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WETLANDS RESTORATION

Effects of the Substrate and Planting Method on *Sphagnum palustre* Growth in Subtropical High-Mountain Regions and the Underlying Mechanisms

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Abstract

Sphagnum wetlands in subtropical high-mountain regions have been severely destroyed by human activities, necessitating restoration efforts. We studied the effects of substrate and planting method on *Sphagnum palustre* L. growth and the underlying mechanisms to determine the optimal conditions for *S. palustre* restoration. *S. palustre* collected from natural wetlands was grown on nine substrates and with four planting methods in a greenhouse. The results show that *S. palustre* grew best in mountain yellow-brown soil without added peat or river sand and when planted as intact plants. Substrate pH and P content and capitula P content negatively correlated with *S. palustre* productivity, while initial biomass of *S. palustre* at planting positively correlated with productivity. *S. palustre* restoration on local mountain soil in subtropical high-mountain regions is practical, which may provide a new perspective for restoring peatlands. Traditional restoration method using the 10 cm upper parts of *S. palustre* as transplanted materials does not destroy the source *S. palustre* populations in habitats where plants are collected. However, we argue that a planting method using only capitula (top 1–2 cm) may be a better choice for *S. palustre* restoration, due to the similar productivity but less impact to source *S. palustre* populations.

Keywords *Sphagnum palustre* · Wetland restoration · Nitrogen · Phosphorus · pH · Substrate

Introduction

Sphagnum wetlands are the most important components of Northern Hemisphere peatlands (Limpens et al. 2017; Bengtsson et al. 2018). Because *Sphagnum* wetlands are located in areas with nutrient-poor (ombrotrophic), waterlogged (anoxic), cold and acidic conditions (Hajek et al. 2011; Rydin and Jeglum 2013; Manninen et al. 2016; Binet et al. 2017), their rate of decomposition is usually lower than their rate of production, which contributes to the significant accumulation of organic matter (OM) that serves as an important carbon pool (Gorham 1991; Clymo et al. 1998; Granath et al. 2014; Hommeltenberg et al. 2014). The genus *Sphagnum* comprises approximately 250–400 species (Shaw et al. 2016), among which *Sphagnum palustre* is a common species with a wide distribution (Daniels and Eddy 1990). In the subtropical regions of southern China, patches of *S. palustre*-dominated wetlands are found in the high-altitude areas of the Huangshan Mountains, Yunnan-Kweichow Plateau and western Hubei Mountains (Ma et al. 2008), which are the sources of the headstreams of a number of rivers and play an important role in water storage. However, large areas of subtropical high-mountain *Sphagnum* wetlands have been diminished because of habitat destruction and overcollection for horticultural purposes, leading to reduced performance of ecological

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functions (Wang et al. 2013), which emphasizes the urgent need for restoring these wetlands.

The growth of *Sphagnum* is determined by a wide variety of environmental factors (Price et al. 2003; Chapin et al. 2004; Thompson and Waddington 2008; Medvedeff et al. 2015). Nutrient availability (especially of nitrogen [N] and phosphorus [P]) is an important factor for *Sphagnum* growth when water availability is sufficient (Weltzin et al. 2001; Hoosbeek et al. 2002; Kim et al. 2014). In natural bogs, *Sphagnum* keeps growing upward from the apical part (capitulum), while the lower part gradually dies, isolating the *Sphagnum* from the underlying mineral soil or minerotrophic groundwater (Clymo 1973; van Breemen 1995). Therefore, it is generally thought that the nutrient supply for *Sphagnum* mainly depends on atmospheric deposition (Bridgham et al. 1996; Malmer et al. 2003; Bragazza and Freeman 2007; Limpens and Heijmans 2008; Granath et al. 2009; Nishimura and Tsuyuzaki 2014). However, during the restoration of destroyed peatlands with bare peat surfaces, transplanted *Sphagnum* plants are in full contact with the substrate, raising the question of whether the substrate will affect *Sphagnum* growth via its background nutrient contents. Until now, research and restoration work have been mostly performed on original peatlands or abandoned cutover peatlands (Rochefort and Price 2003; Vasander et al. 2003; Graf et al. 2008; Andersen et al. 2010; Karofeld et al. 2016) where local peat was the only substrate used. However, whether peat is the only substrate that can be used or if it is the optimal substrate for *Sphagnum* restoration remains uncertain. In addition, *Sphagnum* mires in subtropical high-mountain regions are intermittently distributed in small patches, and peat use is thus limited by the complicated topographic conditions and the distribution of mires. In contrast, mountain yellow-brown soil ("mountain soil" hereafter, which is classified in the Alfisol order, Moist Warm Alfisol suborder, in accordance with the classification system of Chinese soil; Zhu et al. 2010) is widely distributed, and high levels of precipitation commonly create rivulets in these subtropical high-mountain regions. This effect of water flow results in mixed substrates with a wide range of proportions of mountain soil and river sand. Considering these situations in subtropical high-mountain regions in China, we used local mountain soil as an alternative base substrate for *S. palustre*. Moreover, different proportions of peat (to improve the texture and nutritional environment of the substrate) or river sand (to simulate the mixture of mountain soil and river sand caused by rivulets) were mixed into the mountain soil to explore the suitability of different substrates for *S. palustre* as well as understand the possible mechanisms underlying the substrate effects.

In addition to the substrate effects, the effects of water and nutrient transport and supply inside *Sphagnum* mosses are also of key importance (Aldous 2002; Kim et al. 2014). *Sphagnum* mosses grows apically from the capitula (Clymo 1970) and has a well-developed system for water conduction in the capillary spaces among pendent branches around the stem, which provides an effective vertical transport path for water and soluble ions from the basal part to the capitulum (Rydin and Clymo 1989; van Breemen 1995; Thompson and Waddington 2008; Chiwa et al. 2016). Consequently, nutrient transport depends largely on water availability. In addition to the groundwater level, the distance water is transported from the basal part to the capitulum is determined by stem length and may affect water and nutrient supply efficiency, further affecting *S. palustre* growth (Aldous 2002; Kim et al. 2014). This implies that different collection depths and different planting methods for *S. palustre* (i.e., whether *S. palustre* is collected and transplanted with the stem and the length of the stem) could result in differences in final productivity. Additionally, the commonly used transplant materials in previous *Sphagnum* restoration practices have been the upper parts of plants of a certain length (usually within 10 cm) (Clymo and Duckett 1986; Campeau and Rochefort 1996; Bugnon et al. 1997; Rochefort et al. 2003; Waddington et al. 2003; Pouliot et al. 2015). Therefore, most of the attention was focused on the performance of the transplanted upper part of *Sphagnum* diaspores, while the growth status of the damaged *Sphagnum* plants in the source populations was overlooked. As the vitality of *Sphagnum* plant parts decreases sharply with increasing distance from the capitula (Rochefort et al. 2003), the regenerative potential of damaged plants after collection deserves more attention.

We studied the substrate composition and length of shoot fragment as factors influencing the growth of *S. palustre* in subtropical high-mountain regions and the possible mechanisms underlying these effects. Specifically, we tested the following hypotheses: (1) Background nutrient contents in different substrate compositions will affect the N and P contents in the capitula, further affecting *S. palustre* growth; therefore, the growth of *S. palustre* in substrates mixed with peat will be different from that in substrates mixed with river sand. (2) Water and nutrient supply, which will depend on the length of the shoot fragment, will affect the water and NP contents in the capitula, further affecting *S. palustre* growth; therefore, *S. palustre* growth will be different when transplanted with different lengths of shoot fragments. (3) The regenerative ability of *S. palustre* is functional below 10 cm of the capitula, therefore, collecting approximately 10 cm of the upper part of *S. palustre* plants will not have destructive effects on the regenerative potential of the damaged plants.

