involve the dissimilarity in the mean annual temperature between study areas, which was proven by Gunnarsson (2005) to be the single most important factor explaining the global patterns of *Sphagnum* productivity. The abovementioned studies involved favorable temperatures that were near 20 °C, which is considered the optimal temperature for *S. palustre* growth (Fukuta et al. 2012). In contrast, our experiment was performed under a much lower mean annual temperature—approximately 9.4 °C. Thus, the lower mean annual temperature in our experiment resulted in a slower growth rate.

Substrate

Our study showed that, in subtropical mountain regions, the local mountain soil seemed to be a better substrate for the restoration of *S. palustre*, as determined by all four growth indicators. This finding is important because it indicates that peatland ecosystem restoration does not depend on peat availability, potentially allowing restoration practices on large, less restrictive scales.

We initially predicted that *S. palustre* would perform better in the peat than in the mountain soil due to the higher nutrient contents within the peat (Table 1). However, the results suggested that *S. palustre* growth may be limited by factors other than nutrients. Several studies have reported that, as the major component of peatlands, mosses are more responsive to alkalinity-acidity gradients than to nutrient (N and P) gradients (Vitt 1990; Vitt and Chee 1990; Bedford et al. 1999). Species in the genus *Sphagnum* are generally acidophilic calcifuge species; due to the toxicity of Ca–HCO_3^-, these species are intolerant to high pH values and high concentrations of calcium (Ca) and bicarbonate (HCO_3^-) (Clymo 1973; Andrus 1986; Lamers et al. 1999; Smolder et al. 2003; Hajek et al. 2006; Vicherova et al. 2017). The optimal pH range for *S. palustre* is approximately 4.5–6.0 (Andrus 1986; Chen et al. 2009; Wang 2010; Harpenslager et al. 2015); our pH measurements (5.0–6.0) of peat pore water in the *S. palustre* habitats within the Qizimei Mountain National Nature Reserve were in accordance with this optimal range (Wang et al. 2013). In our experiment, the mountain soil exhibited an acidity that was closer to that of the original habitat; the pH values of the mountain soil were 5.58 ± 0.05 and 5.30 ± 0.24 before and after fertilization, respectively. In contrast, the pH values of the peat before and after fertilization were 6.44 ± 0.06 and 6.64 ± 0.15, respectively, both of which were higher than the maximum of the optimal range (4.5–6.0). A high pH is usually associated with high Ca^{2+} concentrations (Clymo 1973), which may cause toxicity symptoms in *S. palustre* by several methods. One possibility is that excessive condensation of Ca on the carboxyl cation-exchange sites of cell walls can create a barrier against the exchange and intracellular uptake of other cations, leading to interference with nutrient uptake (Hajek and Adamec 2009). Another possibility is that, under the combined conditions of high pH and high Ca^{2+} concentrations in the peat, *S. palustre* is unable to control the balance between intracellular Ca^{2+} uptake and efflux (to vacuoles or the apoplast), and excessive cytosolic Ca^{2+} interferes with cellular metabolism (Vicherova et al. 2015). Thus, we speculated that the abovementioned Ca–HCO_3^- toxicity triggered by high pH may worsen the performance of *S. palustre* in the peat substrate, while a more favorable acidic environment provided by the mountain soil affects the better performance of *S. palustre*. However, our speculations require additional experimental verification.

N

The effects of N on *S. palustre* differed from what we predicted. In the mountain soil, *S. palustre* in the control group (N0) seemed to perform the best; in the control group, the N content in the capitula was 8.13 ± 1.06 mg g^{-1}. The effects of N on *Sphagnum* growth depended largely on the N content in the capitula, and a critical value existed at which point the positive effects of N became negative effects (Wiedermann et al. 2007; Limpens and Heijmans 2008; Bonnett et al. 2010). Bragazza et al. (2005) reported a threshold value of 13 mg g^{-1} in the capitula. Kim et al. (2014) speculated that 10.1–10.3 mg g^{-1} was the critical concentration, while other researchers have suggested lower values, ranging from 4.5 to 8 mg g^{-1} (Aerts et al. 1992; Lamers et al. 2000; Gunnarsson 2005). In our study, the N addition of 2 g m^{-2} $year^{-1}$ (N2) corresponded to 13.37 ± 2.51 mg g^{-1} N content in the capitula; this content was greater than previously reported thresholds. Moreover, the N content in the capitula increased as the N addition increased (Fig. 3a) and was negatively correlated with biomass, suggesting that excess N detrimentally affected *S. palustre* growth. Therefore, the background N content in the mountain soil was sufficient for *S. palustre* growth. Additional N supplies can lead to nutrient imbalance or even N toxicity in *S. palustre* (Bridgham 2002).

