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Nutrient dynamics of Sphagnum farming on rewetted bog grassland in NW Germany

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HIGHLIGHTS

- Agricultural nutrient legacy decreases rapidly in Sphagnum farming
- Long-lasting *Sphagnum* biomass accumulation and nutrient sequestration
- Lateral irrigation enables considerable and homogeneous biomass yields
- Sphagnum farming provides a sustainable alternative to drainage-based agriculture
- Sphagnum farming has a high potential for peatland rehabilitation

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ABSTRACT

The agricultural use of drained peatlands leads to huge emissions of greenhouse gases and nutrients. A land-use alternative that allows rewetting of drained peatland while maintaining agricultural production is the cultivation of *Sphagnum* biomass as a renewable substitute for fossil peat in horticultural growing media (Sphagnum farming).

We studied *Sphagnum* productivity and nutrient dynamics during two years in two Sphagnum farming sites in NW Germany, which were established on drained bog grassland by sod removal, rewetting, and the introduction of *Sphagnum* fragments in 2011 and 2016, respectively.

We found a considerable and homogeneous production of *Sphagnum* biomass (>3.6 ton DW ha^{-1} yr^{-1}), attributable to the high nutrient levels, low alkalinity, and even distribution of the irrigation water. The ammonium legacy from former drainage-based agriculture rapidly declined after rewetting, while nutrient mobilization was negligible. CH_4 concentrations in the rewetted soil quickly decreased to very low levels. The *Sphagnum* biomass sequestered high loads of nutrients (46.0 and 47.4 kg N, 3.9 and 4.9 kg P, and 9.8 and 16.1 kg K ha^{-1} yr^{-1} in the 7.5 y and 2.5 y old sites, respectively), preventing off-site eutrophication.

We conclude that Sphagnum farming as an alternative for drainage-based peatland agriculture may contribute effectively to tackling environmental challenges such as local and regional downstream pollution and global climate change.

1. Introduction

Natural peatlands form a substantial carbon (C) store, containing over 30% of global soil C (Eswaran et al., 1993; Batjes, 1996, 2016; Scharlemann et al., 2014). An estimated 15% of global peatlands (~0.4% of global land cover) have been drained for agriculture, forestry or peat extraction (Joosten, 2010; Leifeld and Menichetti, 2018), and are currently responsible for almost 5% of global anthropogenic carbon dioxide (CO_2) emissions (Joosten et al., 2016). Peatland drainage and consequent peat oxidation result in the release of stored C and nutrients, land subsidence, and the loss of vital ecosystem services including water retention and purification, and biodiversity conservation (Bonn et al., 2016; Holden et al., 2004; Joosten et al., 2012; Kasimir-Klemedtsson et al., 1997).

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To decrease emissions and stop subsidence, drained peatlands have to be rewetted, implying – if agricultural production has to be maintained - the cultivation of perennial crops on rewetted peatland as a novel form of land use ('paludiculture'; Wichtmann et al., 2016). The cultivation of peatmosses ('Sphagnum farming'; Gaudig et al., 2014) is such a form of paludiculture. The produced *Sphagnum* biomass can be used as a renewable raw material for horticultural growing media, thereby lowering the demand for fossil peat (Gaudig et al., 2018; Pouliot et al., 2015). Sphagnum farming thus combines the avoidance of environmental burdens of drainage-based peatland use with the supply of a renewable alternative to fossil peat. Compared to the former drained situation, Sphagnum farming may furthermore enhance biodiversity and nutrient sequestration and decrease greenhouse gas (GHG) emissions, C losses, and eutrophication (Günther et al., 2017; Muster et al., 2015; Temmink et al., 2017), making it an attractive landscape rehabilitation option.