Materials and Methods

Study Site and Species

The Qizimei Mountain National Nature Reserve (29° 39′ 30″ ~30° 05′ 15″ N, 109° 38′ 30″~109° 47′ 00″ E) is located in southwestern Hubei, China, and encompasses an area of 34,550 ha (Liu et al. 2006). The region lies in the subtropical zone and is characterized by 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 was set in the reserve of a high-mountain area: altitude of 1800 m, annual average temperature of 8.9 °C, annual precipitation of 1876 mm, and annual sunshine duration of 1520 h.

A total of approximately 940 ha of *Sphagnum* wetlands are distributed from an altitude of 1650 to 1950 m in patches of various sizes. The soil profiles in these *Sphagnum* wetlands have thicknesses ranging from 48 to 100 cm and are divided into three layers: a sod layer (pH 6.7 ± 1.2), deposited peat layer (pH 5.7 ± 1.2) and gleying layer (pH 5.3 ± 1.1) (Mao et al. 2009). The results of the most recent survey indicate that a total of 197 species of embryophytes, including 3 bryophytes, 8 ferns, 4 gymnosperms and 182 angiosperms, exist in the area (Wang et al. 2013; Zhao et al. 2013). *Sphagnum palustre* L. is the only *Sphagnum* species at the study location and is the dominant species in wetland areas with developed hummocks. The other common species have been described in detail in Li et al. (2018).

Experimental Design

A 20-m × 15-m experimental greenhouse was constructed on a wasteland in the core zone of the reserve. The wasteland had been over-grown with weeds dominated by *Erigeron annuus* (L.) Pers. and *Inula japonica* Thunb. before our greenhouse was constructed. To keep the greenhouse ventilated, transparent plastic film and shade nets were placed overhead, while only shade nets were placed around the sides. All experiments were conducted in the greenhouse (data of temperature and humidity are given in Online Resource 1). A two-factor design consisting of nine substrates and four planting methods (see below) was applied to transplanted *S. palustre* plants. Each combination of treatments was replicated five times, and there were 180 samples in total.

In February 2016, large quantities of substrate material [mountain soil, peat, and river sand] were excavated from natural *Sphagnum* wetlands, a nearby wasteland and a rivulet, after which the materials were air-dried for 72 h in the sun and then sifted through a 3-mm mesh screen. Afterward, peat or river sand was mixed evenly into the mountain soil in proportions (on the basis of mass) of 20%, 40%, 60% and 80% (20%M + 80%P, 40%M + 60%P, 60%M + 40%P, 80%M + 20%P, 20%M + 80%R, 40%M+ 60%R, 60%M + 40%R and 80%M + 20%R; M, mountain soil; P, peat; and R, river sand), and equal amounts of the mixtures were placed in plastic pots. A substrate that included only mountain soil, without peat or river sand (M, 0%), was used as a control group. Each substrate was used in 20 pots as replicates. In March 2016, *S. palustre* plants were collected from a local natural *Sphagnum* wetland and assigned to four treatments randomly: P1, intact plant (capitulum with long stem, 20 cm in total); P2, the upper 8 cm of the intact plant (capitulum with short stem); P3, 1 cm of the apical part of the intact plant (capitulum); and P4, the remaining part of the intact plant after the upper 8 cm was removed (long stem). Shoot bundles within the same treatment composed of 5 shoots (or capitula) of similar sizes without side shoots or multiple capitula were weighed to ensure that they were as close as possible to being equal in mass and then were transplanted into plastic pots. The lower part of every shoot bundle in P1, P2 and P4 was inserted into the substrate, leaving an initial aboveground length of 5 cm, while the capitula in P3 were pressed gently to place them in full contact with the substrate surface. Local spring water (pH was approximately 6.0, conductivity was approximately 500 μS cm^{-1}) was sprayed evenly above the *S. palustre* plants 3–5 times per week to ensure sufficient soil and air humidity.

Measurements of Growth Indicators and Elements

Each substrate used in the experiment was subsampled and subjected to physical and chemical analyses in accordance with the methods of Lao (1988). For the physical analyses, we used oven drying (105 °C) to determine the water content (WC), a cutting ring was used to determine the volume-weight (VW), a pycnometer was used to determine the specific gravity (SG), and the formula $Porosity\ (\%) = (1\text{-}\ \frac{VW}{SG}) \times 100$ was used to calculate the porosity. The solid phase ratio (SR), liquid phase ratio (LR) and gas phase ratio (GR) were calculated by the formulae $SR(\%) = (1\text{-}Porosity) \times 100$, $LR(\%)=\frac{WW-DW}{\rho V} \times 100$ (WW, sample wet weight; DW, sample dry weight; ρ, the density of water; V, cutting ring volume), and $GR(\%) = (Porosity\text{-}LR) \times 100$, respectively. For the chemical analyses, a potentiometer was used to determine the pH of each substrate; H_2SO_4–$HClO_4$ was used to digest substrates, and the indophenol blue method and molybdenum-antimony anti-spectrophotometric method were used to analyze the total N (TN) and total P (TP) contents, respectively. Additionally, alkaline hydrolysis diffusion was used to determine soil hydrolysable N (HN) contents, the Olsen method was used to determine available P (AP) content, and the oil-melt method was used to determine the OM content (data are given in Online Resource 2).

From March until November 2016, the number of capitula and average shoot length of *S. palustre* plants in each pot were measured monthly on fixed dates. In addition, a

digital photograph with a reference frame included in it was taken at the same time, and coverage was analyzed using ArcMap (version 10.2, ESRI, USA) (data are given in Online Resources 3, 4).

In November 2016, all tissues of the *S. palustre* plants were harvested, and the fresh weight (biomass) per pot was measured immediately. After which, 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 a fine powder to measure the TN and TP contents (on a dry-mass basis). The methodology was identical to that used for the substrate (data are given in Online Resource 5).

Statistical Analysis

We divided the eight mixed substrates into two groups: one group consisted of the four mixtures with peat, and the other group consisted of the four mixtures with river sand (mixture proportions of 20%, 40%, 60% and 80%). One-way ANOVA was used to test the differences in the physical and chemical properties between the two groups (mixture types) and the differences among the five substrate mixture proportions (including 0% mountain soil) within each group. Two-way ANOVA was used to analyze the effects of the substrate mixture type and planting method, as well as their interactive effects, on *S. palustre* growth (the response variables included length growth, number of capitulum increments, coverage change and biomass accumulation). Moreover, a MANOVA approach was used to evaluate the effects of substrate mixture type and planting method, as well as their interactive effects, on overall *S. palustre* growth (four indicators combined). Within each type of substrate mixture, one-way ANOVA was used to analyze the effects of the substrate mixture proportions on *S. palustre* growth under different planting methods. Analyses were also performed to determine the mechanisms underlying the effects of the substrate composition and planting method on *S. palustre* growth. We used multiple linear regression to test the relationship between *S. palustre* biomass accumulation and all thirteen measured physical and chemical properties of the substrate. One-way ANOVAs were used to test the differences in initial *S. palustre* biomass under different substrate mixture types, different substrate mixture proportions and different planting methods. Two-way ANOVA was performed to analyze the effects of substrate mixture type and planting method, as well as their interactive effects, on N and P contents and the N:P ratio in capitula. Within each type of substrate mixture, one-way ANOVA was used to analyze the effects of the substrate mixture proportion on N and P contents and the N:P ratio in capitula. Finally, multiple linear regression was used to analyze the relationships between *S. palustre* biomass accumulation and initial biomass, capitula N and P contents and the N:P ratio. Pearson's correlation coefficients (r values) were calculated to test the relationships between the N and P contents in substrates and those in capitula.

