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Sphagnum farming in a eutrophic world: The importance of optimal nutrient stoichiometry

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ABSTRACT

Large areas of peatlands have worldwide been drained to facilitate agriculture, which has adverse effects on the environment and the global climate. Agriculture on rewetted peatlands (paludiculture) provides a sustainable alternative to drainage-based agriculture. One form of paludiculture is the cultivation of *Sphagnum* moss, which can be used as a raw material for horticultural growing media. Under natural conditions, most *Sphagnum* mosses eligible for paludiculture typically predominate only in nutrient-poor wetland habitats. It is unknown, however, how the prevailing high nutrient levels in rewetted agricultural peatlands interfere with optimal *Sphagnum* production.

We therefore studied the effect of enriched nutrient conditions remaining even after top soil removal and further caused by external supply of nutrient-rich irrigation water and (generally) high inputs of atmospheric nitrogen (N) to habitat biogeochemistry, biomass production and nutrient stoichiometry of introduced *Sphagnum palustre* and *S. papillosum* in a rewetted peatland, which was formerly in intensive agricultural use.

Airborne N was responsible for the major supply of N. Phosphorus (P) and potassium (K) were mainly supplied by irrigation water. The prevailing high nutrient levels (P and K) are a result of nutrient-rich irrigation water from the surroundings. Peat porewater (10 cm below peatmass surface) CO₂ concentrations were high, bicarbonate concentrations low, and the pH was around 4.2.

Provided that moisture supply is sufficient and dominance of fast-growing, larger graminoids suppressed (in order to avoid outshading of *Sphagnum* mosses), strikingly very high biomass yields of 6.7 and 6.5 t DW ha⁻¹ yr⁻¹ (*S. palustre* and *S. papillosum* [including *S. fallax* biomass], respectively) were obtained despite high N supply and biomass N concentrations. Despite high P and K supply and uptake, N:P and N:K ratios in the *Sphagnum* capitula were still low. *Sphagnum* mosses achieved high nutrient sequestration rates of 34 kg N, 17 kg K and 4 kg P ha⁻¹ yr⁻¹ from May 2013 to May 2014, which shows that the site acted as an active nutrient sink. Nutrient management still needs further improvement to reduce the competitive advantage of fast growing peatmoss species (cf. *S. fallax*) at the expense of slower growing but preferred peatmosses as horticultural substrate (*S. palustre* and *S. papillosum*) to optimize the quality of biomass yields.

In conclusion, *Sphagnum* farming is well able to thrive under high N input provided that there is a simultaneous high input of P and K from irrigation water, which facilitates high production rates. Due to the lack of suitable, nutrient poor sites, it seems to be useful to remove the topsoil (mainly P removal) prior to start growing *Sphagnum* mosses. In addition, bicarbonate concentrations have to stay sufficiently low to ensure a low pH, CO₂ supply from the peat soil should be sufficiently high to prevent C limitation, and graminoids should be mown regularly.

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1. Introduction

Worldwide, large areas of peatlands have been drained to facilitate agriculture, forestry and peat extraction (Grootjans et al., 2006; Zedler and Kercher, 2005). These activities destroy the biodiversity, carbon storage capacity and hydrological regulation function of fens and bogs (Hassan et al., 2005; Lamers et al., 2015; Verhagen et al., 2009; Verhoeven and Setter, 2010). Large-scale drainage of peatlands globally results in carbon dioxide (CO₂) and nitrous oxide (N₂O) emissions of more than 2 Gt CO₂-eq yr⁻¹ (Joosten and Couwenberg, 2009). Apart from increased CO₂ and N₂O emissions, continuation of peatland drainage to sustain agricultural activities leads to severe land subsidence, deterioration of surface and groundwater quality and higher flood risk (Dawson et al., 2010; Lamers et al., 2015; Schothorst, 1977; Verhoeven and Setter, 2010). Currently, agricultural yields on drained peatlands are decreasing and it is becoming more difficult to cover the ever-increasing drainage costs, emphasizing the urgent need for alternative land use for these agriculturally-used peatlands (Joosten and Clarke 2002; Kowatch 2007; Wichtmann and Joosten, 2007).

A solution to these problems would be paludiculture. Paludiculture (from Latin “palus” = “mire, swamp”) is agriculture on wet or rewetted peatlands, with cultivation of wetland species such as *Phragmites australis*, *Typha* spp. or *Sphagnum* moss spp., in a way that preserves the peat body (Joosten et al., 2012). The benefits of paludiculture as opposed to conventional drainage-based land use on peat soils are considerable (cf. Joosten et al., 2012). The high water table associated with paludiculture stops peat oxidation and land subsidence, because less peat is aerated, which results in much lower peat decomposition rates (Dawson et al., 2010; Renger et al., 2002). Nutrient discharge into groundwater and surface water is reduced due to lower mineralization rates. Furthermore, ecosystem services including water purification and water retention in peatlands are restored (Joosten et al., 2012).

In this study we focus on the paludiculture crop *Sphagnum* (peatmoss) as a renewable source of raw material for horticultural growing media, which provides a sustainable alternative to unsustainably extracted *Sphagnum* peat. In pristine bogs and poor fens, *Sphagnum*, a genus of bryophytes, is very common and is often the dominant vegetation and peat forming species (Clymo et al., 1984). Like vascular plants, *Sphagnum* productivity is related to pH, water and nutrient availability. However, *Sphagnum* differs by its adaptation to oligotrophic, acidic and wet environments (Clymo, 1964). As a genuine ecosystem engineer, it keeps its environment oligotrophic by efficient nutrient sequestration and very low mineralization rates, and acidic by proton exchange and the production of organic acids. *Sphagnum* strongly limits nutrient mineralization by its low decomposability and the acidic anaerobic environment created (Aerts et al., 1992; Clymo 1963, 1964; Halsey et al., 2000; Lamers et al., 1999; Limpens et al., 2004; Scheffer et al., 2001). *Sphagnum* mosses do not have roots and take up nutrients efficiently via their leaves and stem (Fritz et al., 2014).

Low nutrient concentrations, however, also limit primary production of *Sphagnum*, like it does for any other plant species. In general, the limiting nutrient in pristine bogs appears to be nitrogen (N) (Bragazza et al., 2005, 2004; Lamers et al., 2000), or a combination of N and phosphorus (P) (Fritz et al., 2012). Increases in N supply by increased anthropogenic N deposition from the atmosphere can at first be sequestered by *Sphagnum* species and used for increased growth (Chiwa et al., 2016; Lamers et al., 2000). N concentrations in the *Sphagnum* capitula may reflect the N-availability from rain and surface water supply (Novak et al., 2015) and from N₂ fixation (Lamers et al., 2000). Depending on whether N is limiting biomass production, N concentrations may be increased by higher N availability (luxury consumption, i.e. when other factors are limiting growth), or remain more or less similar (if N is limit-

ing or co-limiting). By rapidly sequestering N, *Sphagnum* acts as a nutrient filter, decreasing nutrient (pore)water concentrations in the rhizosphere of vascular plants (Chiwa et al., 2016; Fritz et al., 2014; Lamers et al., 2000).

