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RESEARCH PAPER

Sphagnum growth under N saturation: interactive effects of water level and P or K fertilization

G. Gaudig, M. Krebs & H. Joosten

Institute of Botany and Landscape Ecology, University of Greifswald, partner in the Greifswald Mire Centre, Greifswald, Germany

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Correspondence

G. Gaudig, Institute of Botany and Landscape Ecology, University of Greifswald, partner in the Greifswald Mire Centre, Soldmannstr. 15, 17487 Greifswald, Germany.

E-mail: gaudig@uni-greifswald.de

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ABSTRACT

- *Sphagnum* biomass is a promising material that could be used as a substitute for peat in growing media and can be sustainably produced by converting existing drainage-based peatland agriculture into wet, climate-friendly agriculture (paludiculture). Our study focuses on yield maximization of *Sphagnum* as a crop.
- We tested the effects of three water level regimes and of phosphorus or potassium fertilization on the growth of four *Sphagnum* species (*S. papillosum, S. palustre, S. fimbriatum*, *S. fallax*). To simulate field conditions in Central and Western Europe we carried out a glasshouse experiment under nitrogen-saturated conditions.
- A constant high water table (remaining at 2 cm below capitulum during growth) led to highest productivity for all tested species. Water table fluctuations between 2 and 9 cm below capitulum during growth and a water level 2 cm below capitulum at the start but falling relatively during plant growth led to significantly lower productivity. Fertilization had no effect on *Sphagnum* growth under conditions with high atmospheric deposition such as in NW Germany (38 kg N, 0.3 kg P, 7.6 kg K·ha^{-1}·year^{-1}).
- Large-scale maximization of *Sphagnum* yields requires precise water management, with water tables just below the capitula and rising with *Sphagnum* growth. The nutrient load in large areas of Central and Western Europe from atmospheric deposition and irrigation water is high but, with an optimal water supply, does not hamper *Sphagnum* growth, at least not of regional provenances of *Sphagnum*.

INTRODUCTION

Sphagnum biomass is an important renewable raw material that can be used in various products (Pouliot *et al.* 2015; Glatzel & Rochefort 2017). It can substitute for fossil peat, especially for slightly humified *Sphagnum* peat (Emmel 2008; Reinikainen *et al.* 2012; Blievernicht *et al.* 2013; Jobin *et al.* 2014), which, with an annual worldwide consumption of 30 million m^3, is the major constituent of growing media used in professional horticulture (Schmilewski 2017). Its cultivation on rewetted peatlands ('Sphagnum farming') contributes to reducing greenhouse gas emissions from formerly drained agricultural land (Beyer & Höper 2015; Wichtmann *et al.* 2016; Günther *et al.* 2017). Replacing peat with *Sphagnum* biomass, however, requires a substantial expansion of the area under cultivation and of the yield per hectare (Gaudig *et al.* 2014, 2018; Wichmann *et al.* 2017). Maximizing yield implies that conditions for optimal *Sphagnum* growth should be identified.

Sphagnum growth rate is, next to climate factors, determined by water and nutrient availability as well as the *Sphagnum* species (Gunnarsson 2005). Under natural conditions, atmospheric water supply in NW Germany used to provide sufficient water to cover water losses, in particular through evapotranspiration in summer. This is, however, no longer the case. In the present situation of higher atmospheric water demand and larger seepage losses as a result of extensive drainage in the surrounding land, Sphagnum farming now requires an additional water supply (Brust *et al.* 2018) to keep the photosynthetically most active apical capitulum continuously moist (cf. Robroek *et al.* 2007). Several studies have shown that the growth rate of most *Sphagnum* species is highest at water tables just below the capitula, independent of the species (Clymo & Reddaway 1971; Hayward & Clymo 1983; Campeau & Rochefort 1996; Robroek *et al.* 2009; Brown *et al.* 2017).

In NW Germany, with a total atmospheric N deposition of ca. 38 kg·ha^{-1}·year^{-1} (Gauger *et al.* 2002), *Sphagnum* growth is not N-limited, and the N pool of the *Sphagnum* layer is saturated (cf. Malmer 1990; Lamers *et al.* 2000; Berendse *et al.* 2001; Bragazza *et al.* 2004). Additional N input would not result in extra *Sphagnum* growth and could even negatively affect growth, both directly (*e.g.* by lower photosynthesis, increased metabolic costs) and indirectly (by vascular plants increasingly competing with *Sphagnum* for light and water; Berendse *et al.* 2001; Tomassen *et al.* 2004; Limpens *et al.* 2011; Fritz *et al.* 2014). Under high N loads *Sphagnum* growth may furthermore become limited by phosphorus (P) (Aerts *et al.* 1992; Verhoeven *et al.* 1996; Lund *et al.* 2009) and potassium (K) (Bragazza *et al.* 2004). The addition of P may then substantially increase *Sphagnum* biomass production (Limpens *et al.* 2004; Fritz *et al.* 2012), but this effect disappears with insufficient water availability (Aerts *et al.* 2001; Limpens *et al.* 2004; Fritz *et al.* 2012). High *Sphagnum* biomass production was indeed observed in a Sphagnum farming field experiment in NW Germany under high N loads, balanced supply of P and K in irrigation water, and year-round water tables just below the moss surface (Temmink *et al.* 2017). However, the water table varied up to 20 cm over time and around 10 cm in space because of differences in micro-relief (cf. Brust *et al.* 2018).

In this study we address the relationship between nutrient supply, high water level regimes and growth of different *Sphagnum* species for the first time in a glasshouse factorial experiment. We hypothesize that under N-saturated conditions, the highest *Sphagnum* growth rates can be achieved by combining a constantly high water table with extra P and K fertilization.

MATERIAL AND METHODS

The experiment was set up in a full factorial design with three replicates and repeated twice with the same combination of water regime and fertilization level. A total of 216 moss containers (4 species × 3 water regimes × 3 fertilization levels × 3 replicates × 2 repetitions) were placed in 18 (2 repetitions × 9 combinations of water regime and fertilization level) boxes (4 × 60 × 23 cm) filled with culture medium after Rudolph *et al.* (1988) (Table 1). Each box contained 12 containers: three of each species (with the exception of *S. palustre* with lower availability) distributed randomly within the box. To ensure similar conditions within the boxes, 'gaps' due to the lack of *S. palustre* were filled using containers with *S. papillosum* (same section).