The analyses described above included only data from P1, P2 and P3. For P4, we focused on the regenerative potential of damaged *S. palustre* plants. Considering the particular factors in P4 (the capitula were initially removed, and minimal longitudinal growth occurred), we used number of capitulum increments as the growth indicator representing regenerative potential. The growth of P4 plants was compared with that of the plants subjected to the other three planting methods by one-way ANOVAs.

Prior to analysis, the data were checked for normality and homogeneity of variance. 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 Mixture Type on *S. palustre* Growth

Among the physical indicators of the substrates, the WC, porosity, LR and GR were higher in substrates mixed with peat than in substrates mixed with river sand, while the VW, SG and SR were lower in substrates mixed with peat than in substrates mixed with river sand. Among the chemical indicators of the substrate, TN, HN, AP and OM contents were higher in substrates mixed with peat than in substrates mixed with river sand, while the pH and TP content were not significantly different between the two types of substrate mixtures (Table 1).

There were no interactive effects between substrate mixture type and planting method on *S. palustre* growth (Table 2). For each of the four *S. palustre* growth indicators, no significant differences were found between the effects of substrates mixed with peat and the substrates mixed with river sand [length growth: 4.1 ± 1.6 cm (peat), 4.3 ± 1.8 cm (river sand); number of capitulum increments: 4.4 ± 4.3 (peat), 5.3 ± 5.4 (river sand); coverage change: 28.91 ± 16.02 cm^2 (peat), 27.61 ± 16.24 cm^2 (river sand); biomass accumulation: 5.56 ± 3.62 g (peat), 5.33 ± 3.29 g (river sand)]. Therefore, the type of substrate mixture did not significantly affect *S. palustre* growth.

Effects of Substrate Mixture Proportion on *S. palustre* Growth

Among the physical indicators, with increasing proportion of peat, the WC, porosity and GR increased, the VW, SG, SR decreased, and the LR did not show significant differences. All chemical indicators (pH, TN, TP, HN, AP and

Table 1 Comparison of physical and chemical properties between substrates mixed with peat and substrates mixed with river sand

Substrate	WC (%)	VW (g cm^{-3})	SG (g cm^{-3})	Porosity (%)	SR (%)	LR (%)	GR (%)	pH	TN (mg g^{-1})	TP (mg g^{-1})	HN (mg kg^{-1})	AP (mg kg^{-1})	OM (mg g^{-1})
Mixed with peat	102.38 ± 26.65^{A}	0.60 ± 0.13^{A}	2.02 ± 0.30^{A}	70.55 ± 2.52^{A}	29.45 ± 2.52^{A}	58.44 ± 4.18^{A}	12.12 ± 3.63^{A}	6.05 ± 0.22^{A}	4.75 ± 0.86^{A}	1.06 ± 0.06^{A}	311.84 ± 56.23^{A}	20.70 ± 1.74^{A}	127.70 ± 24.15^{A}
Mixed with river sand	35.57 ± 12.19^{B}	1.32 ± 0.20^{B}	2.62 ± 0.08^{B}	50.01 ± 6.06^{B}	49.99 ± 6.06^{B}	44.30 ± 8.76^{B}	5.71 ± 3.67^{B}	6.09 ± 0.27^{A}	2.42 ± 0.20^{B}	1.08 ± 0.07^{A}	90.91 ± 34.72^{B}	11.55 ± 2.16^{B}	60.23 ± 7.18^{B}
$F_{(1,70)}$	187.06	331.10	133.59	352.34	352.34	76.35	55.34	0.36	251.14	1.74	402.32	391.41	258.14
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.55	<0.001	0.19	<0.001	<0.001	<0.001

Different letters next to values (means ± SDs) indicate significant differences ($P < 0.05$) by one-way ANOVA

WC water content, *VW* volume-weight, *SG* specific gravity, *SR* solid phase ratio, *LR* liquid phase ratio, *GR* gas phase ratio, *TN* total nitrogen content, *TP* total phosphorus content, *HN* hydrolysable nitrogen, *AP* available phosphorus, *OM* organic matter content

Table 2 Effects of substrate (S), planting method (P) and their interaction (S*P) on the growth of *Sphagnum palustre* by two-way ANOVA (upper table) and two-way MANOVA (upper table)

Source	*df*	*F*	*P*
(a) Length growth			
S	1113	0.06	0.81
P	2113	44.96	<0.001
S*P	2113	0.96	0.39
(b) Number of capitulum increments			
S	1113	0.06	0.80
P	2113	22.80	<0.001
S*P	2113	1.11	0.34
(c) Coverage change			
S	1113	0.55	0.46
P	2113	61.11	<0.001
S*P	2113	2.09	0.13
(d) Biomass accumulation			
S	1113	1.14	0.29
P	2113	105.96	<0.001
S*P	2113	0.52	0.60

Source	*df*	Wilks' Lambda	*F*	*P*
S	4110	0.98	0.53	0.72
P	8220	0.19	35.07	<0.001
S*P	8220	0.95	0.70	0.69

OM) increased with the increasing proportion of peat. Among the physical indicators, with increasing proportion of river sand, the VW, SG, SR and GR increased, and the WC, porosity and LR decreased. Among the chemical indicators, with increasing proportion of river sand, the pH and TP content increased, and the TN, HN, AP and OM contents decreased (Table 3).

S. palustre biomass accumulation tended to decrease as the proportion of peat increased, irrespective of the planting method (P1: $F_{(4,\ 20)} = 31.02$, $P < 0.001$; P2: $F_{(4,\ 20)} = 11.08$, $P < 0.001$; P3: $F_{(4,\ 20)} = 7.00$, $P = 0.001$) (Fig. 1a). The same trend was also observed in plants growing in substrates mixed with river sand (P1: $F_{(4,\ 20)} = 4.18$, $P = 0.01$; P2: $F_{(4,\ 20)} = 3.00$, $P = 0.04$; P3: $F_{(4,\ 19)} = 7.41$, $P = 0.001$) (Fig. 1b).

Effects of the Planting Method on *S. palustre* Growth

Each of the four growth indicators showed significant differences among the three planting methods (Table 2, Fig. 2). Length growth was highest in P1, intermediate in P2, and lowest in P3, while the other three growth indicators (number of capitulum increments, coverage change and biomass accumulation) responded similarly to the planting method, with the highest values in P1 and no remarkable differences in values between P2 and P3.

Table 3 Comparison of physical and chemical properties among five mixture proportions within each type of mixed substrate