However, when N input becomes too high, P will become limiting for *Sphagnum* growth and excess N cannot be allocated to increased growth (Bragazza et al., 2004; Limpens et al., 2011). This may result in internal ammonium (NH₄⁺) detoxification evident as N-rich amino acid accumulation and even NH₄⁺ poisoning (Bragazza et al., 2012, 2006; Breeuwer et al., 2009; Limpens and Berendse, 2003). Currently, it is debated whether a balanced nutrient stoichiometry can alleviate negative effects of N and if *Sphagnum* can consequently sustain its growth rate under high but balanced nutrient loadings (Bragazza et al., 2004; Jirousek et al., 2011; Limpens et al., 2011).

In this study the peatmoss species *Sphagnum palustre* L., *S. papillosum* Lindb. and *S. fallax* Klinggr. were used (taxonomy follows Michaelis, 2011) as they are common and widespread species with different ecological demands. While the first two species belong to the section *Sphagnum*, *S. fallax* is included in the section *Cuspidata* (Daniels and Eddy, 1985; Michaelis, 2011). Natural habitats for these species are described after Daniels and Eddy (1985) and Frahm and Frey (2003).

S. palustre grows in mesotrophic to eutrophic peatland habitats like in wet fen woodlands, and under more open situations in ditches, along streams and at lake margins. It forms loose carpets or tussocks, is shade tolerant and absent from calcareous and strongly acid locations. *S. papillosum* is mainly found in oligotrophic, but also mesotrophic open acid peatlands. It grows at low hummocks to extensive carpets and lawns and is less tolerant of base-rich conditions than *S. palustre*. *S. fallax* occurs in oligotrophic to mesotrophic, but also minerotrophic peatlands in open to shaded habitats. It forms wide lawns and is tolerant of a fairly wide range of hydrological and chemical conditions.

Here we present a study on *Sphagnum* cultivated in a managed paludiculture field site on a rewetted former agricultural peatland. The goal of this *Sphagnum* biomass production is to provide a sustainable alternative to the ongoing extraction of non-renewable white peat (slightly humified *Sphagnum* peat) that is presently being used as a raw material for horticultural growing media (Emmel, 2008; Gaudig et al., 2014; Gaudig and Joosten, 2002; Reinikainen et al., 2012; Wichmann et al., 2014). We hypothesized that (1) the high N supply at this location limits *Sphagnum* biomass production, (2) *Sphagnum* species differ in their response to nutrient availability and stoichiometry, and (3) *Sphagnum* production rates, and N and P accumulation rates in the peatmoss biomass are dependent on site management.

2. Materials and methods

2.1. Study site

The study site is a former bog, situated near Rastede, North-Western Germany (N 53°26'32.4; E 08°26'84.3), with a peat layer of around 2–2.5 m depth that has been drained and used as intensively fertilized agricultural grassland since the 1950s. In March 2011, the 4 ha study field (which is still surrounded by agricultural grasslands on peat soil) was established (Gaudig et al., 2014). The upper 30–50 cm of degraded peat was removed to expose the underlying hardly decomposed and nutrient poor *Sphagnum* peat (98% organic matter content), which has a high water holding capacity and hydrological conductivity. This resulted in an area with maximum height differences of 9.8 cm.

Two *Sphagnum* species were introduced: *S. palustre* and *S. papillosum*. *S. palustre* or *S. papillosum* donor material consisted of 16% or <1% *S. fallax* (based on volume), respectively. Peatmoss fragments

manually collected from natural sites were spread on the peat in spring 2011 and covered with 300 g m⁻² straw mulch (Gaudig et al., 2014). In May 2014, the vegetation was dominated by *Sphagnum* mosses. *Sphagnum* cover consisted of *S. papillosum* (71%), *S. palustre* (42%) and *S. fallax* (29 and 58% in the *S. papillosum* and *S. palustre* variant, respectively) with a mean lawn thickness (newly formed *Sphagnum* layer) of 10.8 cm. In lower quantities *S. cuspidatum* and *S. fimbriatum* were found. Vascular plant cover (<25%) is dominated by the rush *Juncus effusus*, accompanied by sparse other vascular plant species such as *Drosera intermedia*, *D. rotundifolia*, *Vaccinium oxycoccos* and *Rhynchospora alba* (Gaudig and Krebs, 2016).

The study site contains three production strips of 10 × 270 m, separated by ditches (width 0.5 m, depth 0.5 m) to control the water table, and is surrounded by levees (Fig. 1). Water tables were kept closely below the peatmoss capitula (the top ~5 cm and physiologically most active part of peatmoss plants) by active pumping, whereas a levelled outlet prevented flooding of the peatmoss capitula (Fig. 1). Water tables were similar and independent of the distance to the ditch. The canal (“Schanze”), from which the water originates receives drainage water from surrounding agricultural fields, is slightly acidic (pH 5.6), low in alkalinity (0.35 meq L⁻¹) and can be classified as eutrophic. Based on nutrients concentrations in the canal (12.9–38.7 μmol P L⁻¹, 168.8 μmol KL⁻¹, and 107.1–328.6 μmol NL⁻¹) of the irrigation water (1620 m⁻³ ha⁻¹ in 2014) the estimated nutrient load via irrigation was 0.7–2.4 kg P, 13 kg K, and 3–9 kg N ha⁻¹ yr⁻¹. During the growing season vascular plants were mown twice a month without removing the biomass.

2.2. Porewater and surface water analyses

In March (rainwater surplus) and November 2014 (rainwater deficit – irrigation water supply) porewater samples (2.5 cm below peatmoss surface) were collected along six transects (Fig. 1) ($n=6$). Additionally, in March 2014 at 0.5 and 1 m (10 cm below peatmoss surface) and 2.5 and 5 m distance from the ditch (10, 27.5, 52.5 and 102.5 cm below peatmoss surface) pore water samples were taken ($n=6$). In March and November 2014 surface water samples were taken from the canal, the water inlet, the water outlet and the ditch at the beginning of each transect. Due to logistical constraints no samples were taken during the growing season of 2014. To extract and filter the water, vacuum syringes attached to teflon soil pore water samplers or ceramic cup samplers were used (Rhizon SMS 10 cm; Rhizosphere Research Products, Wageningen, The Netherlands; Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands).

The pH, alkalinity and total inorganic carbon (TIC) were determined within one day after sampling. The pH and alkalinity (cf. Roelofs, 1983) were measured with a handheld meter (pH 330i, pH-Electrode SenTix 41, Wissenschaftlich-Technische Werkstätten GmbH & Co.KG, Germany). TIC was measured using an infrared carbon analyser (IRGA; ABB Analytical, Frankfurt, Germany), after which bicarbonate (HCO₃⁻) and CO₂ were calculated based on the pH equilibrium. Pore water gas samples were analysed for methane (CH₄) with a gas chromatograph (5890 GC, Hewlett Packard, Wilmington, DE, U.S.A.).