Sphagnum species

Pure patches (12 × 12 cm and 10-cm deep) of *Sphagnum papillosum*, *S. palustre*, *S. fimbriatum* and *S. fallax* were collected from natural lawns in Lower Saxony (Esterweger Dose, NW Germany) and placed in containers (12 × 12 × 12 cm) with a perforated base, within the boxes filled with a culture medium.

Water regimes

Three water regimes were applied by adjusting water levels in the boxes each week: (i) water level rising with moss growth and remaining 2 cm below the top of the capitulum ('rising'), (ii) water level alternating between 2 cm (1 week duration) and 8 cm (3 weeks duration) below the top of the capitulum ('fluctuating'), (iii) water level starting 2 cm below the top of the capitulum and remaining at the same absolute level in spite of moss growth ('static').

Fertilization levels

Water with a composition according to Rudolph *et al.* (1988) for microelements and to Gauger *et al.* (2002) for macroelements was sprayed every third week (2 h after sprinkling the mosses with demineralized water in the morning) to control the level to the average annual (1990–1999) atmospheric deposition of Ramsloh (Lower Saxony 53°04′ N, 7°38 O). The other treatments were a five-fold deposition of P (5P: 1.5 kg $P \cdot ha^{-1} \cdot year^{-1}$) and a twofold deposition of both P and K (2P2K: 0.6 kg $P \cdot ha^{-1} \cdot year^{-1}$ and 15 kg $K \cdot ha^{-1} \cdot year^{-1}$) (cf. Table 1). All fertilization treatments received the same amount of N (38 $kg \cdot ha^{-1} \cdot year^{-1}$).

Cultivation conditions

The mosses were cultivated in a glasshouse with a light regime of 12-h light (mostly sunlight, but at light flux densities < 15 klx, supplemented with a sodium vapour lamp – Philips Son-T Agro 400 W – of 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and 12-h dark. Air temperatures in the glasshouse were 18–21 °C during the day and 12 °C at night, without active cooling. Temperatures at the moss surface never exceeded 35 °C and were thus not detrimental to the mosses (cf. Clymo & Hayward 1982). After 2 weeks of adaptation, the experiment ran from September 2006 to June 2007 (280 days). Sprinkler irrigation (~0.25 mm demineralized $water \cdot m^{-2}$) was applied twice a day (06:00 and 18:00 h) for 1 min, simulating morning dew and rain (Rudolph 1963). Different growth rates between containers within a box were corrected weekly by adjusting the height position of the containers. After 54 and 146 days, all mosses of the 'rising' and 'fluctuating' treatments were cut back from the base to a length of 10 cm to maintain similar water levels within a box for all containers. In the 'static' treatment, container walls were regularly elongated to avoid interaction between the growing mosses.

Table 1. Nutrient availability during the experiment (280 days) – calculated from nutrient concentrations in the boxes at the beginning of the experiment ('culture medium', pH 5.8) and the nutrients added by fertilization (fertilization solution: pH 8.7–9.0, weakly buffered) – depending on fertilization treatment compared to mean concentration of the culture medium in the boxes at the end of the experiment (in $kg \cdot ha^{-1} \pm$ SEM, $n = 6$ for each fertilization treatment). N availability was the same for all treatments, with N at 6.67 $kg \cdot ha^{-1}$ by culture medium + 28.98 $kg \cdot ha^{-1}$ by adding fertilizer = 35.65 $kg \cdot ha^{-1}$ total. C = control, P5 = five-fold addition of phosphorus, 2P2K = double addition of both phosphorus and potassium.

		fertilization treatment								
		C			5P			2P2K		
	culture medium start	applied by fertilization	total nutrient availability	culture medium end	applied by fertilization	total nutrient availability	culture medium end	applied by fertilization	total nutrient availability	culture medium end
K	1.64	5.81	7.45	3 ± 1	5.81	7.45	2 ± 1	11.61	13.25	3 ± 1
NO_3-N	2.86	7.02	9.88	n.d.	7.02	9.88	n.d.	7.02	9.88	n.d.
NH_4-N	3.81	21.96	25.77	1 ± 0.5	21.96	25.77	1 ± 0.6	21.96	25.77	1 ± 0
PO_4-P	0.55	0.23	0.78	0.5 ± 0	1.15	1.70	0.4 ± 0	0.46	1.01	0.5 ± 0
N/P	12.1	126	45.7		25.2	21		63	35.3	
N/K	4.1	5	4.8		5	4.8		2.5	2.7	

Growth measurements

At the beginning of the experiment, five moss shoots per container were marked with nylon zip ties (width 2 mm, length 100 mm) fixed between the capitulum and the subjacent branches (cf. Overbeck & Happach 1957; Clymo 1970). At the end of the experiment (day 280) all mosses were cut at the level of the zip ties and at 1 cm below the surface to separate the capitula (0–1 cm). Length increase was measured, and biomass weight of each marked moss shoot and each container determined after drying for at least 48 h at 60 °C. Annual biomass productivity was calculated by extrapolating the subcapitulum weight (dry mass) of each entire container to hectares and year, assuming that the biomass of the capitula had not changed since the end of the initial adaptation period. Weight per length unit was calculated for each marked moss shoot to characterize compactness.

Fruiting bodies of the fungus *Sphagnurus paluster* were removed from 28 of the 216 containers during the experiment to prevent further distribution of the fungus. The cover (% of the container area) of *Sphagnum* tissue with necrosis (bleached capitula) and with algal infestation (dark green capitula) was estimated at the end of the experiment.