A lack of responses to N addition occurred for *S. palustre* in the peat substrate with respect to length growth, coverage change and biomass, suggesting that N fertilization did not affect the growth or productivity in peat. One possibility is that pH-linked positive effects together with N-linked toxic effects cancelled each other out, resulting in non-significant growth indicators following N addition. Clymo (1987) suggested that the uptake of ammonium by *Sphagnum* under conditions of higher N addition rates is compensated by the excretion of protons, resulting in a lower pH. Our results confirmed that, as the addition of NH_4NO_3 increased, the pH in the peat continuously decreased from 6.78 ± 0.06 to 6.43 ± 0.11, making the environment increasingly favorable for *S. palustre* growth. Alternatively, several studies have reported that *Sphagnum* can synthesize specific amino acids such as arginine, asparagine and glutamine under high N conditions to prevent ammonium toxicity (Nordin and Gunnarsson 2000; Smolders et al. 2001; Tomassen et al. 2003). In our study, the greatest negative effects of N on *S. palustre* biomass in the mountain soil occurred during the change in N addition from N0 to N4; no pronounced effects were observed when the addition was higher than N4, which could suggest that *Sphagnum* can avoid further damage from increasing N addition via the abovementioned detoxification mechanism. In the peat substrate, the N content in the capitula at N2 was 17.17 ± 2.23 mg g^{-1}, which was similar to that of N4 in the mountain soil (16.63 ± 2.82 mg g^{-1}). Therefore, the slight increase in N for *S. palustre* in the peat was already at a high rate and triggered the detoxification process, causing little response as N addition as increased from 0.

N addition promoted the number of capitula to increase in both substrates. This phenomenon may have occurred because our experimental period covered only one growing season; the new capitula may have been too small to increase clearly in biomass. However, an increase in the number of capitula implies a stronger ability of clonal expansion for *S. palustre*, which is undoubtedly beneficial to *S. palustre* restoration and lateral expansion. Hence, a longer experimental period is needed to carefully examine the effects of N addition on the different growth indicators of *S. palustre*.

P

Although the effects of N on *Sphagnum* growth varied spatially, the effects of P on *Sphagnum* growth were relatively consistent. Researchers (Boyer and Wheeler 1989; Verhoeven and Schmitz 1991; Chapin et al. 2004) have suggested that, during succession from minerogenous fens to ombrogenous bogs, nutrient shifts from N limitation to P limitation occur, as P from the parent mineral material becomes immobilized in organic-bound pools or is bound by geochemical processes. Therefore, it is likely that the growth of the dominant species in ombrogenous bogs—*Sphagnum*—is limited by P availability in most regions. Bu et al. (2011) performed a fertilization experiment involving three *Sphagnum* species in a boreal Hani peatland in China. Their results showed that both *S. palustre* length growth and the number of capitula increased as P addition increased and that the maximum occurred at P0.2, which is in agreement with our results using peat as a substrate. In the mountain soil, however, *S. palustre* exhibited a higher demand for P addition (0.5 g m^{-2} $year^{-1}$), probably because the background P content was lower in the mountain soil than in the peat substrate (Table 1). On the whole, in subtropical high-mountain regions, *S. palustre* grew best under 0.2–0.5 g m^{-2} $year^{-1}$, which resulted in a P content in the capitula ranging from approximately 1.67–2.03 mg g^{-1} (Fig. 3b).

Therefore, our results supported those of previous studies, as P addition positively affects *Sphagnum* growth. However, significant correlations exhibiting unimodal patterns between *S. palustre* growth (biomass) and the P content in the capitula for both substrates indicated that a threshold existed for P demand; once the threshold was exceeded, the effects on *Sphagnum* growth became negative. With respect to *S. palustre* in subtropical mountain regions, ~ 2 mg g^{-1} P (Fig. 3b) in the capitula was the critical amount at which the effects change from positive to negative.