A 10 mL subsample of each sample was conserved by adding 0.1 mL of nitric acid (HNO₃) (65%) and stored at 4 °C until P and calcium (Ca) analysis by inductively coupled plasma emission spectrophotometry (ICP-OES; model IRIS Intrepid II XDL, Thermo Fisher Scientific, Franklin, USA). The rest of each sample was stored in polyethylene bottles at -20 °C prior to analyses. Nitrate (NO₃⁻), ammonium (NH₄⁺), phosphate (PO₄³⁻) and chloride (Cl) were measured colorimetrically with an auto analyser (Auto Analyser III, Bran and Luebbe GmbH, Norderstedt, Germany), as in Geurts et al. (2008). Potassium (K) was determined by flame photometry (FLM3 Flame Photometer, Radiometer, Copenhagen, Denmark).

2.3. Soil analyses

In March 2014 peat soil samples were collected along the 6 transects (Fig. 1). Samples were taken at each transect 5 m from the ditch at 0–10 cm, 10–30 cm and 30–50 cm below the newly formed moss layer ($n=6$ per depth). At transect 2 (T₂) and 4 (T₄) additional soil samples were taken at similar depths at 2.5 m from the ditch ($n=2$ per depth). For the top 10 cm a root auger (15 cm long, Ø 8 cm), and for other depths a half-cylinder chamber peat corer (50 cm long, Ø 5 cm) was used to collect soil samples of known volumes. Subsamples were dried at 70 °C for 48 h to determine soil dry weight and to calculate bulk density.

Dried soil samples were ground for 4 min at 400 RPM to ensure homogeneity (Fritsch Pulverisette Ball Mill, Fritsch GmbH, Idar-Oberstein, Germany). Bio-available P (Olsen-P extract) was determined by incubating 3 g dried soil in 60 mL 0.5 M sodium carbonate (NaHCO₃) for 30 min at 105 RPM (Henriksen 1965) and bio-available NH₄⁺ and NO₃⁻ were determined by incubating 17.5 g fresh soil in 50 mL of 0.2 M sodium chloride (NaCl) for 120 min at 105 RPM after which the extract was collected under vacuum conditions with teflon pore water samplers. Total-P and K soil contents were determined by digesting 200 mg soil in 4 mL HNO₃ (65%) and 1 mL H₂O₂ (35%) in Teflon vessels, heated in an Ethos D microwave (Milestone, Sorisole Lombardy, Italy). Samples were measured using ICP-OES analyses (Olsen-P, Total-P and K) and the Auto Analyzer system (NH₄⁺ and NO₃⁻).

2.4. Plant biomass analyses

In May 2013 five single *Sphagnum* shoots were marked in plots (size: 15 × 15 cm, *S. palustre* variant $n=7$; *S. papillosum* variant $n=3$) with a nylon cable tie (width 2 mm, length 100 mm) directly below the moss capitulum (0–1 cm, shoot apex with branches not fully developed, cf. Clymo, 1973). One year later in May 2014 all above-ground biomass, grown since installation, was harvested with scissors at 24 plots of the *S. palustre* variant and 14 plots of the *S. papillosum* variant including the plots with the marked mosses. After the harvest the capitula were cut and entire samples with marked peatmosses were additionally divided into the upper part above (=one-year biomass yield) and the lower part below the cable tie (=residual biomass of previous years). All samples were sorted into *Sphagnum* species, other mosses, vascular plants, and litter and subsequently dried to constant weight (80 °C for 48 h) (Hendry and Grime, 1993). Most samples included next to *S. palustre* or *S. papillosum* also *S. fallax*.

Additionally to the capitula from May 2014 from all plots the capitula from May 2013 of 18 plots (15 × 15 cm) for *S. palustre* variant and 10 plots for *S. papillosum* variant were harvested. The differences in the nutrient amount of capitula layer in 2013 and 2014 as well as the nutrient accumulation in the one-year biomass yields (2013–2014, $n=10$) were used to calculate annual nutrient sequestration. Total accumulated biomass (2011–2014) including capitula was determined to investigate the relation of biomass growth and nutrient supply with regard to the distance to the irrigation inlet and the ditches and also to peat surface height.

All plots were distributed randomly at the entire three production stripes, thus having different distances to the irrigation inlet and to the ditches to allow the gradient analyses.

Sphagnum capitula of the three *Sphagnum* species of the harvested plots from 2013 and 2014, and also the annual biomass yield (2013–2014) were used for elemental analysis. Dried *Sphagnum* was ground to ensure sample homogeneity (18,000 RPM, 0.2 mm screen) (Fritsch GmbH, Idar-Oberstein, Germany). Nutrient content was measured in the living capitula where major nutrients (N, P and K) are concentrated (Fritz et al., 2012; Malmer, 1988), and also in the annual biomass yield (2013–2014). Total-P and K contents

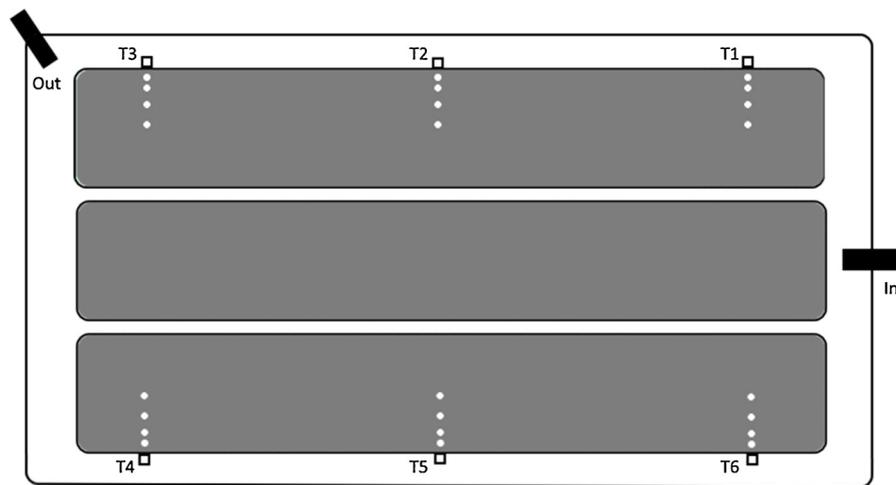


Fig. 1. Schematic overview of the study site with the production strips embedded by ditches (10×270 m; ditch width 0.5 m), the water inlet (In) and outlet (Out), locations of the transects (T_x) and sampling plots (squares indicate surface water sampling sites; circles represent pore water sampling sites at 0.5, 1, 2.5, 5 m from the ditch).

were determined by microwave digesting as described above. N contents of homogenized dried plant material (3 mg) were determined by an elemental CNS analyser (NA 1500, Carlo Erba; Thermo Fisher Scientific, Franklin, USA).