Nutrient measurements

The biomass of all capitula per container was dried and milled in a centrifugal ball mill (Pulverisette 14, Fritsch Idar-Oberstein; for 1–2 min at RCF: 15,580 *g*), and total N concentration and C/N ratio determined with a dry-combustion C/N analyser (CHNOS element analyser; Vario EL III, Elementar Analysensysteme, Hanau, Germany). After dry ashing (in a muffle furnace at 550 °C for 4 h), the ash was dissolved in 10% H_2SO_4 (Kalra 1998) and the solution treated with an acidic molybdate solution containing ascorbic acid (modified molybdenum blue method; Temminghoff 2004) to measure total P using a UV/Visible spectrophotometer (Cecil CE 1021, 890 nm wavelength). Potassium (K) was determined with an atomic absorption flame spectrometer (CD-ContrAA 300, analytic Jena) directly after microwave digestion (START 1500, MLS Enterprises). The K concentration of the water in the boxes was determined as described for the biomass samples but without digestion. Orthophosphate (ortho-P) in the water was measured after filtration (cellulose acetate filter with 0.45-μm pore size) using the modified molybdenum blue method (Temminghoff 2004), and ammonium (NH_4^+) was measured spectrophotometrically using the salicylate method (Krom 1980).

Data analysis

We analysed the effects and possible interactions of the treatments, *Sphagnum* species, water regime and fertilization level, on *Sphagnum* dry mass productivity and length increase, moss compactness, N, P and K concentrations and N/P and N/K quotients ratios in the *Sphagnum* capitula, and cover of necrosis and algae (dependent variable). As we had different sample sizes (number of replicates) and no homogeneity among the datasets, assumptions necessary for applying linear regression models (including ANOVA models) were not met (Zuur *et al.* 2009). To accommodate possible spatial correlation of *Sphagnum* containers of the same species in one box, we thus applied linear mixed effect models with fixed and random components (Pinheiro *et al.* 2009; Zuur *et al.* 2009). We also applied linear mixed effect models to compare the results of dry mass productivity ($t{\cdot}ha^{-1}{\cdot}year^{-1}$), rate of increase in length ($cm{\cdot}year^{-1}$), compactness ($mg{\cdot}cm^{-1}$) and cover of necrosis and algae (% per container) for each *Sphagnum* species (*S. fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum*) with regard to the treatments water regime and fertilization level.

Restricted maximum likelihood estimation (REML) was used to calculate estimates of coefficients for the models (Zuur *et al.* 2009). To identify the optimal model, we used the Akaike information criterion (AIC), which measures goodness-of-fit and model complexity (the lower the AIC value, the better the model).

Furthermore, we measured the strength and direction of association between dry mass productivity and necrosis, algae and N, P and K concentrations in the *Sphagnum* capitula using Pearson product-moment ('standard') or Spearman rank-order correlation, depending on whether the data were normally or not normally distributed, respectively. Correlation between *Sphagnum* dry mass productivity and N/P ratio was analysed with a generalized additive model with integrated smoothness estimation (Wood 2006).

Data exploration, computation and figure design were done with the software R (R Development Core Team 2009) and the packages' 'nlme' (Pinheiro *et al.* 2009), 'mgcv' (Wood 2006) and 'stats' (R Development Core Team 2009).

RESULTS

Length increase and biomass productivity

Differences in productivity between *Sphagnum* species were significant (Fig. 1; Table 2). Most values of dry mass productivity ranged between 4 and 8 $t{\cdot}ha^{-1}{\cdot}year^{-1}$. Differences in length increase were also significant (Fig. 1; Table 2), with *S. fallax* growing fastest (max. $48{\cdot}cm{\cdot}year^{-1}$ and $10.8\ t{\cdot}ha^{-1}{\cdot}year^{-1}$) and *S. papillosum* slowest (max. $22\ cm{\cdot}year^{-1}$ and $7\ t\ ha^{-1}{\cdot}year^{-1}$).

Length increases and biomass productivity of all *Sphagnum* species were highest with the water table staying constantly 2 cm below the capitulum (treatment 'rising'; Table 2). Moss growth decreased with lower water tables, even if lowering was only periodic and only a few centimetres. As long as high water tables (2 cm below capitulum) occurred periodically, *S. palustre* grew better than with a water level not rising with moss growth (treatment 'static', *i.e.* water table sinking relative to the moss growth; $P = 0.027$). At the end of the experiment, the water level in the 'static' water level treatment was: *S. fallax* 1–9 cm (mean 5.6 cm), *S. fimbriatum* and *S. palustre* 4.0–8.5 cm (mean 6.3 cm) and *S. papillosum* 3.0–7.5 cm (mean 5.3) cm below the capitulum. The 'static' water level led to the lowest biomass and length values for all species, except biomass productivity of *S. fallax*, which was similar to that with a fluctuating water table (Fig. 1, Table 2).

Fertilization with P or with P and K had no effect on *Sphagnum* growth (Table 2).

Compactness

Compactness, *i.e.* dry mass per unit moss length, determines water-holding capacity and capillarity (cf. Hayward & Clymo 1982; Titus & Wagner 1984). Compactness was used as a proxy