Growth indicators

Sphagnum growth can be measured by various indicators, such as length growth, number of capitula, coverage change and biomass. These indicators sometimes respond oppositely to changes in nutrient contents within an environment (Rincon and Grime 1989; Dorrepaal et al. 2003; Bu et al. 2011; Kim et al. 2014). For instance, in our study, as N addition increased, the number of capitula markedly increased, while length growth significantly decreased in the mountain soil. This phenomenon is probably due to the trade-off between allocation to elongation and lateral branching (Rydin 2009), which is also suggested by the negative correlation between the two parameters in the mountain soil, although these correlations were not significant at the individual level per se. Traditional studies in which *Sphagnum* growth has been evaluated have often focused on longitudinal elongation (shoot length growth) and final biomass. However, Bu et al.

(2011) highlighted the importance of measuring lateral growth (number of capitula), as it represents the potential for clonal expansion. Although the four growth indicators measured in our study were generally positively correlated with each other (Table 3), exceptions occurred, and each indicator had its own significance and application in evaluating *Sphagnum* growth. Specifically, length growth (or height growth) reflects the ability to acquire light resources, while number of capitula reflects the ability for clonal expansion. Coverage change can be used to estimate restoration achievement, and biomass is a typical measurement of green plant productivity. Therefore, the combined use of the four growth indicators can predict *Sphagnum* responses to nutrient environments more accurately than their individual use can.

Conclusion and implications

The results of this study showed that substrate type and nutrient level significantly influenced the growth of *S. palustre*, which is the dominating peat-forming species in the subtropical high-mountain peatland regions of China. Compared with peat, which is typically believed to be a superior substrate for *Sphagnum* growth, the mountain soil obtained from nearby sites produced improved growth results, which may provide a new approach for restoring peatland ecosystems in these regions. Furthermore, *Sphagnum* growth was limited by P availability instead of N availability, and 0.2–0.5 g m^{-2} $year^{-1}$ P addition (corresponding to 1.67–2.03 mg g^{-1} P in the capitula) could significantly increase growth; this range of fertilization rates is thus beneficial for the rapid restoration of *S. palustre*. Fertilization- and substrate-induced changes in pH and the N and P contents in the capitula both underlie different patterns of *S. palustre* growth. In addition, using a combination of multiple growth indicators can evaluate *Sphagnum* growth more accurately than use of the individual indicators and to meet the needs of fundamental and applicable interests. However, for the purposes of nondestructive surveys, we recommend using coverage change as a substitute for biomass, as both are strongly positively related in *S. palustre*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving in human and animal participants This article does not contain any studies with human participants or animals performed by any of the authors.

References

Aerts R, Wallen B, Malmer N (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low a high atmospheric nitrogen supply. J Ecol 80:131–140. https://doi.org/10.2307/2261070

Andrus RE (1986) Some aspects of *Sphagnum* ecology. Can J Bot 64:416–426. https://doi.org/10.1139/b86-057

Arroniz-Crespo M, Leake JR, Horton P et al (2008) Bryophyte physiological responses to, and recovery from, long-term nitrogen deposition and phosphorus fertilization in acidic grassland. New Phytol 180:864–874. https://doi.org/10.1111/j.1469-8137.2008.02617.x

Bedford BL, Walbridge MR, Aldous A (1999) Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–2169. https://doi.org/10.1890/0012-9658(1999)080[2151:PINAAP]2.0.CO;2

Beilman D, Joe S, Olivia S et al (2014) Poster Presentation. Growth and ecological impacts of an invasive bryophyte in Hawaii: the strange tale of *Sphagnum palustre*. In: International Conference on Island Evolution, Ecology and Conservation (ICIE)

Berendse F, Breemen NV, Rydin H et al (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. Globa Chang Biol 7:591–598. https://doi.org/10.1046/j.1365-2486.2001.00433.x

Bonnett SAF, Ostle N, Freeman C (2010) Short-term effect of deep shade and enhanced nitrogen supply on *Sphagnum capillifolium* morphophysiology. Plant Ecol 207:347–358. https://doi.org/10.1007/s11258-009-9678-0

Boyer M, Wheeler B (1989) Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. J Ecol 77:597–609. https://doi.org/10.2307/2260772