2.5. Nutrient sequestration

Nutrient sequestration (NSQ) by *S. palustre*, *S. papillosum* and *S. fallax* (May 2013– May 2014) was determined as:

$$NSQ_{Capitula_{species}} = (BC_{t_2} * NC_{t_2}) - (BC_{t_1} * NC_{t_1}) \quad (1)$$

$$NSQ_{Stem_{species}} = (BS_{t_2} * NS_{t_2}) \quad (2)$$

Where *BC* represents biomass capitulum, *NC* capitulum nutrient content, *BS* biomass stem (=biomass yield), *NS* stem nutrient content at t_2 (May 2014) and t_1 (May 2013). Nutrient sequestration values of all *Sphagnum* species present were added according to its biomass proportion. Due to a lack of stem nutrient data, the nutrient content of the stem was estimated using capitula:stem ratios, following:

$$Nutrient\ content\ stem_{species} = \frac{NC_{t_2}}{ratio\ capitula : stem} \quad (3)$$

Elemental capitulum:stem ratios of *S. magellanicum* (section *Sphagnum*) were obtained from Fritz et al. (2012) for N (1.67), K (1.12) and P (1.29), that were similar to those of *S. fallax* (section *Cuspidata*) obtained by Tomassen et al. (2003).

2.6. Statistical analyses

Normal distribution and homogeneity of variance of the data were tested with the Shapiro-Wilk test and the Levene's test. ANOVA was used to test the differences in nutrient status of the canal, inlet, and outlet water (NH_4^+ , NO_3^- , PO_4^{3-} , K, Cl). When tested significant, a post hoc test was applied (Tukey multiple comparisons of means). Because ANOVA's assumptions were not met, differences in *Sphagnum* capitula contents, capitula weight, stem weight within the *S. palustre* or *S. papillosum* variants were tested with the Kruskal Wallis Test (N, P, K content [2013,2014] and N:P, N:K and C:N ratios [2014], $P \leq 0.05$).

A multivariable regression including a model reduction procedure was applied to identify important variables explaining the variety of *Sphagnum* nutrient content as well as the variation in pore water concentrations in 2014 (Crawley, 2007). Models were treated as significant at $P \leq 0.05$. For identifying the optimal model

the Akaike information criteria (AIC) were used (Zuur et al., 2009). N, P and K *Sphagnum* capitula content (Explanatory variables set 1) was tested with different *Sphagnum* species, biomass yield, distance to the water inlet, elevation of the plots, and distance to the ditch (Response variables). PO_4^{3-} , NH_4^+ and K concentrations in the water (Explanatory variables set 2) were tested with distance to the water inlet, elevation of the plots and distance to the ditch (Response variables).

All analyses were performed in R (version 3.1.2) (R Core Team, 2014). The following packages were used for statistical analyses: psych (Revelle, 2015), car (Fox and Weisberg, 2011), rcmdr (Fox, 2005), and plyr (Wickham, 2011).

3. Results

3.1. Site conditions and nutrient input

3.1.1. Characteristics of the underlying peat

Peat characteristics and extractable nutrient concentrations of the peat layer below peatmoss surface showed no large differences between 2.5 and 5 m from the ditch at similar depths in March 2014 (Table S1). NO_3^- concentrations were similar at all depths. However, concentrations of bio-available P, Total-P, NH_4^+ and Total-K decreased with depth. At 2.5 m distance from the ditch, for example, bio-available P was higher in the upper 10 cm of this original peat layer ($134.2 \pm 1.7 \mu\text{mol L}^{-1}$ fresh peat) than in deeper peat layers, where bio-available P was very low ($15.1 \pm 2.3 \mu\text{mol L}^{-1}$ fresh peat). Total-P and Total-K concentrations were also highest in the top layer (774 ± 195 and $987 \pm 3 \mu\text{mol P and KL}^{-1}$ fresh peat, respectively) and decreased with depth (358 ± 190 and $308 \pm 136 \mu\text{mol P and KL}^{-1}$ fresh peat, respectively). Extractable NH_4^+ was also highest in the top layer ($65.8 \pm 15.2 \mu\text{mol L}^{-1}$ fresh peat) and lower in the deeper layer ($25.9 \pm 4.8 \mu\text{mol L}^{-1}$ fresh peat).

3.1.2. Porewater depth profiles

Porewater pH increased from 4.2 ± 0.05 at 2.5 cm below peatmoss surface to 4.8 ± 0.07 at 102.5 cm below peatmoss surface, and alkalinity from 0 to $0.3 \pm 0.03 \text{ meq L}^{-1}$ in March 2014 (Table S2). HCO_3^- concentrations were very low ($0.8 \pm 0.3 \mu\text{mol L}^{-1}$) at 2.5 cm and increased to $151.5 \pm 26 \mu\text{mol L}^{-1}$ at 102.5 cm below peatmoss surface. There also was a steep increase in CO_2 concentrations with increasing depth, from around $100 \pm 47 \mu\text{mol L}^{-1}$ at 2.5 cm, 1135 ± 97 at 10 cm to $5400 \pm 636 \mu\text{mol L}^{-1}$ at 102.5 cm. PO_4^{3-} levels were highest close to the surface ($12.8 \pm 2.5 \mu\text{mol L}^{-1}$),

Table 1

Mean capitula and stem weight (ton ha⁻¹ yr⁻¹), capitulum N, P and K content (mg g⁻¹) in May 2013 and 2014 (±SE, 2013: variant *S. palustre* n = 18; *S. fallax* n = 18, variant *S. papillosum* n = 10, *S. fallax* n = 10, 2014: variant *S. palustre* n = 24; *S. fallax* n = 24, variant *S. papillosum* n = 14, *S. fallax* n = 13). Significant differences within each variant are indicated by different letters.

Variant	Species	2013				2014				
		Capitula weight	N	P	K	Capitula weight	Stem weight	N	P	K
<i>S. palustre</i>	<i>S. palustre</i>	0.46 ± 0.1 ^b	13.6 ± 0.5	1.7 ± 0.1	8.0 ± 0.5	0.3 ± 0.1	3.5 ± 0.5	17.4 ± 0.4 ^b	2.0 ± 0.05 ^b	6.6 ± 0.2
	<i>S. fallax</i>	0.26 ± 0.1 ^a	14.7 ± 0.2	1.9 ± 0.2	9.1 ± 0.7	0.64 ± 0.2	2.3 ± 0.3	13.8 ± 0.2 ^a	1.4 ± 0.07 ^a	7.0 ± 0.3
<i>S. papillosum</i>	<i>S. papillosum</i>	0.48 ± 0.1 ^b	16.2 ± 0.5	2.7 ± 0.2	9.5 ± 1.2	0.51 ± 0.3	3.4 ± 0.9	18.0 ± 0.5 ^b	2.1 ± 0.1 ^b	6.9 ± 0.5
	<i>S. fallax</i>	0.26 ± 0.1 ^a	15.3 ± 0.8	2.4 ± 0.2	10.3 ± 0.7	0.57 ± 0.3	1.7 ± 0.9	11.2 ± 0.6 ^b	2.4 ± 0.09 ^a	4.5 ± 0.1

decreased with depth until 52.5 cm (~2 μmol L⁻¹) and were higher again at 102.5 cm depth (17.5 ± 4.9 μmol L⁻¹). NH₄⁺ was also high at the surface (18.2 ± 6.3 μmol L⁻¹), compared to concentrations found in the surface water. Substantial concentrations of NH₄⁺ were only found at 102.5 cm depth (42.6 ± 28.8 μmol L⁻¹). NO₃⁻ was absent throughout the depth profile. A modest increase of Cl, HCO₃⁻ and Ca (Ca – data not shown) concentrations with depth, suggesting the dominance of rainwater in March 2014. Furthermore, CH₄ concentrations in the pore water increased with depth; from 0.2 ± 0.07 μmol L⁻¹ at 27.5 cm to 133.6 ± 59.2 μmol L⁻¹ at 102.5 cm depth.