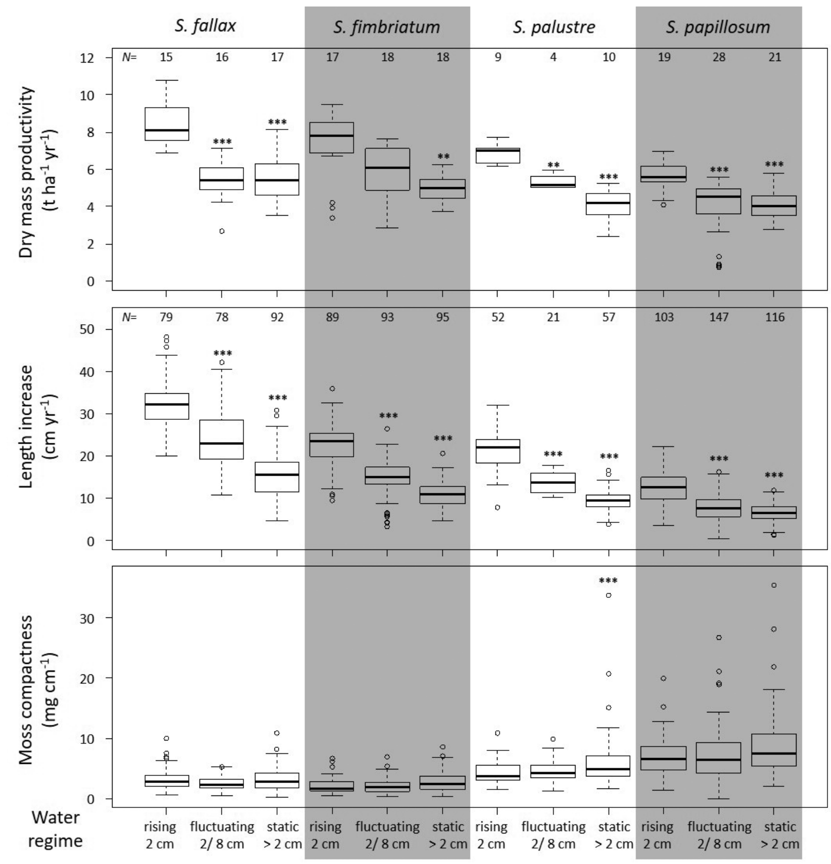

Fig. 1. Dry mass productivity (t·ha^{-1}·year^{-1}), length increase (cm·year^{-1}) and compactness (mg·cm^{-1}) of *Sphagnum fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* as a function of water regime (see text for details), with levels of significance for comparison to 'rising' water level within one species (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$) and total number of measurements (*N* compactness is similar to *N* length increase). The 'box and whisker' graphs show the median (bold line), the upper and lower quartiles (which include 50% of the data and create the box), whiskers representing the lowest value within 1.5 IQR (=interquartile range) of the lower quartile and the highest value within 1.5 IQR of the upper quartile, and outliers (o, *i.e.* values outside these ranges).

for the suitability of *Sphagnum* biomass as a raw material for growing media (cf. Jacobs *et al.* 2009).

Sphagnum papillosum and *S. palustre* were significantly more compact than *S. fallax* and *S. fimbriatum* (Fig. 1; Table 2). A 'static' water level resulted in more compact growth of all species, but this was only significant for *S. palustre* (Fig. 1; Table 2). Fertilization had no significant influence on the morphological characteristics of these peat mosses.

Nutrient concentrations in *Sphagnum* capitula

The N concentrations in all *Sphagnum* species were similar (mean N 14.4 mg·g^{-1} DW). Generally, biomass productivity decreased with increasing N concentration in the capitulum (Pearson correlation: $r = -0.23$, $n = 190$, $P \leq 0.01$). *Sphagnum papillosum* had the lowest biomass production with highest N values (max. 26.2 mg·g^{-1} DW).

The P concentrations ranged between 0.63 and 2.36 mg·g^{-1} DW (mean 1.3 mg·g^{-1} DW), K concentrations were between 2.9 and 11.9 mg·g^{-1} DW (mean 6.0 mg·g^{-1} DW). While lowest P concentrations were in *S. papillosum* (mean 1.1 mg·g^{-1} DW), the highest K concentrations were in *S. palustre* and *S. fallax* with 'rising' water level (Table 3). Fertilization did not influence N, P or K concentrations in the capitula nor the growth (Tables 2 and 3). Both P and K concentrations were lowest at the 'static' water level (Table 2). Biomass productivity decreased with increasing N/P values (Table 2; Fig. 3), with highest N/P ratio reached in *S. papillosum* (N/P = 7–24).

The N/K ratio ranged between 1.1 and 5.3 but had no relationship to biomass productivity. On the other hand, N/K values were significantly lowest in the 'rising' water table, except for *S. fallax* (Table 3).

Necrosis and algae

Algae (leading to dark green capitula) were recorded in 38% of the containers. Also, in 38% of the containers, more than 5% of the *Sphagnum* plants suffered from necrosis, probably because of fungal infection. With higher water tables there were fewer necrosis and algal infections (Fig. 2). Containers with *S. fimbriatum* experienced the highest level of necrosis per container (up to 92%), but proportionally more containers of *S. palustre* were affected. *Sphagum fallax* experienced the highest level of algal infestations (up to 55% of the moss; Fig. 2).

We excluded six containers with *S. fallax* from data analysis because these mosses collapsed and lost their structure, making further measurements impossible. The reasons for the die-off are unclear. There was no link between die-off and treatment.

Biomass productivity values as a function of cover of necrosis (% per container) were wide ranging (Fig. 4), but decreased

Table 2. Results of linear modelling of the response variables biomass productivity, length increase and compactness.

variable	factor	estimate of the slope	SE	*t*-value	*P*
Dry mass	*S. fimbriatum*[a]	−0.26	0.16	−1.65	0.099
productivity	*S. palustre*[a]	−0.96	0.21	−4.56	**<0.001**
n = 192, df 186	*S. papillosum*[a]	−1.24	0.16	−7.96	**<0.001**
	Water regime 'fluctuating'[b]	−1.51	0.33	−4.55	**<0.001**
	Water regime 'static'[b]	−1.71	0.33	−5.16	**<0.001**
Length	*S. fimbriatum*[a]	−7.64	0.38	−20.06	**<0.001**
increase	*S. palustre*[a]	−8.37	0.48	−17.26	**<0.001**
n = 1022, df: 1016	*S. papillosum*[a]	−14.56	0.36	−40.40	**<0.001**
	Water regime 'fluctuating'[b]	−7.26	1.02	−7.09	**<0.001**
	Water regime 'static'[b]	−11.21	1.02	−10.98	**<0.001**
Moss	*S. fimbriatum*[a]	−0.59	0.05	−5.05	**<0.001**
compactness	*S. palustre*[a]	2.08	0.06	8.91	**<0.001**
n = 1021, df: 1015	*S. papillosum*[a]	4.65	0.05	21.49	**<0.001**
	Water regime 'fluctuating'[b]	0.03	0.07	−0.50	0.615
	Water regime 'static'[b]	0.96	0.07	2.24	**<0.05**
Phosphorus	*S. fimbriatum*[a]	−0.04	0.04	−0.79	0.42
concentration	*S. palustre*[a]	−0.11	0.05	−1.89	0.06
in *Sphagnum*	*S. papillosum*[a]	−0.39	0.04	−9.03	**<0.001**
capitula	Water regime 'fluctuating'[b]	−0.05	0.11	−0.53	0.59
n = 192, df: 186	Water regime 'static'[b]	−0.27	0.11	−2.57	**<0.05**
Potassium	*S. fimbriatum*[a]	−0.53	0.23	−2.31	**<0.05**
concentration in	*S. palustre*[a]	1.20	0.29	−4.07	**<0.001**
Sphagnum	*S. papillosum*[a]	−0.15	0.22	−0.66	0.50
capitula	Water regime 'fluctuating'[b]	−1.71	0.54	−3.15	**<0.05**
n = 184, df: 178	Water regime 'static'[b]	−2.44	0.54	−4.49	**<0.001**

Generalized least squares fitted by REML, Correlation structure (boxes): biomass productivity Rho = 0.149; rate of increase in length Rho = 0.134; compactness Rho = 0.026; phosphorus concentration Rho = 0.359; potassium concentration Rho = 0.389.

df, degrees of freedom; *P*, level of significance; significant values are marked in bold.