Bragazza L, Rydin H, Ferdol R (2005) Multiple gradients in mire vegetation: a comparison of a Swedish and an Italian bog. Plant Ecol 177:223–236. https://doi.org/10.1007/s11258-005-2182-2

Bragazza L, Buttler A, Habermacher J (2012) High nitrogen deposition alters the decomposition of bog plant litter and reduces carbon accumulation. Glob Change Biol 18:1163–1172. https://doi.org/10.1111/j.1365-2486.2011.02585.x

Breeuwer A, Heijmans MMPD, Gleichman M et al (2009) Response of *Sphagnum* species mixtures to increased temperature and nitrogen availability. Plant Ecol 204:97–111. https://doi.org/10.1007/s11258-009-9571-x

Bridgham SD (2002) Nitrogen, translocation and *Sphagnum* mosses. New Phytol 156:137–144. https://doi.org/10.1046/j.1469-8137.2002.00521.x

Bu ZJ, Rydin H, Chen X (2011) Direct and interaction-mediated effects of environmental changes on peatland bryophytes. Oecologia 166:555–563. https://doi.org/10.1007/s00442-010-1880-1

Bubier J, Moore TR, Bledzki LA (2007) Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. Glob Change Biol 13:1168–1186. https://doi.org/10.1111/j.1365-2486.2007.01346.x

Chapin CT, Bridgham SD, Pastor J (2004) pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen. Wetlands 24:186–201. https://doi.org/10.1672/0277-5212(2004)024[0186:PANEOA]2.0.CO;2

Chen X, Bu ZJ, Wang SZ et al (2009) Niches of seven bryophyte species in Hani peat land of Changbai Mountains. Chin J Appl Ecol 20:574–578. https://doi.org/10.13287/j.1001-9332.2009.0076

Clymo RS (1973) The growth of S*phagnum*—some effects of environment. J Ecol 61:849–869. https://doi.org/10.2307/2258654

Clymo RS (1983) Peat. Mires: swamp, bog, fen and moor. Ecosyst World 4A:159–224

Clymo RS (1987) The growth of *Sphagnum*: some effects of environment. J Ecol 61:849–869. https://doi.org/10.2307/2258654

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388. https://doi.org/10.2307/3547057

Damman AWH (1978) Distribution and movement of elements in ombrotrophic peat bogs. Oikos 30:480–495. https://doi.org/10.2307/3543344

Daniels RE, Eddy A (1990) Handbook of European *Sphagna*, 2nd edn. Institute of Terrestrial Ecology, Huntingdon

Dorrepaal E, Aerts R, Cornelissen JHC et al (2003) Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. Glob Change Biol 10:93–104. https://doi.org/10.1111/j.1365-2486.2003.00718.x

Fukuta E, Sasaki A, Nakatsubo T (2012) Microclimate and production of peat moss *Sphagnum palustre* L. in the warm-temperate zone. Plant Spec Biol 27:110–118.

Gerdol R, Brancaleoni L (2015) Slow recovery of mire vegetation from environmental perturbations caused by a heat wave and experimental fertilization. Wetlands 35:769–782. https://doi.org/10.1007/s13157-015-0668-9

Gerdol R, Siffi C, Bombonato L (2010) Aboveground production and nutrient status of the vegetation of different mire types in the South-eastern Alps (Italy). Bot Helv 120:85–93. https://doi.org/10.1007/s00035-010-0077-x

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195. https://doi.org/10.2307/1941811

Gunnarsson U (2005) Global patterns of *Sphagnum* productivity. J Bryol 27:269–279. https://doi.org/10.1179/174328205X70029

Gunnarsson U, Rydin H (2000) Nitrogen fertilization reduces *Sphagnum* production in bog communities. New Phytol 147:527–537. https://doi.org/10.1046/j.1469-8137.2000.00717.x

Hajek T, Adamen L (2009) Mineral nutrient economy in competing species of *Sphagnum* mosses. Ecol Res 24:291–302. https://doi.org/10.1007/s11284-008-0506-0

Hajek M, Horsak M, Hajkova P et al (2006) Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. Perspect Plant Ecol Evol Syst 8:97–114. https://doi.org/10.1016/j.ppees.2006.08.002