3.1.3. Surface water quality

The water in the ditch surrounding the *Sphagnum* field had an average pH of 4.9 ± 0.1 and 5.7 ± 0.3 in March and November 2014, respectively (Table S3). The alkalinity ranged from 0.1 to 0.5 meq L⁻¹. Both in March and November no NO₃⁻ was detected in the water, and NH₄⁺ was low with a maximum value of 23.5 in November 2014 (Table S3). Also, in November 2014, the NH₄⁺ concentration was 228.2 ± 4.6 μmol L⁻¹ at the water inlet and <5 μmol NH₄⁺ L⁻¹ at the outlet, the PO₄³⁻ concentration 35.8 ± 1.3 μmol L⁻¹ and 18.5 ± 0.6 μmol PO₄³⁻ L⁻¹, respectively. Additional information on surface water composition is shown in Table S3.

3.1.4. Horizontal porewater transects

From the ditches toward the middle of the *Sphagnum* strip, a decline in porewater pH and alkalinity was observed in March and November 2014 (Fig. 2). Cl was considerable higher in March than in November. In March 2014, PO₄³⁻ and K concentrations showed a large variation, especially at 5 m from the ditch, while NH₄⁺ showed varying results at 2.5 and 5 m from the ditch. In November 2014, however, PO₄³⁻ and K concentrations significantly decreased with increasing distance from the ditch (Fig. 2, Table S4). In November 2014 PO₄³⁻ and K concentrations were respectively 5 and 7 times lower at 5 m in the *Sphagnum* field (3.8 ± 0.6 and 22.7 ± 16, respectively), than in the ditch (18.3 ± 3 and 155.6 ± 14, respectively). NH₄⁺ concentrations were already very low in the ditches, and remained low in the *Sphagnum* field (<5 μmol L⁻¹; Fig. 2), while NO₃⁻ was absent.

3.2. *Sphagnum* biomass yield

Between May 2013 and May 2014 a mean annual biomass yield of around 6.5 t DW ha⁻¹ yr⁻¹ was obtained (Fig. 3). In both variants *S. fallax* had a 40% contribution to the biomass. The *S. palustre* variant yielded on average 6.7 t DW ha⁻¹ yr⁻¹ to which *S. fallax* contributed 2.9 t DW ha⁻¹ yr⁻¹. The *S. papillosum* variant yielded on average 6.5 t DW ha⁻¹ yr⁻¹ to which *S. fallax* contributed 2.6 t DW ha⁻¹ yr⁻¹.

From the installation until May 2014 on average 3.4 t DW peatmoss biomass ha⁻¹ yr⁻¹ accumulated, resulting in 10.2 t accumulated DW *Sphagnum* biomass in 3 years. There was no spatial relationship between accumulated biomass of *S. palustre*, *S. papil-*

Table 2

Mean capitulum N:P, N:K and C:N ratios (g g⁻¹) in May 2014 (±SE, variant *S. palustre* n = 24; *S. fallax* n = 24, variant *S. papillosum* n = 14, *S. fallax* n = 13). Significant differences within each variant are indicated by different letters.

Variant	Species	N:P	N:K	C:N
<i>S. palustre</i>	<i>S. palustre</i>	9.0 ± 0.2 ^a	2.5 ± 0.08 ^b	3.6 ± 0.08 ^a
	<i>S. fallax</i>	10.6 ± 0.5 ^b	2.0 ± 0.07 ^a	4.6 ± 0.08 ^b
<i>S. papillosum</i>	<i>S. papillosum</i>	8.8 ± 0.3 ^a	2.7 ± 0.1 ^b	3.5 ± 0.1 ^a
	<i>S. fallax</i>	11.2 ± 0.6 ^b	2.4 ± 0.09 ^a	4.5 ± 0.1 ^b

losum and *S. fallax* (2011–2014) and ditch proximity, elevation of the plots, or distance from the water inlet.

3.3. *Sphagnum* nutrient contents and nutrient sequestration rates

Nutrient concentrations in *Sphagnum* capitula were high in both variants. *S. palustre* and *S. papillosum* showed similar values with respect to N and P, while significantly lower nutrient concentrations were found for *S. fallax* in 2014 (Table 1). K content was equally high in all three species. Elemental ratios differed within the variants among *Sphagnum* species (Table 2). N:K ratios (g g⁻¹) in the moss capitula were significantly higher in *S. palustre* and *S. papillosum* than in *S. fallax*, whereas *S. fallax* showed significantly higher N:P and C:N ratios (Table 2). In all *Sphagnum* capitula, on average, N:K ratios were below 3. For *S. palustre* and *S. papillosum* N:P ratios were below 10, while for *S. fallax* N:P ratio was slightly higher than 10. Based on the capitula weight (2013 and 2014), stem weight (2014), their measured capitula nutrient content and their calculated stem nutrient contents (Table 1), on average 34 kg N, 17 kg K and 4 kg P ha⁻¹ yr⁻¹ was sequestered by *Sphagnum* biomass from May 2013 to May 2014.

3.4. Influence of nutrients on *Sphagnum* biomass accumulation

Interestingly, biomass accumulation and N contents in moss capitula showed a strong negative correlation for *S. papillosum* (Fig. 4) and for *S. fallax* (Fig. S1), and no significant relation for *S. palustre* (Fig. S2). For *S. papillosum* accumulated biomass was, on average, 134% higher for *S. papillosum* with low N contents, while this was 270% for *S. fallax* and only 36% for *S. palustre*. Furthermore, there is a positive relationship between accumulation of *S. fallax* biomass and N content (indicative for N availability) in the capitula of *S. papillosum* (R² = 0.55, p < 0.01, y = 0.27x – 3.9) and *S. palustre* (R² = 0.41, p < 0.01, y = 0.14x – 1.6). There was no such relationship between accumulation and P, K contents and nutrient ratios (N:P and N:K) in the capitula of *S. papillosum*, *S. palustre* and *S. fallax*.