Sphagnum species require humid to wet, oligotrophic to mesotrophic conditions (Clymo, 1973; Hájek and Adamec, 2009; Hayward and Clymo, 1983; Joosten, 1993), and a moisture content close to saturation in the upper 5–10 cm to maintain high growth rates (Gaudig et al., 2020; Hayward and Clymo, 1983; Robroek et al., 2007). In contrast, high alkalinity and bicarbonate (HCO_3^-) concentrations combined with high pH (>8.0) are detrimental (Harpenslager et al., 2015b; Koks et al., 2019; Vicherová et al., 2017). *Sphagnum* productivity can be limited by nitrogen (N) or phosphorus (P), also depending on atmospheric N deposition rates (Aerts et al., 1992; Bragazza et al., 2004; Fritz et al., 2012). When low P and potassium (K) availability inhibits high productivity, high N supply can become toxic to *Sphagnum* (Limpens and Berendse, 2003). Next to causing physiological stress, high nutrient levels will favour more competitive bryophyte and vascular plant species, which may overgrow and outcompete the desired *Sphagnum* species by shading, litterfall, and uptake of nutrients and water (Limpens and Berendse, 2003; Tomassen et al., 2004, 2003). Therefore, an optimal nutrient balance is required to maximize *Sphagnum* biomass production (Gaudig et al., 2018, 2017; Temmink et al., 2017).

As Sphagnum farming sites generally experience substantial lateral and vertical water losses (especially by evapotranspiration; Brust et al., 2018; Pouliot et al., 2015), irrigation with water from external sources is required to optimize water supply (Gaudig et al., 2018; Pouliot et al., 2015; Van de Riet et al., 2017). *Sphagnum* productivity and the farm's nutrient balance will then be determined by the quality and proportion of both atmospheric deposition and irrigation water. Additionally, the peat soil on site may show a nutrient legacy from former agricultural practice, which may be counteracted by removing the top soil prior to rewetting (Harpenslager et al., 2015a; Huth et al., 2020).

Despite these challenges, *Sphagnum* farming appears to be successful even under high nutrient conditions, at least in the short term (Gaudig et al., 2018; Temmink et al., 2017). Over the last two decades, small scale Sphagnum farming pilots have been carried out across the world (for overviews, see Gaudig et al., 2018 and Pouliot et al., 2015) and these have recently been followed up by larger scale practical implementation in Germany (Gaudig et al., 2017, 2018; this paper) and Canada (Pouliot et al., 2015). The long-term effects of high nutrient inputs on *Sphagnum* performance and on water and soil nutrient contents have, however, not yet been studied.

In this study, we report on the biogeochemistry (nutrients, cations and methane (CH_4)) and *Sphagnum* productivity of two Sphagnum farming sites in NW Germany differing in age (established in 2011 and 2016) and size (net production area: 0.82 ha and 2.8 ha, respectively). We characterize nutrient inputs from different sources (atmospheric deposition, irrigation water, peat soils, and levees) to test the following hypotheses:

1) lateral infiltration of irrigation water allows optimal *Sphagnum* growth and leads to homogeneous biomass yields and nutrient sequestration,
2) the agricultural soil nutrient legacy rapidly decreases after topsoil removal, rewetting and *Sphagnum* establishment,
3) Sphagnum farming supports long term C and nutrient sequestration,
4) nutrient input from irrigation water eventually leads to elevated nutrient concentrations in the upper soil layers.

2. Materials & methods

2.1. Study site

The studied Sphagnum farm is located in the Hankhauser Moor (Lower Saxony, NW Germany, 53° 15.80′ N, 08° 16.05′ E), a former raised bog with a 2–2.5 m thick peat layer overlaying sand. The bog has been intensively drained for over six decades to allow agricultural use as grassland. The Sphagnum farm was established on 4.5 ha in 2011 (with experimental site S2011, including net 0.82 ha *Sphagnum* production fields) and extended with 9.5 ha in 2016 (with experimental site S2016, including net 2.8 ha *Sphagnum* production fields) (Fig. 1; Wichmann et al., 2020). Establishment included the removal of 30–50 cm of topsoil from the 10 m wide *Sphagnum* production fields, the digging of 0.5 m wide and deep irrigation ditches, and the construction of levees (1 m height, 15 m basal width) used as causeways. *Sphagnum* fragments were spread over the bare and even peat surface, after which the site was rewetted. Site S2011 was inoculated (in 2011) with mainly *S. palustre* and *S. papillosum* fragments, whereas site S2016 was inoculated (in 2016) with material harvested from S2011, which had a higher proportion of *S. fallax* (on average 75% cover at S2011 in 2016).