Harpenslager SF, van Dijk G, Kosten S et al (2015) Simultaneous high C fixation and high C emissions in *Sphagnum* mires. Biogeosciences 12:4465–4494. https://doi.org/10.5194/bgd-12-4465-2015

Joe SM (2015) Controlling the invasive moss *Sphagnum palustre* at Ka'ala, Island of O'ahu. In: Pacific Cooperative Studies Unit Technical Report 192. University of Hawai'i at Mānoa, Department of Botany. Honolulu, HI, p 18

Kim S, Kim Y, Kim Y et al (2014) Effects of planting method and nitrogen addition on *Sphagnum* growth in microcosm wetlands. Paddy Water Environ 12(5):185–192. https://doi.org/10.1007/s10333-014-0427-1

Lamers LPM, Farhoush C, van Groenendael JM et al (1999) Calcareous groundwater raises bogs; the concept of ombrotrophy revisited. J Ecol 87:639–648. https://doi.org/10.1046/j.1365-2745.1999.00380.x

Lamers LPM, Bobbink R, Roelofs JGM (2000) Natural nitrogen filter fails in raised bogs. Glob Change Biol 6:583–586. https://doi.org/10.1046/j.1365-2486.2000.00342.x

Lao JC (1988) Handbook of soil agro-chemistrical analysis. Agricultural Publishing House, Beijing

Limpens J, Berendse F (2003) Growth reduction of *Sphagnum magellanicum* subjected to high nitrogen deposition: the role of amino acid nitrogen concentration. Oecologia 135:339–345. https://doi.org/10.1007/s00442-003-1224-5

Limpens J, Heijmans MMPD (2008) Swift recovery of *Sphagnum* nutrient concentrations after excess supply. Oecologia 157:153–161. https://doi.org/10.1007/s00442-008-1046-6

Limpens J, Tomassen HBM, Berendse F (2003) Expansion of *Sphagnum fallax* in bogs: striking the balance between N and P availability. J Bryol 25:1–8. https://doi.org/10.1179/037366803235001733

Limpens J, Berendse F, Klees H (2004) How phosphorus availability affect the impact of nitrongen deposition on *Sphagnum* and vascular plants in bogs. Ecosystems 7:793–804. https://doi.org/10.1007/s10021-004-0274-9

Limpens J, Bohlin E, Nilsson MB (2017) Phylogenetic or environmental control on the elemental and organo-chemical composition of *Sphagnum* moss? Plant Soil 417:69–85. https://doi.org/10.1007/s11104-017-3239-4

Liu SX, Qu JP, Jiang YF et al (2006) Hubei Qizimeishan nature reserve scientific survey and research report. Hubei Publishers of Science and Technology, Wuhan

Ma GL, Lei Y, Wang ZX et al (2008) Plant diversity of *Sphagnum* mire at Qizimei mountations in Western Hubei Province. J Wuhan Bot Res 26(5):482–488

Medvedeff CA, Bridgham SD, Meister LP et al (2015) Can *Sphagnum* leachate chemistry explain differences in anaerobic decomposition in peatlands? Soil Biol Biochem 86:34–41. https://doi.org/10.1016/j.soilbio.2015.03.016

Nishimura A, Tsuyuzaki S (2015) Plant responses to nitrogen fertilization differ between post-mined and original peatlands. Folia Geobot 50:107–121. https://doi.org/10.1007/s12224-015-9203-2

Nordin A, Gunnarsson U (2000) Amino acid accumulation and growth of *Sphagnum* under different levels of N deposition. Ecoscience 7:474–480. https://doi.org/10.1080/11956860.2000.11682619

Paavilainen E, Päivänen J (1995) Peatland Forestry. In: Ecology and principles, ecological studies, vol. 111, Springer, Berlin, pp 31–101. https://doi.org/10.1007/978-3-662-03125-4

Pan RZ, Wang XJ, Li NH (2008) Plant physiology, 3rd edn. Higher Education Press, Beijing

Price JS, Heathwaite AL, Baird AJ (2003) Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetl Ecol Manage 11:65–83. https://doi.org/10.1023/A:1022046409485

Quinty F, Rochefort L (2003) Peatland restoration guide, 2rd edn. Canadian *Sphagnum* peat moss association and New Brunswick Department of Natural Resources and Energy. Québec