4. Discussion

4.1. High *Sphagnum* biomass production and accumulation

The *Sphagnum* farm in our study reached a very high productivity compared to other productivity studies in natural or constructed *Sphagnum*-dominated systems. Next to higher nutrient availability

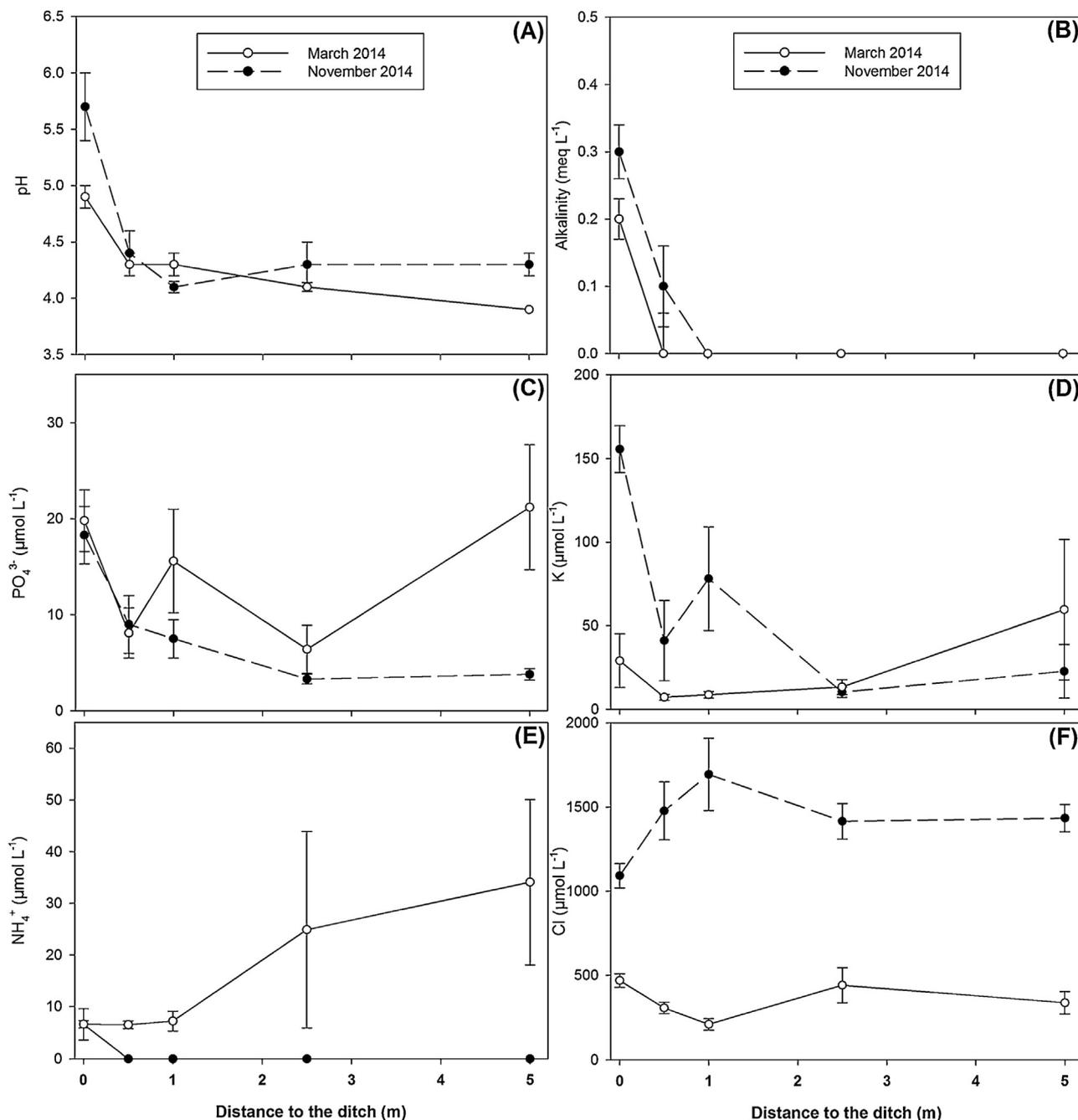


Fig. 2. pH (A), alkalinity (meq L⁻¹, B), PO₄³⁻ (C), K (D), NH₄⁺ (E) Cl (F, all in μmol L⁻¹) of the porewater at 2.5 cm below peat surface as a function of distance to the ditch ($n = 6 \pm SE$) in March and November 2014. NH₄⁺ (E) concentrations were lower than the detection limit of 5 μmol NH₄⁺ L⁻¹ and set to 0 (0.5, 1, 2.5 and 5 m from the ditch) in November 2014. All NO₃⁻ concentrations were below the detection limit of 5 μmol L⁻¹.

(see below), this is probably due to the release of vascular plant competition (Tomassen et al., 2003) and optimal irrigation management (Clymo, 1973; Hayward and Clymo, 1983) in which water levels were adjusted to increasing *Sphagnum* lawn height. Average annual *Sphagnum* biomass yield (6.5 t DW ha⁻¹ yr⁻¹, dominant peatmosses *S. palustre*, *S. papillosum* and *S. fallax*) was higher compared to the mean biomass yield (3.6 t DW ha⁻¹ yr⁻¹, dominant peatmoss *S. papillosum*) at another *Sphagnum* farming site on cut-over bog in Germany after an initial establishment phase of 3.5 years (Gaudig et al., 2014), which is probably attributable to the better water supply in our study. In a Canadian *Sphagnum* farm a mean annual yield of 1.12 t DW ha⁻¹ yr⁻¹ was obtained after seven growing seasons (Pouliot et al., 2015), which is considerably lower than

yields obtained in the third year after installation in our study. The Canadian site, however, had no active water management, whereas average temperature was lower and the growing season shorter, which will have limited peatmoss growth (cf. Gunnarsson, 2005; Haraguchi and Yamada, 2011). A global meta-analysis of *Sphagnum* dominated wetlands (Gunnarsson, 2005), found a mean productivity of natural pure *Sphagnum* stands of approximately 2.8 (*S. palustre*), 2.4 (*S. papillosum*) and 4 t DW ha⁻¹ yr⁻¹ (*S. fallax*). The highest productivities of *S. papillosum* and *S. palustre* in natural bogs were recorded for the Kolkhetti Lowlands (Georgia) with 4.3 and 5.9 t DW ha⁻¹ yr⁻¹ respectively, which is explained by year-round growth facilitated by high and frequent precipitation in combination with high temperatures (Krebs et al., 2016).

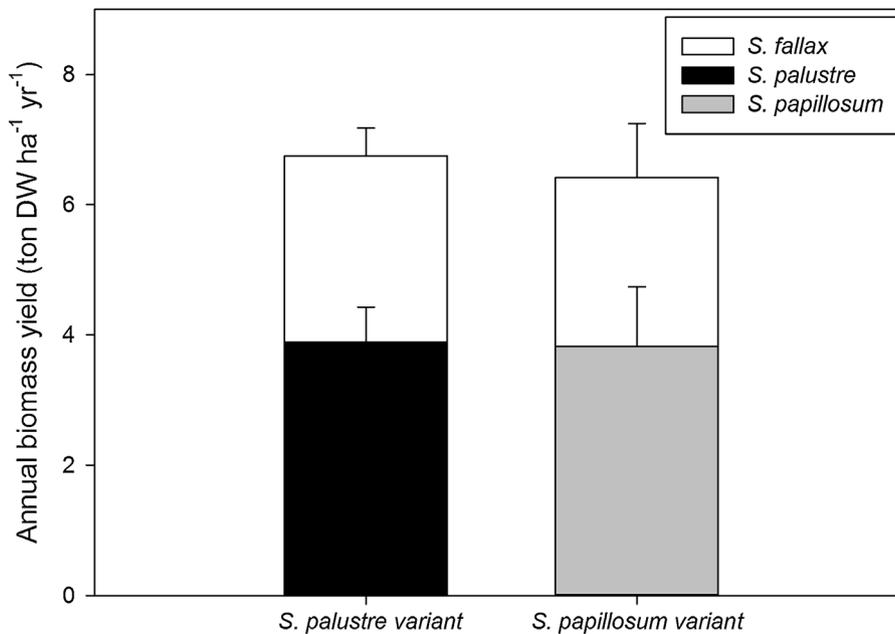


Fig. 3. Annual biomass yields of *S. palustre* (n=7) and *S. papillosum* (n=3), and additional *S. fallax* yields for both variants from May 2013 till May 2014 (3rd year after installation). Including small amount of biomass from *S. fimbriatum* and *S. cuspidatum*.