[a]Compared with *S. fallax*.

[b]Compared with the water regime 'rising'.

with increasing percentage of necrosis, particularly in the 'rising' water table, were less distinct in the 'fluctuating' water table, whereas in the 'static' water level biomass productivity was independent of necrosis (Fig. 4). We observed an association between decreasing *Sphagnum* dry mass and an increase in algae (Spearman correlation: $r_s = -0.42$, $n = 191$, $P \leq 0.001$). Fertilization had no significant effect on necrosis or algae, but algal occurrence was higher in the 5P treatment. Furthermore, there was no relationship between nutrient concentration (N, P, K) in the moss capitula and percentage of necrosis or algae.

DISCUSSION

Water level

Our results show that constantly high water tables, *i.e.* continuously rising with the growing moss, lead to the highest growth rates for all four *Sphagnum* species. As soon as the relative water table falls by only a few centimetres, *Sphagnum* growth is significantly hampered. The 'static' water level, which sank relative to the up-growing moss, apparently hampered *Sphagnum* growth more than an alternating water level (treatment 'fluctuating'). This concurs with the results of Robroek *et al.* (2007), who found a lower capitulum water content and a consequent growth reduction in lawn species growing with a water table of 15 cm compared to a water table 5 cm below the top of the capitulum. In contrast, Breeuwer *et al.* (2009) found the productivity of the lawn species *Sphagnum magellanicum* increased with summer water table fluctuations of between 7 and 23 cm in comparison to somewhat wetter conditions (water table 3–15 cm below moss surface), and they attributed this to a competitive advantage of *S. magellanicum* in the drier conditions over the co-occurring *S. cuspidatum*. Without competition, growth of lawn species is generally highest at high water levels (Hayward & Clymo 1983; Grosvernier *et al.* 1997; Johnson 1998; Stokes *et al.* 1999).

Despite their more dense and compact growth form, our mosses obviously could not compensate for lower water levels through more effective capillarity (cf. Clymo & Hayward 1982). The water content of the capitulum is a good indicator of whether water supply is sufficient for optimal CO_2 assimilation (cf. Robroek *et al.* 2009). We did not measure capitulum water content in our study, but several other studies have found a rapid decrease when lowering water levels by only a few centimetres (Hayward & Clymo 1982; Robroek *et al.* 2009; Strack & Price 2009). On the other hand, even small amounts of precipitation (0.5–1.0 mm) may rewet the capitulum sufficiently to reduce the negative effect of low water levels (Robroek *et al.* 2009; Strack & Price 2009; Nijp *et al.* 2014; Krebs *et al.* 2016). As we sprinkled water on our mosses twice a day, with 0.5 mm per day, and each week replenished water loss in the boxes, capitulum water content will only have varied very slightly.

Table 3. Mean nitrogen, phosphorus and potassium concentrations ($mg{\cdot}g^{-1}$ dry mass ± SEM) and N/K quotient in capitula of different *Sphagnum* species as a function of water regime and fertilization level.

Sphagnum species	*S. fallax*	*S. fimbriatum*	*S. palustre*	*S. papillosum*
$mg\ N{\cdot}g^{-1}$ dry mass				
Water regime				
Rising	14.2 ± 0.07 (14)[a]	15.2 ± 0.10 (17)[a]	14.6 ± 0.11 (9)[a]	14.3 ± 0.06 (19)[a]
Fluctuating	16.7 ± 0.06 (15)[b]	16.3 ± 0.07 (18)[a]	13.2 ± 0.14 (4)[a]	15.3 ± 0.07 (27)[a]
Static	12.6 ± 0.07 (17)[a]	13.1 ± 0.07 (18)[a]	13.8 ± 0.15 (10)[a]	12.7 ± 0.04 (21)[a]
Fertilization level				
C	14.7 ± 0.08 (14)[a]	16.3 ± 0.07 (18)[a]	14.6 ± 0.26 (6)[a]	14.1 ± 0.06 (23)[a]
5P	14.6 ± 0.11 (15)[a]	15.0 ± 0.09 (18)[a]	14.5 ± 0.13 (6)[a]	14.6 ± 0.09 (20)[a]
2P2K	14.0 ± 0.07 (17)[a]	13.3 ± 0.07 (17)[a]	13.4 ± 0.11 (11)[a]	14.0 ± 0.06 (24)[a]
$mg\ P{\cdot}g^{-1}$ dry mass				
Water regime				
Rising	1.6 ± 0.01 (14)[a]	1.5 ± 0.01 (17)[a]	1.7 ± 0.01 (9)[b]	1.2 ± 0.01 (19)[a]
Fluctuating	1.6 ± 0.01 (15)[a]	1.6 ± 0.01 (18)[a]	1.2 ± 0.02 (4)[a]	1.1 ± 0.00 (27)[a]
Static	1.3 ± 0.01 (17)[a]	1.3 ± 0.01 (18)[a]	1.2 ± 0.01 (10)[a]	1.0 ± 0.01 (21)[a]
Fertilization level				
C	1.5 ± 0.01 (14)[a]	1.5 ± 0.01 (18)[a]	1.3 ± 0.03 (6)[a]	1.1 ± 0.00 (23)[a]
5P	1.6 ± 0.01 (15)[a]	1.6 ± 0.01 (18)[a]	1.6 ± 0.03 (6)[a]	1.2 ± 0.01 (20)[a]
2P2K	1.4 ± 0.01 (17)[a]	1.3 ± 0.01 (17)[a]	1.3 ± 0.01 (11)[a]	1.0 ± 0.00 (24)[a]
$mg\ K{\cdot}g^{-1}$ dry mass				
Water regime				
Rising	6.0 ± 0.02 (14)[a]	6.7 ± 0.03 (17)[b]	9.6 ± 0.07 (9)[b]	8.1 ± 0.05 (19)[b]
Fluctuating	6.3 ± 0.02 (15)[a]	5.3 ± 0.03 (17)[a]	6.1 ± 0.02 (4)[ab]	5.4 ± 0.02 (27)[a]
Static	5.8 ± 0.05 (12)[a]	4.7 ± 0.04 (18)[a]	5.4 ± 0.06 (10)[a]	4.7 ± 0.02 (21)[a]
Fertilization level				
C	5.9 ± 0.03 (14)[a]	5.9 ± 0.04 (17)[a]	6.6 ± 0.24 (6)[a]	6.3 ± 0.06 (23)[a]
5P	6.2 ± 0.03 (10)[a]	5.2 ± 0.04 (18)[a]	7.7 ± 0.21 (6)[a]	5.7 ± 0.04 (20)[a]
2P2K	6.1 ± 0.03 (17)[a]	5.6 ± 0.04 (17)[a]	7.2 ± 0.08 (11)[a]	5.7 ± 0.03 (24)[a]
N/K quotient				
Water regime				
Rising	2.4 ± 0.01 (14)[ab]	2.3 ± 0.01 (17)[a]	1.5 ± 0.01 (9)[a]	1.8 ± 0.01 (19)[a]
Fluctuating	2.7 ± 0.01 (15)[b]	3.1 ± 0.01 (17)[b]	2.2 ± 0.03 (4)[ab]	2.9 ± 0.01 (27)[b]
Static	2.2 ± 0.02 (12)[a]	3.0 ± 0.02 (18)[b]	2.6 ± 0.04 (10)[b]	2.8 ± 0.01 (21)[b]
Fertilization level				
C	2.5 ± 0.01 (14)[a]	2.9 ± 0.02 (17)[a]	2.4 ± 0.06 (6)[a]	2.6 ± 0.02 (23)[a]
5P	2.5 ± 0.02 (10)[a]	3.0 ± 0.02 (18)[a]	2.1 ± 0.08 (6)[a]	2.7 ± 0.02 (20)[a]
2P2K	2.3 ± 0.01 (17)[a]	2.5 ± 0.02 (17)[a]	2.0 ± 0.02 (11)[a]	2.5 ± 0.01 (24)[a]