Rincon E, Grime JP (1989) An analysis of seasonal patterns of bryophyte growth in a natural habitat. J Ecol 77:447–455. https://doi.org/10.2307/2260761

Rochefort L, Quinty F, Campeau S et al (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. Wetl Ecol Manage 11:3–20. https://doi.org/10.1023/A:1022011027946

Rydin H (2009) Population and community ecology of bryophytes. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambrige University Press, Cambridge, pp 393–444

Shaw AJ, Devos N, Liu Y et al (2016) Organellar phylogenomics of an emerging model system: *Sphagnum* (peatmoss). Ann Bot 118:185–196. https://doi.org/10.1093/aob/mcw086

Smolder AJP, Tomassen HBM, van Mullekom M et al (2003) Mechanisms involved in the re-establishment of *Sphagnum*-dominated vegetation in rewetted bog remnants. Wetl Ecol Manage 11:403–418. https://doi.org/10.1023/B:WETL.0000007195.25180.94

Smolders AJP, Tomassen HBM, Pijnappel HW et al (2001) Substrate-derived CO_2 is important in the development of *Sphagnum* spp. New Phytol 152:325–332. https://doi.org/10.1046/j.0028-646X.2001.00261.x

Tomassen HBM, Smolders AJP, Lamers LPM et al (2003) Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition. J Ecol 91:357–370. https://doi.org/10.1046/j.1365-2745,2003.00771.x

Verhoeven JTA, Schmitz MB (1991) Control of plant growth by nitrogen and phosphorus in mesotrophic fens. Biogeochemistry 12:135–148. https://doi.org/10.1007/BF00001811

Vicherova E, Hajek M, Hajek T (2015) Calcium intolerance of fen mosses: physiological evidence, effects of nutrient availability and successional drivers. Perspect Plant Ecol Evol Syst 17:347–359. https://doi.org/10.1016/j.ppees.2015.06.005

Vicherova E, Hajek M, Smilauer P et al (2017) *Sphagnum* establishment in alkaline fens: importance of weather and water chemistry. Sci Total Environ 580:1429–1438. https://doi.org/10.1016/j.scitotenv.2016.12.109

Vitt DH (1990) Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. Bot J Linn Soc 104:35–59. https://doi.org/10.1111/j.1095-8339.1990.tb02210.x

Vitt DH, Chee WL (1990) The relationship of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87–106. https://doi.org/10.1007/BF00032163

Vitt DH, Wieder K, Halsey LA (2003) Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada. The Bryologist 106:235–245. https://doi.org/10.1639/0007-2745(2003)106[0235:ROSFTN]2.0.CO;2

Wang XY (2010) Effect of pH and nutrition elements on growth of *Sphagnum* plants. Guizhou Agric Sci 38:80–83

Wang ZX, Lei Y, Xiong KC et al (2013) Comprehensive scientific investigation and research of *Sphagnum* wetlands for Qizimei mountains national nature reserve in Hubei. China Forestry Publishing House, Beijing

Warner BG, Asada T (2006) Biological diversity of peatlands in Canada. Aquat Sci 68:240–253. https://doi.org/10.1007/s00027-006-0853-2

Wiedermann MM, Nordin A, Gunnarsson U et al (2007) Global change shifts vegetation and plant-parasite interactions in a boreal mire. Ecology 88:454–464. https://doi.org/10.1890/05-1823

Williams BL, Silcock DJ (1997) Nutrient and microbial changes in the peat profile beneath *Sphagnum magellanicum* in response to additions of ammonium nitrate. J Appl Ecol 34:961–970. https://doi.org/10.2307/2405286

Yu ZC, Loisel J, Brosseau DP et al (2010) Global peatland dynamics since the last glacial maximum. Geophys Res Lett 37:L13402. https://doi.org/10.1029/2010GL043584

Zaccone C, Lobianco D, Shotyk W et al (2017) Highly anomalous accumulation rates of C and N recorded by a relic, free-floating peatland in Central Italy. Sci Rep 7:43040. https://doi.org/10.1038/strep43040

Zhao ST, Li EH, Cai XB et al (2013) Research on the higher plant diversity of subalpine *Sphagnum* mire in western Hubei province, China. Resour Environ Yangtze Basin 22:468–475

Zhu HJ, Chen JF, Chen SL et al (2010) Soil geography, 2nd edn. Higher Education Press, Beijing