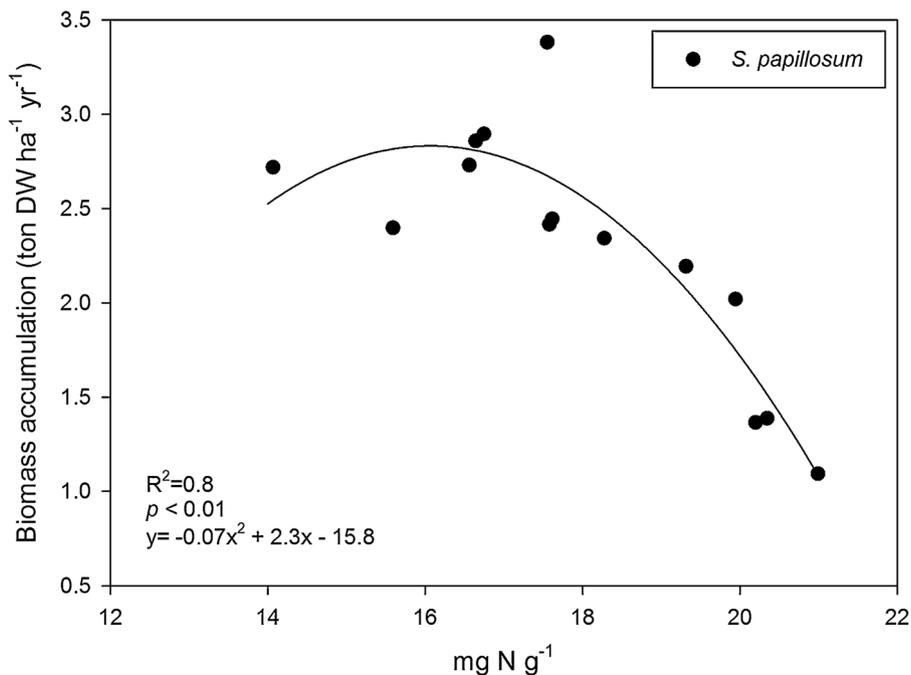


Fig. 4. Average biomass accumulation (ton DW ha⁻¹ yr⁻¹, 2011–2014) of *S. papillosum* in relation to the capitula N content (mg N g⁻¹) in 2014.

4.2. High nutrient availability

Nutrient availability in our managed site is much higher than in most natural mires (Tahvanainen et al., 2002). Eutrophication of natural mires generally leads to the expansion of vascular plants at the expense of peatmosses (Lamers et al., 2000; Tomassen et al., 2003). In our site, with high nutrients availability, vascular plants were mown to suppress competition with peatmosses. The water used for irrigation at our site is low in alkalinity, and therefore not toxic (Harpenslager et al., 2015), and acidic, which is favourable for *Sphagnum* growth (Hayward and Clymo, 1983; Lamers et al., 1999). In addition, high porewater CO₂ concentrations were also

favourable for growth (Harpenslager et al., 2015; Smolders et al., 2003), because at low CO₂ concentrations plants can be C-limited, thus missing the major biomass component, but it also may result in weak stems that do not remain upright (Smolders et al., 2001).

Analysis of horizontal pore water transects (Fig. 2) showed that P, N and K accumulation in the pore water did not occur in November 2014. However, in March, for PO₄³⁻ at 5 m and for NH₄⁺ at 2.5 and 5 m from the ditch concentrations were high, but with a large variation, which may indicate local nutrient mobilisation from the soil. In March, the site was influenced by a rainwater surplus, indicated by low Cl and K concentrations and a lower pH. Water infiltration into the *Sphagnum* farm seems sufficient, because high

Cl concentrations were found after summer from the ditch into the Sphagnum field (main irrigation period). Denitrification, also in the ditches, may play an important role in N-removal, as does settlement of P in ditches (Vymazal, 2007). Regular dredging of ditch sediment could thus lead to additional nutrient removal from the system by removing settled or bound P or removing easily degradable compounds.

Besides denitrification, rapid sequestration of N in *Sphagnum* or vascular plant biomass efficiently reduces N levels in the pore water and prevents the build-up of N in the uppermost soil layers (Chiwa et al., 2016; Lamers et al., 2000). However, sequestration (filter) capacity differs between species and depends on growth rate and nutrient content. At high N supply, the N content in the capitulum is substantially higher than under low N deposition (Bragazza et al., 2004; Jirousek et al., 2011; Lamers et al., 2000; Limpens et al., 2011). Responses of *Sphagnum* to high P loads have hardly been studied. Fritz et al. (2012) added high amounts of P ($10 \text{ kg P ha}^{-1} \text{ yr}^{-1}$), but found P concentrations in the peatmosses ($1.0\text{--}1.5 \text{ mg g}^{-1}$) to be lower than in our field study ($0.75\text{--}2.6 \text{ mg g}^{-1}$), suggesting luxury P consumption. The high annual productivity and high nutrient content of our *Sphagnum* mosses results in high annual nutrient sequestration rates of 34 kg N , 17 kg K and $4 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (May 2013–May 2014). In the current situation *S. palustre* and *S. papillosum* contribute more to nutrient retention at the study site than *S. fallax* due to their higher biomass and higher nutrient content, but may change over time.

In addition to input with irrigation water (estimated to $3\text{--}9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), input from local atmospheric N deposition is high ($20 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (UBA, 2009). N input via irrigation is thus only 13–31% of the total input by atmospheric N deposition. N input from the subsoil will play a minor role as the underlying peat is low in N, and the infiltrating surface water hardly contains N as a result of denitrification and/or N sequestration in biomass. N-input from irrigation water is incomplete, because we miss summer NO_3^- peaks and we have insufficient data on the outflow during irrigation and after heavy rains. In contrast, P load by irrigation was $0.7\text{--}2.4 \text{ kg P ha}^{-1} \text{ yr}^{-1}$, which is higher than atmospheric P deposition, being $0.1\text{--}0.3 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (Tomassen et al., 2004), whereas irrigation water was also the major supply source of K ($13 \text{ kg K ha}^{-1} \text{ yr}^{-1}$), which is also higher than atmospheric K deposition, being $2.5\text{--}3.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Tomassen et al., 2004). In conclusion, the trophic status is not-influenced by the former land-use on site, but by supply of nutrient-rich irrigation water due to active drainage in the surroundings. Pre-treating irrigation water by using for instance a helophyte filter to reduce N-loads, especially during summer months when N-removal is efficient (Beutel et al., 2009), might be a tool to manage nutrient input of the Sphagnum farming site. However, additional space and infrastructure is needed though for a constructed wetland.