	WC (%)	VW (g cm^{-3})	SG (g cm^{-3})	Porosity (%)	SR (%)	LR (%)	GR (%)	pH	TN (mg g^{-1})	TP (mg g^{-1})	HN (mg kg^{-1})	AP (mg kg^{-1})	OM (mg g^{-1})
M	81.96 ± 7.63^{a}	0.78 ± 0.01^{a}	2.40 ± 0.02^{a}	67.65 ± 0.66^{a}	32.35 ± 0.66^{a}	62.62 ± 3.86^{a}	5.04 ± 3.76^{a}	5.58 ± 0.01^{a}	2.72 ± 0.10^{a}	0.87 ± 0.01^{a}	176.83 ± 4.33^{a}	15.56 ± 0.60^{a}	72.51 ± 3.85^{a}
2P	78.22 ± 8.32^{a}	0.74 ± 0.03^{b}	2.36 ± 0.04^{a}	68.57 ± 1.50^{a}	31.43 ± 1.50^{a}	57.85 ± 4.07^{a}	10.72 ± 3.50^{bc}	5.76 ± 0.03^{b}	3.67 ± 0.25^{b}	0.98 ± 0.01^{b}	239.36 ± 2.47^{b}	18.57 ± 0.31^{b}	97.45 ± 5.68^{b}
4P	87.22 ± 14.11^{a}	0.69 ± 0.05^{c}	2.21 ± 0.05^{b}	68.91 ± 1.99^{a}	31.09 ± 1.99^{a}	59.36 ± 5.33^{a}	9.55 ± 3.39^{b}	5.95 ± 0.02^{c}	4.31 ± 0.24^{c}	1.04 ± 0.02^{c}	278.05 ± 3.68^{c}	19.59 ± 0.57^{c}	117.26 ± 3.61^{c}
6P	107.51 ± 7.87^{b}	0.54 ± 0.03^{d}	1.93 ± 0.01^{c}	71.90 ± 1.23^{b}	28.10 ± 1.23^{b}	58.19 ± 2.26^{a}	13.71 ± 2.11^{bc}	6.14 ± 0.02^{d}	5.35 ± 0.38^{d}	1.14 ± 0.04^{d}	356.30 ± 8.02^{d}	22.27 ± 0.57^{d}	138.23 ± 13.59^{d}
8P	136.55 ± 22.77^{c}	0.43 ± 0.04^{e}	1.59 ± 0.02^{d}	72.84 ± 2.15^{b}	27.16 ± 2.15^{b}	58.35 ± 5.00^{a}	14.49 ± 3.28^{c}	6.35 ± 0.05^{e}	5.68 ± 0.25^{d}	1.09 ± 0.01^{e}	373.66 ± 5.72^{e}	22.38 ± 0.38^{d}	157.86 ± 4.67^{e}
$F_{(4,40)}$	29.04	176.93	1041.58	17.97	17.97	1.90	12.06	1056.02	194.88	184.49	2224.01	288.47	189.10
P	<0.001	<0.001	<0.001	<0.001	<0.001	0.13	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
M	81.96 ± 7.63^{A}	0.78 ± 0.01^{A}	2.40 ± 0.02^{A}	67.65 ± 0.66^{A}	32.35 ± 0.66^{A}	62.62 ± 3.86^{A}	5.04 ± 3.76^{AB}	5.58 ± 0.01^{A}	2.72 ± 0.10^{A}	0.87 ± 0.01^{A}	176.83 ± 4.33^{A}	15.56 ± 0.60^{A}	72.51 ± 3.85^{A}
2R	52.06 ± 4.07^{B}	1.05 ± 0.02^{B}	2.54 ± 0.03^{B}	58.46 ± 0.85^{B}	41.54 ± 0.85^{B}	54.54 ± 2.81^{B}	3.92 ± 2.55^{A}	5.76 ± 0.05^{B}	2.56 ± 0.10^{AB}	1.04 ± 0.04^{B}	136.61 ± 3.18^{B}	14.73 ± 0.88^{A}	66.19 ± 3.42^{B}
4R	39.72 ± 2.80^{C}	1.24 ± 0.02^{C}	2.57 ± 0.03^{B}	51.83 ± 0.99^{C}	48.17 ± 0.99^{C}	48.50 ± 2.00^{C}	3.34 ± 2.20^{A}	5.93 ± 0.02^{C}	2.55 ± 0.15^{B}	1.03 ± 0.06^{B}	104.73 ± 4.65^{C}	11.41 ± 0.42^{B}	65.68 ± 3.52^{B}
6R	29.38 ± 3.93^{D}	1.40 ± 0.03^{D}	2.65 ± 0.02^{C}	47.35 ± 1.28^{D}	52.65 ± 1.28^{D}	40.91 ± 4.70^{D}	6.45 ± 3.59^{AB}	6.19 ± 0.04^{D}	2.41 ± 0.08^{B}	1.12 ± 0.05^{C}	78.47 ± 2.42^{D}	11.02 ± 0.53^{B}	58.58 ± 3.82^{C}
8R	21.13 ± 2.65^{E}	1.58 ± 0.02^{E}	2.74 ± 0.03^{D}	42.41 ± 0.69^{E}	57.59 ± 0.69^{E}	33.26 ± 3.74^{E}	9.15 ± 3.29^{B}	6.46 ± 0.02^{E}	2.18 ± 0.18^{C}	1.14 ± 0.07^{C}	43.85 ± 2.57^{E}	9.02 ± 0.57^{C}	50.45 ± 1.69^{D}
$F_{(4,40)}$	241.68	1416.19	262.44	1033.72	1033.72	93.75	4.93	939.39	22.15	38.36	1883.98	171.59	56.81
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.003	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Different letters next to values (means ± SDs) indicate significant differences ($P < 0.05$) by one-way ANOVA, and Tukey tests were used for multiple comparisons tests

M stands for 100% mountain soil, 2P stands for mixed substrate with 20% peat and 80% mountain soil, and so on; 2R stands for mixed-substrate of 20% river sand and 80% mountain soil, and so on

WC water content, *VW* volume-weight, *SG* specific gravity, *SR* solid phase ratio, *LR* liquid phase ratio, *GR* gas phase ratio, *TN* total nitrogen content, *TP* total phosphorus content, *HN* hydrolysable N, *AP* available phosphorus, *OM* organic matter content