The sites are equipped with an automatic irrigation system that controls the in- and outflow of water to maintain the water table just below the *Sphagnum* capitula. Irrigation water is pumped from the adjacent canal 'Schanze', which collects the drainage water of the surrounding agriculturally used peatlands, and enters at one point per experimental site. The outflow for each site is situated on the opposite side. Within each site, irrigation ditches of separate production fields are connected by pipes running through the causeways. To maintain the water table around 5 cm below the *Sphagnum* surface, a mean annual irrigation volume of 160 mm (i.e. 1600 m^3 ha^{-1} yr^{-1}), in dry years up to 360 mm (i.e. 3600 m^3 ha^{-1} yr^{-1}) is required (Brust et al., 2018).

2.2. Setup of transects

In June 2017, transects were installed perpendicular to the irrigation ditches covering half the width of the production fields (Fig. 1). The six transects in S2011 coincided with those of Temmink et al. (2017). In S2016, we installed nine new transects on three different production fields. Transects had different distances to the water inlets (56–270 m in S2011 and 50–371 m in S2016) and measurement points where we took pore water and biomass samples at 0, 0.5, 1.0, 2.5 and 5.0 m distance from the nearest irrigation ditch (Fig. 1B). At 5.0 m distance from the ditch, we also sampled pore water and soil at various depths. Surface water, pore water, and soil were sampled in June and November 2017 and in March, June and November 2018. Ditch sediment was collected in March and November 2018. Collection of plant biomass and levee soil took place in November 2018.

2.3. Sphagnum biomass accumulation

To study how the growth of *Sphagnum* and other plants was affected by the proximity to the irrigation ditch, vegetation composition and biomass accumulation were assessed in the transects in November 2018. Vegetation (species and cover) was recorded in quadrats of 25 by 25 cm ($n = 24$ in S2011 and $n = 36$ in S2016). *Sphagnum* biomass accumulation was evaluated by cutting out 9 by 9 cm plugs from the *Sphagnum* lawn down to the old peat surface. Lawn thickness was determined in situ by measuring the distance of the peatmoss surface to the old