Number of replicates per water level or fertilization treatment of each species are in brackets.
Different letters indicate significant differences within single treatments (water regime, fertilization level) for each single species. $P \leq 0.05$.

A high water level not only leads to optimal water supply to the capitulum, but also to an improved nutrient supply (cf. Clymo & Hayward 1982), higher vitality (indicated by less necrosis and algal infestation) and a looser growth form, allowing light to penetrate deeper into the *Sphagnum* lawn, resulting in an increased active assimilation area (Sliva 1997; cf. Robroek *et al.* 2009). Continuous optimal growth requires a high water table that continuously rises with the growing moss. A water drawdown would result in a growth reduction or – in the case of low stem density – even death of the peat mosses (Fritz *et al.* 2012).

Fertilization

Since *Sphagnum* growth is not N-limited at atmospheric deposition rates exceeding 18 $kg{\cdot}ha^{-1}{\cdot}year^{-1}$ (Malmer 1990; Aerts *et al.* 1992; Verhoeven *et al.* 1996 Lamers *et al.* 2000) and our control (38 $kg{\cdot}ha^{-1}{\cdot}year^{-1}$; Gauger *et al.* 2002; Table 1) far exceeded this value, we refrained from testing additional N fertilization. The mean *Sphagnum* tissue N concentration of 14.4 $mg{\cdot}g^{-1}$ DW found at the end of our experiment, indeed confirms the prevalence of N-saturated conditions (Lamers *et al.* 2000).

Over the entire dataset there was a negative correlation between N tissue concentration and biomass productivity, but this effect was most distinct in *S. papillosum* ($r = -0.53$, $P \leq 0.01$). Its growth strongly decreased at capitulum N concentrations >20 (max. 26.2) $mg{\cdot}g^{-1}$ DW, resulting in the lowest biomass productivity values measured in this study. For the other species, N tissue concentration had no effect on growth (cf. Limpens & Berendse 2003). Berendse *et al.* (2001) proposed a maximum N concentration in *Sphagnum* tissues of 20 $mg{\cdot}g^{-1}$ DW, which was exceeded in both the study of Breeuwer *et al.* (2009) and in our study. According to van der Heijden *et al.* (2000), a capitulum N concentration in *S. fallax* of 15 $mg{\cdot}g^{-1}$ DW indicates N pollution stress in bogs. However, our study shows that even a maximum N value of 20.5 $mg{\cdot}g^{-1}$ DW has no negative effect on growth of *S. fallax*.

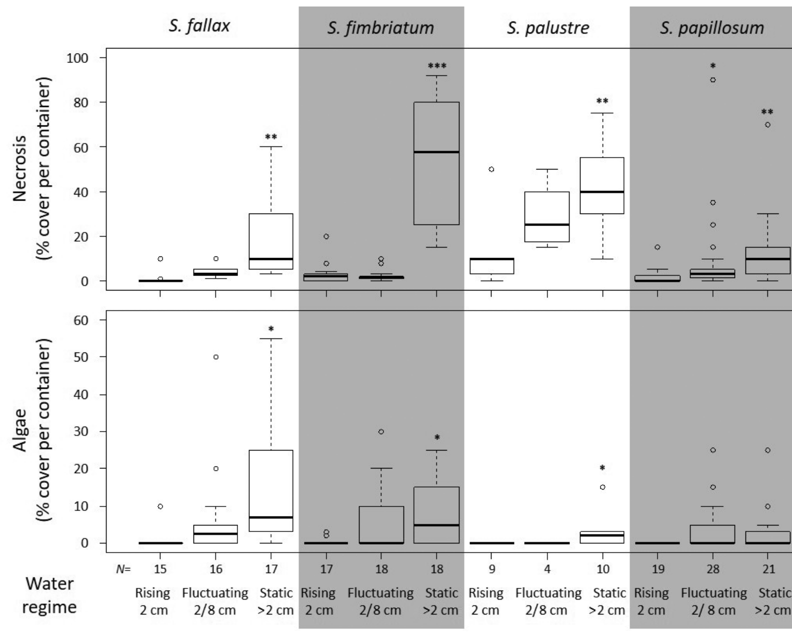

Fig. 2. Cover of necrosis and algae (% per container) on *Sphagnum fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* as a function of water regime (see text for details and caption of Fig. 1 for further explanation).