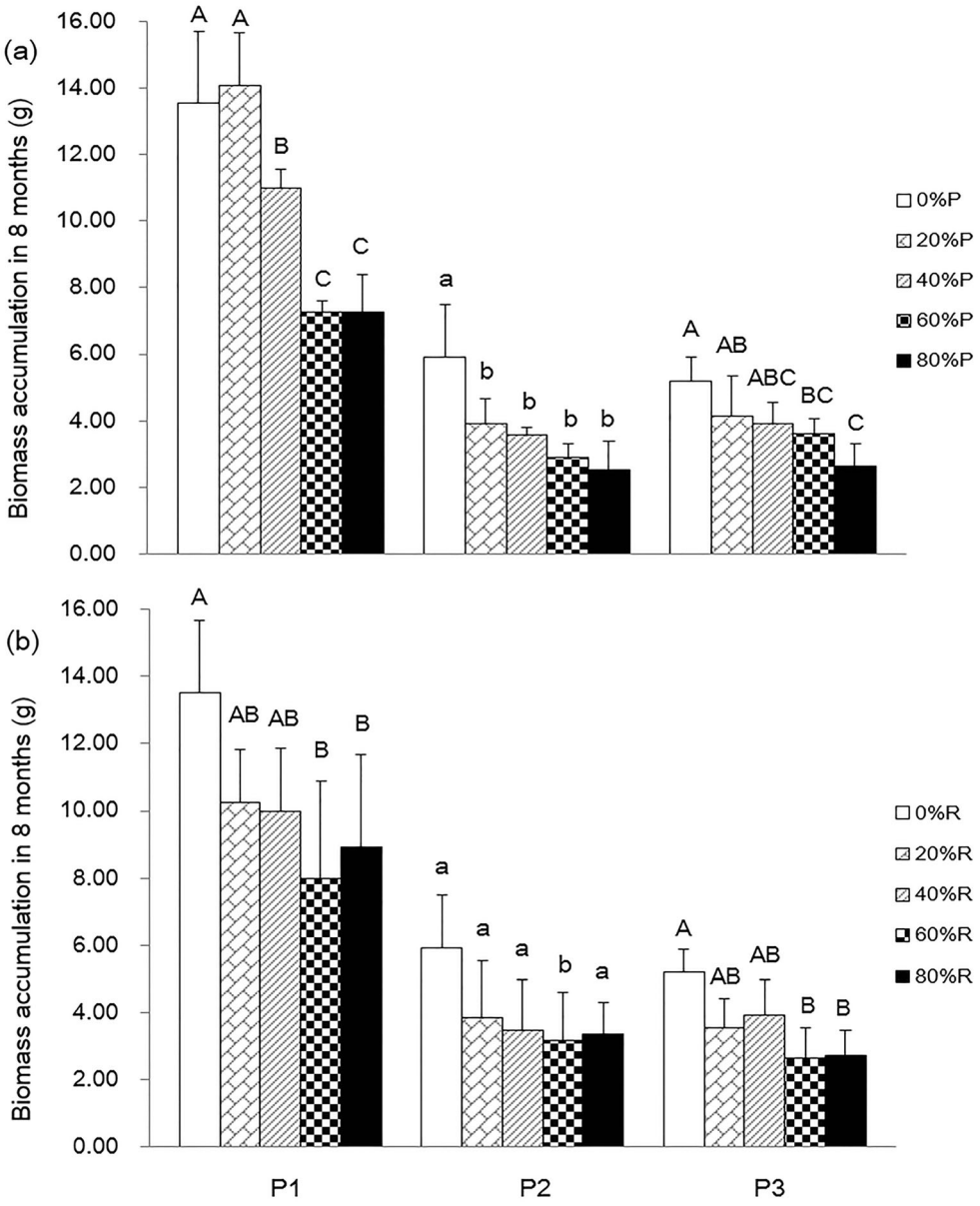

Fig. 1 Effects of the proportion (0%, 20%, 40%, 60%, 80%) of (a) peat (P) or (b) river sand (R) in the mixture on the biomass accumulations (means ± SDs, during eight months) of *Sphagnum palustre* under three planting methods (P1, P2 and P3). [$n = 25$ for each planting method in the two substrate mixtures, except for P3 in mixtures with river sand ($n = 24$). Different letters above the bars indicate significant differences ($P < 0.05$) by one-way ANOVA; Tukey tests were used for multiple comparisons. Each part (a, b) of the figure was created by Microsoft Excel 2013, and the whole figure was created by Photoshop]

S. palustre Growth in Planting Method 4

Ninety-eight percent of the transplanted *S. palustre* plants in P4 were able to grow new capitula from their stems though the upper 8 cm, and all initial capitula were removed; moreover, new capitula were able to grow from any part of the plant stem. The number of capitulum increments in P4 (5.2 ± 3.6) was significantly lower than that in P1 (10.9 ± 5.0) ($F_{(1,88)} = 38.51$, $P < 0.001$) but significantly higher than that in P2 (2.6 ± 3.1, $F_{(1,88)} = 19.15$, $P < 0.001$) and P3 (3.1 ± 2.7, $F_{(1,88)} = 12.47$, $P < 0.001$).

Similar to *S. palustre* growth under the other three planting methods, the number of capitulum increments in P4 was not affected by the type of substrate mixture (peat: 4.4 ± 2.4, river sand: 4.8 ± 3.8, $F_{(1,37)=}0.11$, $P = 0.74$), but tended to decrease as the proportions of peat or river sand increased (peat: $F_{(4,\ 20)} = 9.69$, $P < 0.001$; river sand: $F_{(4,\ 20)} = 5.09$, $P = 0.005$) (Fig. 3).

Effects of Physical and Chemical Properties on *S. palustre* Growth

According to the multiple linear regression analysis, among the thirteen indicators of the physical and chemical properties of the substrate, only TP and pH showed significant correlations with biomass accumulation (biomass accumulation = −7.53 TP-1.81 pH + 24.53; $F_{(2,78)} = 4.70$, $P = 0.01$), and both indicators were negatively correlated with biomass accumulation.

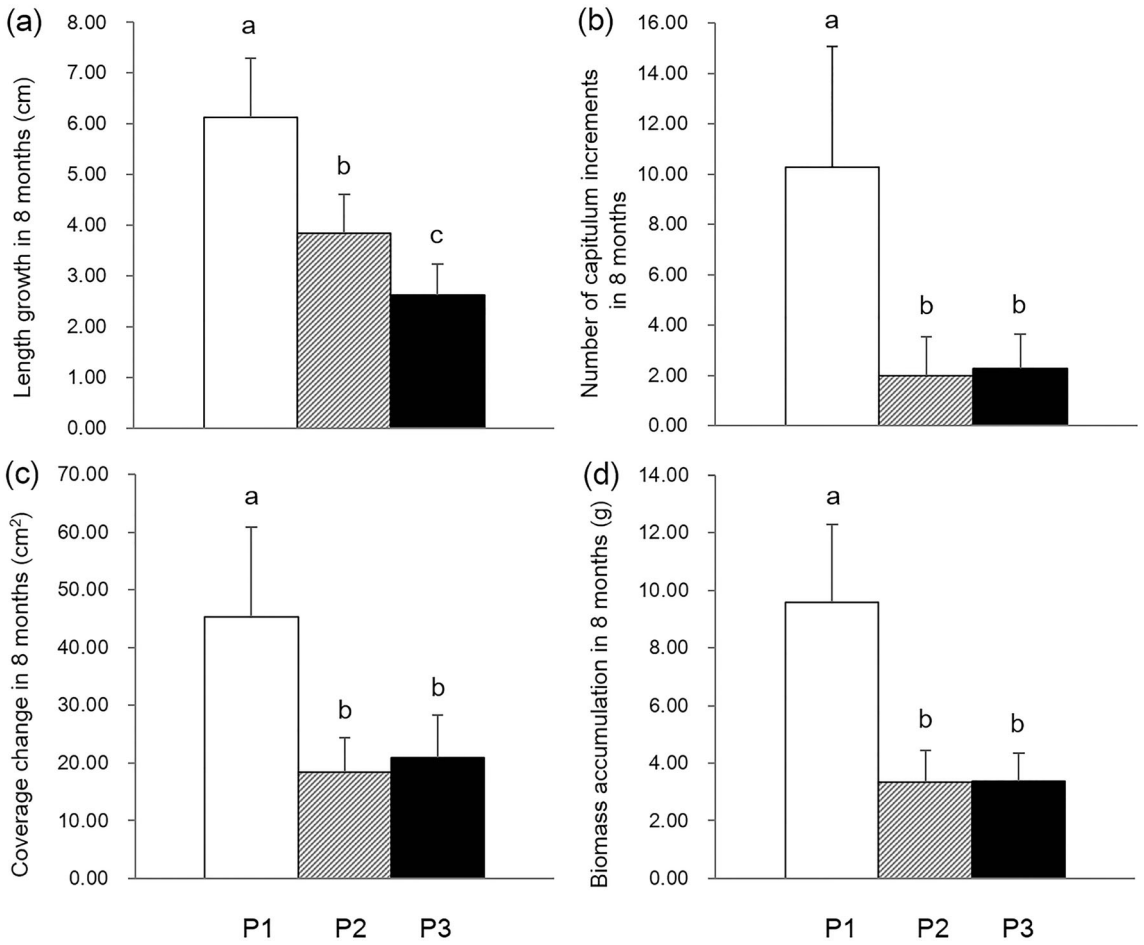

Fig. 2 Effects of planting method (P1, P2 and P3) on **a** length growth, **b** number of capitulum increments, **c** coverage change and **d** biomass accumulation (means ± SDs, during 8 months) ($n = 119$ for each growth indicator) in *Sphagnum palustre*. [Different letters above the bars indicate significant differences ($P < 0.05$) by two-way ANOVA; Tukey tests were used for multiple comparisons. Each part (a, b, c and d) of the figure was created by Microsoft Excel 2013, and the whole figure was created by Photoshop]