Before the onset of this Sphagnum farm, 30–50 cm of the original topsoil had been removed, exposing to a peat layer below the newly formed *Sphagnum* (0–10 cm depth) that is extremely poor in P (Bio-available P $167 \pm 23 \mu\text{mol PL}^{-1}$ fresh soil) compared to the surface peat layer of adjacent agricultural fields (Bio-available P $669 \pm 50 \mu\text{mol PL}^{-1}$ fresh soil) determined in May 2014. Bio-available P concentrations can be $2500 \mu\text{mol PL}^{-1}$ fresh soil or even higher in P polluted sites, whereas concentrations of $300 \mu\text{mol}$ are maximum reported values for species-rich peat meadows (Smolders et al., 2008), illustrating that P availability in the peat layer of our study site was reduced by topsoil removal and was not enriched after three years of irrigation. With regard to high soil P availability, it has been shown in other agricultural peatlands that it is best practice to remove topsoil to expose the nutrient poor peat soil to limit vascular plant growth (cf. *Juncus effusus* or algae) (Harpenslager et al., 2015; Smolders et al., 2008). The removal of litter after mowing may also help to reduce nutrient release of litter

decomposition (Bragazza et al., 2013; Scheffer et al., 2001) and to facilitate growth limitation of *J. effusus*. Also K had apparently been removed by the removal of the topsoil. Total-K in the surface peat layer of adjacent agricultural fields was $5970 \pm 2244 \mu\text{mol KL}^{-1}$ fresh soil, against $920 \pm 102 \mu\text{mol KL}^{-1}$ fresh peat in the peat layer below the newly formed *Sphagnum* of the Sphagnum farming field (0–10 cm depth).

4.3. High production despite high N availability

Despite high atmospheric N loads, the overall annual *Sphagnum* biomass yield at our site was very high on a site scale (Fritz et al., 2012; Gaudig et al., 2014; Gunnarsson, 2005; Krebs et al., 2016; Limpens and Heijmans, 2008; Pouliot et al., 2015). N saturated *Sphagnum* metabolism, at a tissue content of $>14.5 \text{ mg N g}^{-1}$, may result in impeded growth (Fritz et al., 2012; Granath et al., 2012, 2009b; Jirousek et al., 2011; Lamers et al., 2000; Limpens and Berendse, 2003; Limpens et al., 2011; Tomassen et al., 2003). The long-term effects may, however, differ from observed short-term responses and for N-polluted and pristine sites (Aerts et al., 1992). *Sphagnum* seems to possess an adaptive mechanism to cope with high N loads. Fritz et al. (2014) showed for *S. magellanicum* that N uptake efficiency decreases when mosses experience long-term exposure (decades) to high N supply, avoiding N toxicity. Also, it has been shown that *S. capillifolium* can filter wet N deposition up to $32 \text{ kg N h}^{-1} \text{ yr}^{-1}$ for at least a decade (Chiwa et al., 2016). Furthermore, a high P supply may alleviate the negative effects of high N availability (Limpens et al., 2004), but this effect may only be temporary, when the metabolic burden of N cannot be alleviated by increased biomass production (Fritz et al., 2012).

Bragazza et al. (2004) and Jirousek et al. (2011) showed that in natural systems higher N-deposition rates lead to co-limitation by P at $\text{N:P} > 30$, and by K at $\text{N:K} > 3$. In our study we found for all *Sphagnum* species capitulum N:P ratios lower than 10, and N:K ratios lower than 3, implying that despite the high influx of N, P and K are available in sufficient amounts to attain optimal stoichiometric ratios (cf. Arróniz-Crespo et al., 2008; Granath et al., 2009a, 2012). This favourable stoichiometry probably alleviates the physiologically detrimental effects of a high N supply (Bragazza et al., 2004; Limpens et al., 2011; Limpens and Heijmans, 2008). This falsifies our hypothesis that high N supply would frustrate *Sphagnum* biomass production at our site.

Despite the favourable stoichiometry there is an indication that high N levels still cause problems for *Sphagnum* biomass accumulation, particularly for *S. papillosum*. The negative correlation between N content and accumulation may either indicate dilution of N in *S. papillosum* tissue at higher growth rates, or decreased growth rates at higher accumulation of N in the living plant tissue. However, the fact that there were no correlations between N:P or N:K ratios and biomass accumulation (i.e. more balanced nutrient ratios for higher growth rates), suggests that higher N levels in *Sphagnum* (due to small-scale differences in availability and/or uptake) lead to relatively lower growth rates.

Well balanced nutrient ratios at high N-deposition also facilitate the growth of vascular plant (mainly *Juncus effusus*) and *Sphagnum* species that are stronger competitors because of their high specific growth rate or higher nutrient use efficiency (Limpens et al., 2003; Twenhöven, 1992). We showed that *S. fallax* growth rate (40% of total production) is positively correlated with N content in *S. papillosum* and *S. palustre*, which seems to be the result of the much smaller negative effect of increased N in *S. fallax*. The higher C:N ratios of this species (Table 2) indeed indicate higher growth efficiency at similar N availability. This relative advantage of *S. fallax* at high N levels may lead, on the long term, to a shift in species composition at the expense of less competitive *Sphagnum* species, and has indeed been shown in manipulation experiments

(Limpens et al., 2003; Twenhöven, 1992). Limpens et al., (2003) showed that the competitive strength of *S. fallax* is related to N and P availability. Improved management should target optimal nutrient supply allowing high production of promising *Sphagnum* species for suitable horticultural substrates, while reducing stress by less attractive competitors.

5. Conclusions for Sphagnum farming

Our study shows that Sphagnum farming (paludiculture) can thrive under high N input and produce very large volumes of *S. palustre* or *S. papillosum* biomass (6.7 and 6.5 t DW ha⁻¹ yr⁻¹, respectively [including *S. fallax* biomass]), as long as alkalinity of irrigation water is low and *Sphagnum* stoichiometry is optimal due to a balanced supply of P and K by irrigation water. Additionally, other factors like water supply and cover of vascular plants has also to be taken into account. Nutrient dynamics should therefore be monitored and managed. Because of their dominance, *Sphagnum* donor material (*S. palustre* or *S. papillosum*) should not be polluted with *Sphagnum* species less suitable for horticultural purposes and atmospheric N loads should be reduced to avoid the strong growth of these species. As former agricultural lands rich in P promotes dominance of algae and *Juncus* (Smolders et al., 2008), research prior to installation is needed to determine optimal removal depth of nutrient rich topsoil to improve the establishment and growth of *Sphagnum* mosses. Depending on the prevalent *Sphagnum* species and their growth rates, irrigation water should not have HCO₃⁻ concentrations above 250–500 μmol L⁻¹ (this study, Harpenslager et al., 2015, Fritz unpublished data) to avoid *Sphagnum* die-off due to high pH. Furthermore, our study shows that a Sphagnum farm can be utilized to effectively sequester nutrients into *Sphagnum* biomass.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2016.10.069>.

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