Similarly, Granath *et al.* (2009) found no detrimental effects on the photosynthetic apparatus at N tissue concentrations up to 20 mg·g^{-1} DW in *S. balticum* (a species of the *Cuspidata* section, like *S. fallax*). Bragazza *et al.* (2005) suggested that *Sphagnum* plants in polluted regions have a metabolic adaptation (with lower rates of N absorption) to high N supply, which was confirmed by Fritz *et al.* (2014). This ability seems, however, to be differently developed between species, as also suggested in Fig. 3. In our study (as in Temmink *et al.* 2017 with N concentrations >18 mg·g^{-1} DM), a toxic effect (growth reduction) of a high N tissue concentration >20 mg·g^{-1} DM was observed only in *S. papillosum*. Chiwa *et al.* (2016) found that an *S. capillifolium* lawn can filter wet N deposition of up to 32 kg N·ha^{-1}·year^{-1} for least a decade, leading to N concentrations in the capitula of around 14 mg·g^{-1} DM.

In our study, P fertilization had no significant effect on *Sphagnum* growth, indicating the absence of P limitation. This is corroborated by the failing correlation between P concentration in the capitula (mean 1.3 up to 2.4 mg·g^{-1} DW) and fertilization (cf. Li *et al.* 1993, Table 2), as well as N/P ratio <30 (cf. Bragazza *et al.* 2004). In other studies, with low P concentrations in the pore water, similarly high P concentrations in the mosses were found only after P fertilization (Chiwa *et al*. 2018, Limpens *et al.* 2003b; Limpens *et al.* 2004; Limpens & Heijmans 2008; Fritz *et al.* 2012). As in our study, *Sphagnum* did not respond significantly to additional P (Li *et al.* 1993; Limpens *et al.* 2004) at sites with similar water P concentrations as in our experiment (0.23 mg·l^{-1}) and in natural bogs in Lower Saxony (Bertram 1988; Lütt 1992). Only at 'rising' water level (remaining 2 cm below the capitulum) did P fertilization (5P) slightly (but not significantly) increased growth of *Sphagnum palustre*, *S. fimbriatum* and *S. fallax* in our study. The P concentrations in the culture medium were similar at the end of the experiment irrespective of the treatment (see Table 1). This can be explained by P fixation into forms that are unavailable to the plants, as only orthophosphate was determined in the solutions.

The N/P ratios in the *Sphagnum* capitula at the end of the experiment ranged between 7.2 and 23.6, with a mean value of 11.3, indicating optimal nutrient supply (cf. Aerts *et al.* 1992). With increasing N/P ratio, biomass productivity significantly decreased (Fig. 3). Nevertheless, no P

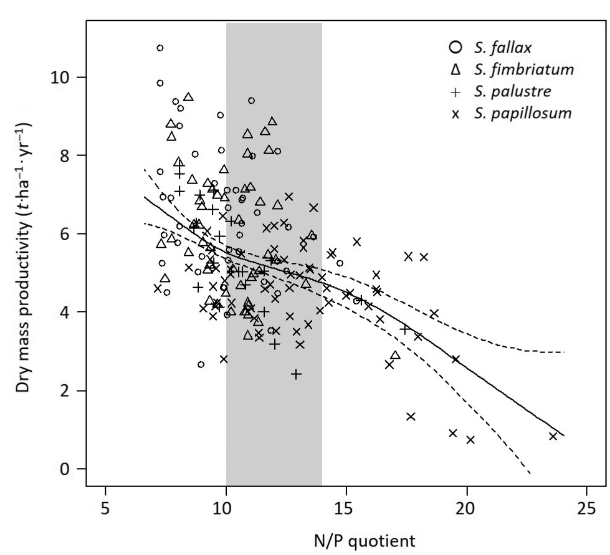

Fig. 3. Correlation between dry mass productivity (t·ha^{-1}·year^{-1}) and N/P quotient for different *Sphagnum* species; grey: N/P quotient with optimal *Sphagnum* growth (after Aerts *et al.* 1992). Model results (generalized additive model), $N = 191$: estimated degrees of freedom for the smoother = 3.23, explained deviance (R^2) = 30.5%, variance of the residuals = 1.25, $P < 0.001$. The curve is estimated using LOESS smoother and point-wise 95% confidence bands (dotted lines) (Zuur *et al.* 2009).

limitation can be found in our study (see above). According to Aerts *et al.* (1992), N/P ratios below ten indicate N limitation, which would apply to about 40% of our values. As all mosses received the same (high) N amount, P fertilization had no influence, and *Sphagnum* species did not differ in N/P ratios, the suggestion of N limitation is implausible.

Compared to studies in natural habitats with 2.5–5.2 mg $K \cdot g^{-1}$ DW (Bragazza *et al.* 2004; Fritz *et al.* 2012), the K concentration in the capitula in our study (mean 4.7–9.6 $g \cdot g^{-1}$ DW; Table 3) was higher, but similar to a Sphagnum farming site (irrigated with eutrophic water) with 4.5–10.3 g $K \cdot g^{-1}$ DW (Temmink *et al.* 2017). Bragazza *et al.* (2004) suggest K limitation at N/K ratios above 3.3, which was only found in a single case in our study (N/K 1.1–5.3, mean 2.6). However, K fertilization did not lead to either significantly higher biomass productivity nor higher K concentrations or lower N/K ratios in the moss capitula. Similarly, the K concentration in the culture medium at the end of the experiment was independent of the fertilization treatment. These facts indicate K-saturated conditions.