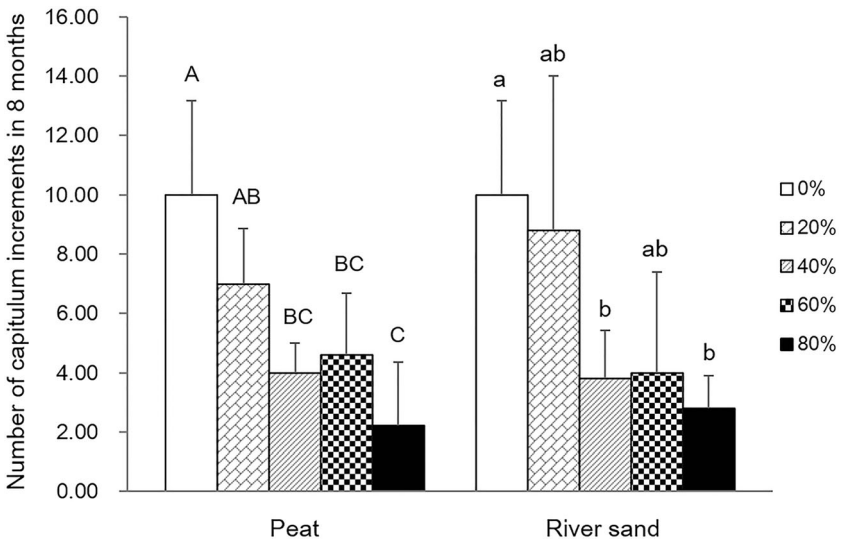

Fig. 3 Effects of the proportion (0%, 20%, 40%, 60%, 80%) of peat or river sand in the mixture on the number of capitulum increments (means ± SDs, during 8 months) of *Sphagnum palustre* under planting method 4. [$n = 25$ for each substrate mixture. Different letters above the bars indicate significant differences ($P < 0.05$) by one-way ANOVA; Tukey tests were used for multiple comparisons. The figure was created by Microsoft Excel 2013]

Effects of Initial Biomass and Capitula N and P Contents on *S. palustre* Growth

No significant differences in the initial biomass of *S. palustre* were found between the two types of substrate mixture ($F_{(1,117)} = 0.06$, $P = 0.80$) or among the different substrate mixture proportions (peat: $F_{(4,70)} = 0.11$, $P = 0.98$; river sand: $F_{(4,69)} = 0.08$, $P = 0.99$). However, pronounced differences in the initial biomass of *S. palustre* existed among the three planting methods ($F_{(2,116)} = 899.44$, $P < 0.001$), with the highest values in P1 (7.24 ± 1.00 g), intermediate values in P2 (3.28 ± 0.34 g) and lowest values in P3 (1.53 ± 0.03 g).

There were no interactive effects between the substrate mixture type and the planting method on N and P contents and N:P ratios in the capitula of *S. palustre* (ANOVA results are given in Online Resource 6); however, each affected the N and P contents and N:P ratios in the capitula of *S. palustre* (Fig. 4). The N contents and N:P ratios were significantly higher in substrates mixed with peat than in substrates mixed with river sand (Fig. 4a and c), but the P contents were not obviously different (Fig. 4b). The N content remained unchanged under all three planting methods (Fig. 4d). P content was highest in P2, while no obvious difference existed between P contents in P1 and P3 (Fig. 4e). N:P ratios were the lowest in P2, while no obvious difference existed between ratios in P1 and P3 (Fig. 4f).

The substrate mixture proportion also affected the N and P contents and N:P ratios in the capitula of *S. palustre* (Fig. 5). For plants grown in substrates mixed with peat, as the proportions of peat increased, the N contents increased, N:P ratios remained unchanged, and P contents showed a slight but not significant increase. For plants grown in substrates mixed with river sand, as the proportions of sand increased, the N contents remained unchanged, P contents increased, and N:P ratios decreased.

According to the multiple linear regression analysis, among the four factors, only the initial biomass and P content in capitula showed significant correlations with biomass accumulation (biomass accumulation = 1.16 initial biomass-7.14 P + 6.19; $F_{(2,78)} = 135.84$, $P < 0.001$). Initial biomass was positively correlated with biomass accumulation, while the P content in capitula was negatively correlated with biomass accumulation.

Correlations Between the N and P Contents in Capitula and those in the Substrate

Both the N and P contents in the capitula of *S. palustre* were positively correlated with those in the substrate in

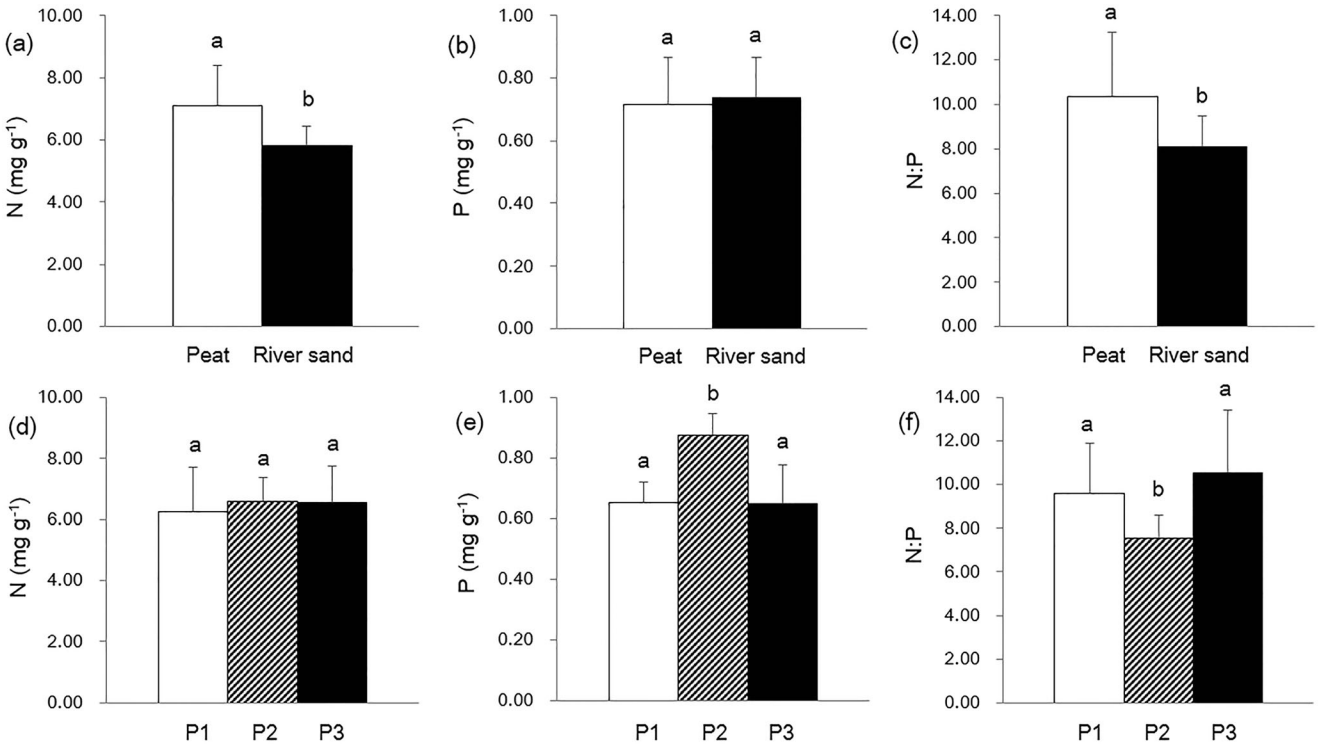

Fig. 4 Effects of the **a**, **b**, **c** substrate mixture type (peat and river sand) ($n = 72$ for each indicator) and **d**, **e**, **f** planting method (P1, P2, P3) ($n = 72$ for each indicator) on N and P contents and the N:P ratios (means ± SDs) in capitula of *Sphagnum palustre*. [Different letters above the bars indicate significant differences $P < 0.05$ by two-way ANOVA; Tukey tests were used for multiple comparisons. Each part (a, b, c, d, e and f) of the figure was created by Microsoft Excel 2013, and the whole figure was created by Photoshop]

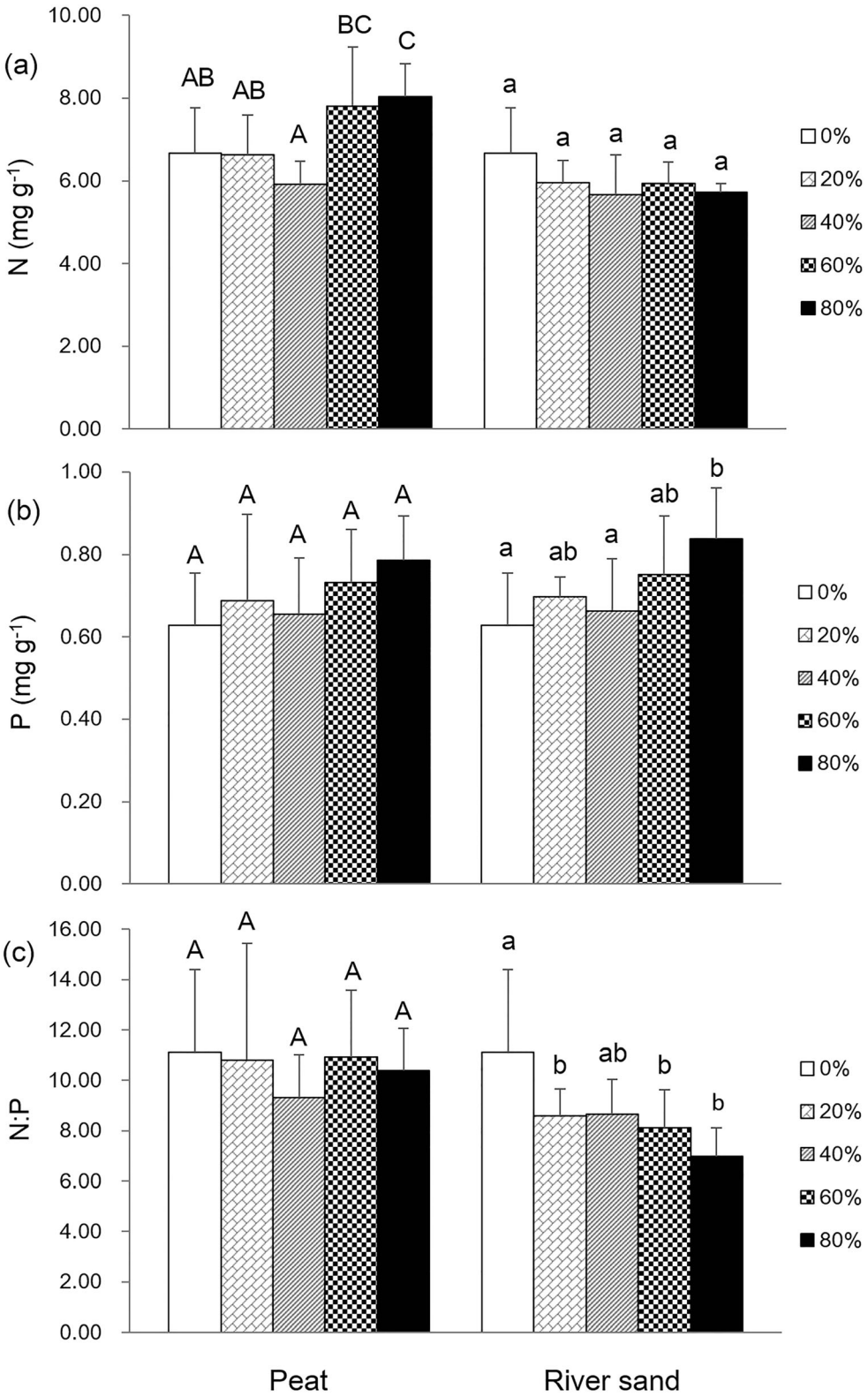

Fig. 5 Effects of the proportion (0%, 20%, 40%, 60%, 80%) of peat ($n = 45$ for each indicator) or river sand ($n = 45$ for each indicator) in the mixture on **a** N and **b** P contents and **c** the N:P ratios (means ± SDs) in capitula of *Sphagnum palustre*. [Different letters above the bars indicate significant differences $P < 0.05$ by one-way ANOVA; Tukey tests were used for multiple comparisons. Each part (a, b and c) of the figure was created by Microsoft Excel 2013, and the whole figure was created by Photoshop]

which *S. palustre* was cultivated [the r values for the correlations between N contents in the substrate and that in the capitula of *S. palustre* in P1, P2 and P3 were 0.54 ($P = 0.003$), 0.58 ($P = 0.002$) and 0.52 ($P = 0.005$), respectively; the r values for the correlations between the P contents in the substrate and that in the capitula of *S. palustre* in P2 and P3 were 0.62 ($P = 0.001$) and 0.68 ($P < 0.001$), respectively]. However, there was no significant correlation

between the P content in capitula and that in the substrate for P1 ($r = 0.09$, $P = 0.66$).

Discussion

Composition and Proportion of the Mixed Substrate

The effects of substrate mixture type on *S. palustre* growth differed from what we predicted. We initially expected significant differences in *S. palustre* growth between plants grown in substrate mixed with peat and those grown in substrate mixed with river sand as a result of differences in the physical and chemical properties of the substrates. However, the results show that *S. palustre* growth in the two substrate mixture groups was not obviously different even though the physical and chemical properties showed obvious and expected differences (Table 1). On the other hand, within each substrate mixture group, as the proportion of peat or river sand increased and the physical and chemical properties changed (Table 3), *S. palustre* growth decreased (Figs. 1 and 3).

This seems to be a contradictory result. We speculated that, although the growth of *S. palustre* can be affected by various biotic and abiotic factors (Gunnarsson 2005; Pouliot et al. 2015), in this particular situation, growth would be primarily limited by only one or few factors. In our results, the negative correlation between *S. palustre* productivity (biomass accumulation) and P contents in capitula suggested that the growth of *S. palustre* depends on this P content. Furthermore, the negative correlation between *S. palustre* productivity and P content in the substrate and the highly positive correlation between the N and P contents in the substrate and those in the capitula of *S. palustre* confirmed our speculation: the nutrient contents in the substrate affected the amount of nutrients taken up and assimilated in capitula and further affected *S. palustre* growth. This may be the main mechanism underlying the effects of substrate on *S. palustre* growth. Therefore, we speculated that the lack of an obvious difference in the background P contents between the two substrate mixture groups (Table 1) led to no obvious difference in the P contents of capitula (Fig. 4b). This resulted in no detectable differences in *S. palustre* growth when transplanted into two different substrates mixtures (Table 2). Similarly, the continuous increase in the substrate P content with increasing proportion of peat or river sand (Table 3) caused a corresponding increase (or a slight increase) in the P content in capitula (peat: from 0.63 ± 0.13 mg g^{-1} to 0.79 ± 0.11 mg g^{-1}; river sand: from 0.63 ± 0.13 mg g^{-1} to 0.84 ± 0.12 mg g^{-1}) (Fig. 5b), which further resulted in a continuous decrease in *S. palustre* growth (Figs. 1 and 3). On the other hand, the multiple regression analysis suggested that in addition to the P content, the increased pH of the substrate also negatively affected *S. palustre* growth. Therefore, another possibility was that no significant difference in the pH between the two substrate mixture groups (Table 1) resulted in no differences in *S. palustre* growth. In contrast, the continuous increase in pH in substrates with increasing proportions of peat or river sand (Table 3) resulted in a continuous decrease in *S. palustre* growth (Figs. 1 and 3).