Higher N, P and K concentrations in the capitula at constantly high water levels ('rising' treatment) may result from increased nutrient uptake by the larger moss surface with permanent water contact (cf. Clymo & Hayward 1982). The values for N, P and K are known to be more concentrated in the *Sphagnum* capitula (Malmer 1988), but under nutrient-saturated conditions their accumulation in stems cannot be ruled out (cf. Chiwa *et al.* 2018); unfortunately, this was not measured in our study. Li *et al.* (1993), however, we did not find changes in P concentration either in the capitula (0–1 cm) or in the stem (1–4 cm) of *S. papillosum* at different P fertilization levels. Nevertheless, nutrients will have been removed from the rather closed box system in our study through the cutting and removal of the basal parts (see Methods).

Both the N/P and N/K ratios in our study indicate that conclusions from studies of natural systems cannot simply be transferred to systems with high nutrient loads and high nutrient concentrations in the moss tissue.

We used the culture medium of Rudolph *et al.* (1988), which is optimized for *Sphagnum* growth and was apparently sufficient and had a favourable stoichiometry, thus no stimulating effect of additional P and K fertilization on *Sphagnum* growth was found. In practice, even larger amounts of nutrients, in particular N, P and K, are supplied to the moss layer when the irrigation water of the Sphagnum farming site is obtained from the surrounding fertilized agricultural areas (Krebs *et al.* 2012; Temmink *et al.* 2017). Nutrient-rich conditions (as in our study) are representative for extensive areas of Western and Central Europe. Our study demonstrates that *Sphagnum* grows well under nutrient-rich conditions, as long as an optimal water supply is guaranteed. These results might also be useful for bog restorations. The long-term effects of such site conditions, *e.g.* on *Sphagnum* growth and species composition, still have to be investigated.

In contrast to the results of Fritz *et al.* (2012) for a nutrient-poor site, we did not find changes in *Sphagnum* morphology as a result of fertilization since N, P and K supply in our study were apparently sufficient for *Sphagnum* growth, including in the control.

Sphagnum species

Of the four studied *Sphagnum* species (*S. palustre*, *S. papillosum*, *S. fimbriatum*, *S. fallax*), *S. fallax* had the highest productivity, which corresponds to results from a global meta-analysis (Gunnarsson 2005). Both high water level and an adequate nutrient supply promote growth of all four tested species, but the minerotrophic species *S. fallax* profits most (cf. Lee & Studholme 1992; Twenhöven 1992; Limpens *et al.* 2003b). On the other hand, *S. fallax* decomposes faster than *S. papillosum* (Limpens & Berendse 2003) and has a lower water-holding capacity (Overbeck & Happach 1957), which might make this species less suitable for use in horticultural substrates, at least for some applications (Emmel & Kennett 2007).

Necrosis and algae

Necrotic diseases of peat mosses are often caused by pathogenic fungi, such as *Sphagnurus paluster* (syn. *Lyophyllum palustris*, *Tephrocybe palustris*) (Redhead 1981; Untiedt & Müller 1985; Limpens *et al.* 2003a); this parasitic basidiomycete is only found on *Sphagnum* (Untiedt & Müller 1985). Although no molecular identification of the fungal mycelium was conducted, the typical pattern of damage and sporocarps in our study indicate the occurrence of *Sphagnurus paluster*.

In contrast to Limpens *et al.* (2003a), our study found a negative effect of infection on biomass production of *Sphagnum* (Fig. 4). This contradiction may be explained by the increased fungal biomass being included in the biomass values of Limpens *et al.* (2003a) and by the intensity of necrosis being lower at high water levels (Fig. 2). Similarly, in contrast to Limpens *et al.* (2003a), we did not find any relationship between necrosis or algae and fertilization treatment or N/P ratio. The N/P ratio in our study, however, did not exceed 25, *i.e.*

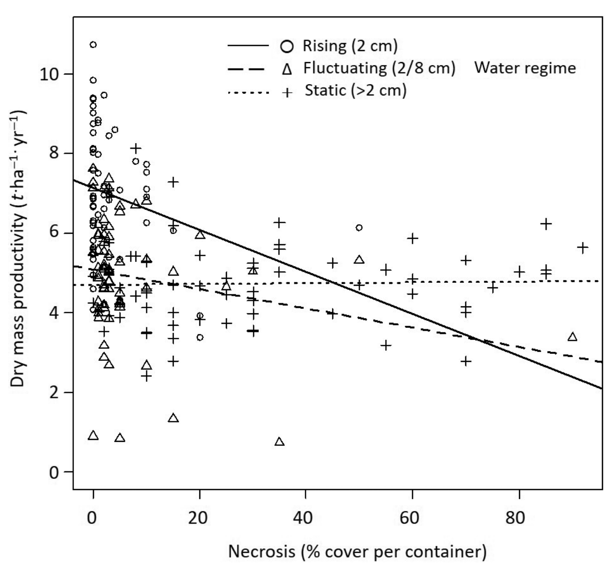

Fig. 4. Relation between dry mass productivity ($t \cdot ha^{-1} \cdot year^{-1}$) and necrosis (% cover per container) for different water regimes with regression lines, including all species. Overall model with dry mass productivity (dependent variable) and necrosis (explanatory variable) and its interaction with the different water regime model results (linear mixed effect model), $N = 192$: degrees of freedom = 188, F-value = 3.58, $P < 0.05$, Rho (induced correlation structure of containers of the same moss species within a box) = 0.53.

remained in the range where Limpens *et al.* (2003a) also failed to see any correlation. Our results indicate that *Sphagnum* vitality and growth rate are stimulated by high water levels, where they are less vulnerable to fungal or algal infection despite high nutrient loads.

While *Sphagnurus paluster* infects only small areas in nature, it often kills most peat mosses in glasshouses where there is a favourable environment for rapid fungal dispersal (Untiedt & Müller 1985; Landry *et al.* 2011). Since *Sphagnum* farming sites on rewetted bogs are also artificial systems, the risk potential for diseases from fungi and algae must be assessed. Effective measures to limit *Sphagnurus paluster* without affecting *Sphagnum* are the fungicide Myclobutanil (Landry *et al.* 2011) or *Trichoderma virens* as an antagonist (Irrgang *et al.* 2012), which have only been tested and might only be applicable in glasshouse cultivation.

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