The effects of P on *S. palustre* growth are usually influenced by other nutrients, especially N (Gusewell and Koerselman 2002; Bubier et al. 2007; Wendel et al. 2011). Koerselman and Meuleman (1996) posited that the N:P ratio reflects relative nutrient availability and can be used as an indicator to evaluate the limiting nutrient. For species in the genus *Sphagnum*, some studies (Bragazza et al. 2004; Hajek and Adamec 2009; Chiwa et al. 2016) proposed that growth would be limited by N availability at N:P ratios less than 30, in which case P would have a negative effect on *Sphagnum* growth. In our experiment, the N:P ratio (9.22 ± 2.51) in *S. palustre* capitula was much lower than 30. In addition, Bragazza et al. (2005) suggested that N would play a limiting role when its concentration in *Sphagnum* capitula was approximately 6 mg g^{-1}; this value is similar to ours (6.46 ± 1.19 mg g^{-1}). Also, other studies reported higher concentrations of N with lower (or similar) concentrations of P in *Sphagnum* capitula from unpolluted areas (Brock and Bregman 1989; Heijmans et al. 2002; Limpens et al. 2003; Fritz et al. 2012). Therefore, one possibility for the negative effects of P on *Sphagnum* are related to imbalances in nutrient stoichiometry triggered by the low N concentration. However, this speculation requires additional experimental verification.

Species of the genus *Sphagnum* are generally acidophilic calcifuges and are highly sensitive to acidity and alkalinity (Quinty and Rochefort 2003; Vicherova et al. 2017). Previous studies showed that the optimal pH range for *S. palustre* is 4.5–6.0 (Andrus 1986; Chen et al. 2009; Ye et al. 2012; Tahvanainen and Haraguchi 2013; Harpenslager et al. 2015; Riegel and Wilde 2016) and that above pH 6.0, the growth of *S. palustre* decreases as pH increases (Wang 2010), which was in accordance with our results. There are two possible reasons for the negative effects of increased pH on *S. palustre* productivity in our study. On the one hand, pH was strongly and positively related to the P content in the substrate (Pearson coefficient $r = 0.79$, $P < 0.001$), and increased P content with increased substrate pH likely caused the decrease in *S. palustre* productivity. On the other hand, the increased substrate pH is usually associated with increased concentrations of Ca^{2+}, Mg^{2+} and HCO_3^- (Clymo 1973; Gorham and Janssens 1992; Lamers et al. 1999), which may cause toxicity symptoms in *S. palustre* by interfering with cellular uptake of monovalent cations (such as K^+ and NH_4^+) (Hajek and Adamec 2009), or by interfering with cellular metabolism (Vicherova et al. 2015, 2017), negatively affecting *S. palustre* growth (Hajek et al. 2006; Bengtsson et al. 2018).

Our results demonstrate that the yellow-brown soil, which is distributed widely in subtropical regions, is an optimal substrate for *S. palustre* growth, probably due to its favorable pH and P content. This finding has important implications as it indicates that *S. palustre* restoration does not dependent on the use of peat, allowing for *S. palustre* restoration on large, less restrictive scales.

Planting Method

As expected, different planting methods resulted in differences in *S. palustre* growth, with the best performance in P1 and no pronounced differences in growth between P2 and P3 (Fig. 2). The multiple regression analysis suggested that *S. palustre* productivity was positively correlated with initial biomass and negatively correlated with P content in capitula. Therefore, compared to values for the other two planting methods, the higher initial biomass and the lower P contents in capitula (Fig. 4e) in P1 contributed to the greatest amount of growth. For the remaining two planting methods, both the initial biomass and capitula P contents were higher in P2 than in P3 (Fig. 4e). Therefore, it is likely that the positive effects related to initial biomass together with the negative effects related to P content cancelled each other out, resulting in non-significant growth differences between P2 and P3.

The negative correlation between *S. palustre* productivity and the P contents in capitula has been discussed previously. The positive effects of initial biomass (or initial fragment size) on *Sphagnum* growth have been reported by earlier studies. Gunnarsson and Soderstron (2007) compared *Sphagnum angermanicum* growth under four planting methods and found that a larger diaspore size resulted in better growth; moreover, *S. angermanicum* showed the greatest growth when transplanting whole shoots. Robroek et al. (2007, 2009) reported similar results. These authors explained that the ability of *Sphagnum* species to supply its capitula with water increased with increasing fragment size, suggesting that *Sphagnum* diaspores of a larger size are better at creating and maintaining microhydrological conditions that are favorable for growth. In contrast, *Sphagnum* diaspores of a smaller size are more sensitive to the environment and to seasonal variations in temperature and moisture conditions, leading to less growth. In addition, Robroek et al. (2009) found that at the early stage of *Sphagnum* plant transplantation, the differences between the microenvironment in the new locality and that in the original habitat led to decreased competitive ability and further reduced coverage. In our experiment, compared to the growth environment in P2 and P3, that of the upper viable parts of *Sphagnum* plants in P1 was closer to the original environment in natural *Sphagnum* wetlands, as they grow on the same basal material, i.e., senescent but undecomposed parts of *Sphagnum* plants (also called 'white peat'). This may also contribute to the better performance of *S. palustre* in P1.

In terms of planting method 4, 98 % of the damaged *S. palustre* plants were able to grow new capitula from any part of the plant stem, suggesting that damaged plants can still regenerate and were no longer affected by apical dominance after their capitula were removed (Rydin and Clymo 1989; Daniels and Eddy 1990). The number of capitulum increments in P4 was lower than that in P1, but higher than that in P2 and P3, suggesting that the regenerative potential of the damaged *S. palustre* plants was decreased when the upper parts were removed, but was stronger than that of *S. palustre* plants with only several centimeters of the upper part of the plant. Therefore, our study demonstrated that the common peatland restoration method using the upper parts of *S. palustre* as transplanted materials is practical and has no destructive effects on the source *S. palustre* populations in the areas where they are collected. However, because *Sphagnum* vitality decreases continuously with increasing distance from the capitula, and the depth at which fragments of *Sphagnum* plants can regenerate new capitula varies greatly between species (Rochefort et al. 2003), the collection depth needs to be determined carefully. From this perspective, we can expect that planting intact plants would cause greatest effects on the source *Sphagnum* populations, while planting only the capitula would cause minimal effects. Therefore, compared with the traditional transplanting method (P2), the method involving transplanting only capitula has the similar productivity but does less damage to the source *S. palustre* populations, making it more suitable for *S. palustre* restoration.

Conclusion and Implications

The results of this study show that the substrate composition and length of shoot fragment significantly affect the growth of *S. palustre*, which is the dominant peat-forming species in the subtropical high-mountain peatland regions of China. The substrate can affect *S. palustre* growth via its background nutrient contents. Although close correlations between the nutrient contents in soils and those in vascular plants have been reported by other studies, our results still have important implications for the transplantation and restoration of *Sphagnum* mosses considering their absence of roots and vascular tissues. In addition to the nutrient contents in the substrate, the pH of the substrate also plays an important role in *S. palustre* growth. Compared with peat, which is used as the only substrate in traditional peatlands restoration technique, the local yellow-brown soil, which is widely distributed in subtropical mountain regions, seemed to be a better substrate for *S. palustre* growth. The results show that *S. palustre* restoration practices can be independent of the distribution and range of peatlands, which may provide a new approach for restoring

peatland ecosystems in these regions. Furthermore, our study demonstrated that the common restoration technique of collecting the upper parts of *S. palustre* plants for transplantation does not destroy the source populations in natural *Sphagnum* wetlands. However, considering the similar productivity and less impact to the source *S. palustre* populations, a planting method using only capitula may be a better choice for *S. palustre* restoration.

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Data Availability All data generated or analysed during this study are included in this published article and its supplementary information files.

Compliance with Ethical Standards

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

Statement of Human and Animal Rights This article does not contain any studies with human participants or animals performed by any of the authors.

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