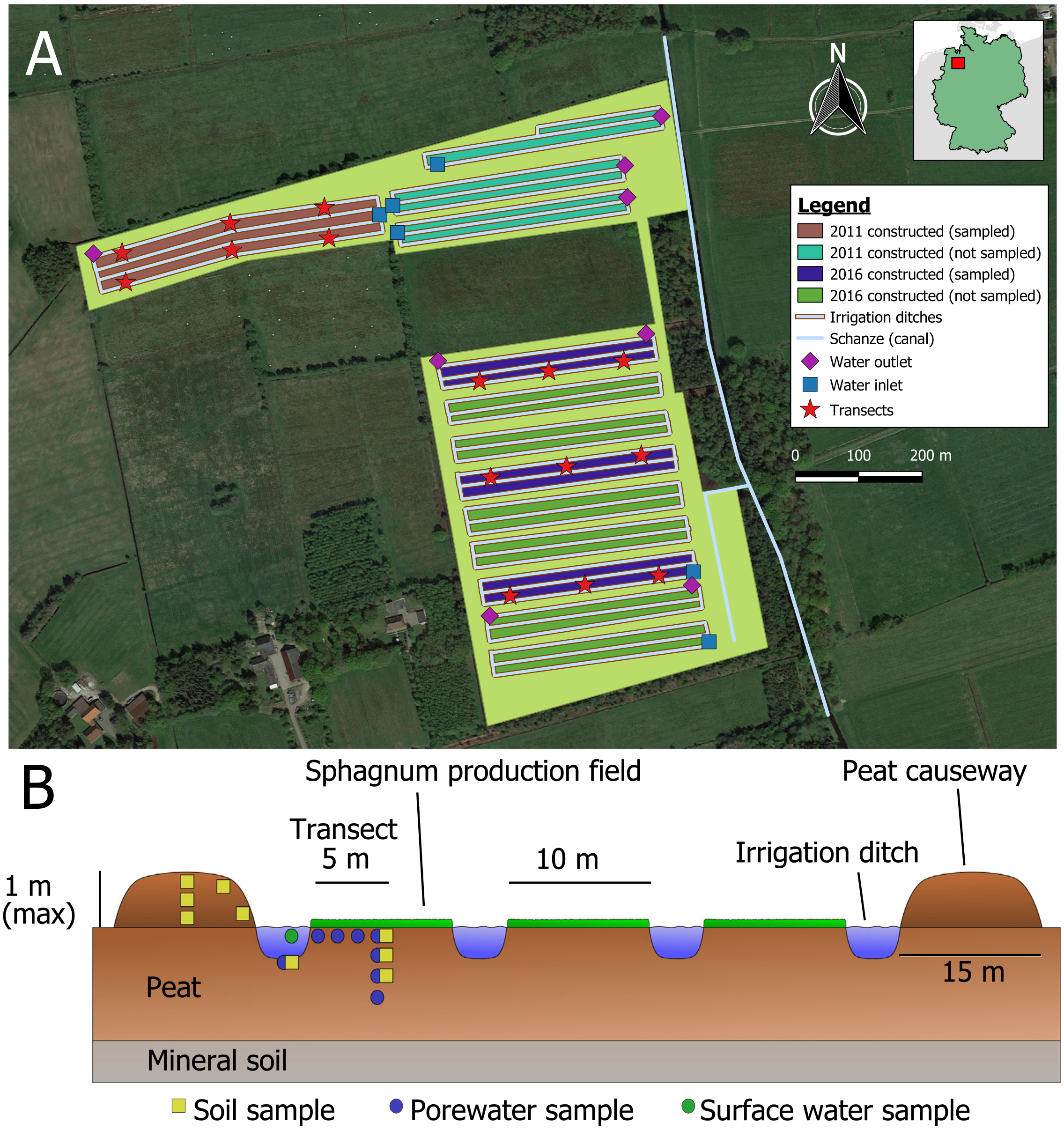

Fig. 1. A. Overview of sampling sites. B. Cross section of the Sphagnum farm with the sampling scheme of a transect. Map background: Microsoft product screen shot(s) reprinted with permission from Microsoft Corporation.

peat. Brownmosses, vascular plants, *Sphagnum* capitula and other *Sphagnum* biomass were separated, weighed (fresh weight), dried for 48 h at 70 °C, and weighed again (dry weight). Samples were stored in a dry place until chemical analysis.

2.4. Surface and pore water quality in horizontal transect

The chemical composition of the pore water was determined to investigate if the *Sphagnum* lawns were fully irrigated up to the maximum distance to the ditch (5 m), and whether the sites accumulated nutrients over time. During every field campaign ($n = 5$), pore water was extracted in each transect at 0.5, 1.0, 2.5 and 5.0 m distance from the ditch ($n = 24$ for S2011; $n = 36$ for S2016) using syringes under vacuum attached to a rhizon (Rhizosphere Research Products, Wageningen, the Netherlands), placed at 0.06 m depth. Surface water was sampled the ditch adjacent to every transect ($n = 6$ for S2011, $n = 9$ for S2016). Additionally, surface water samples were regularly taken in between campaigns ($n = 3$ for 2017, $n = 7$ for 2018) in S2016 at the irrigation inlet ($n = 1$) and outlets ($n = 2$), in ditches with different distances to the inlet ($n = 7$), and in the 'Schanze' ($n = 1$). Surface water was collected using syringes under vacuum connected to ceramic cups to filter out large suspended particles. All water samples were stored at 4 °C until further analysis on the next day (see below).

2.5. Changes in water quality in depth profiles

To evaluate the effect of Sphagnum farming on the nutrient stock that had accumulated in the soil during drained-based land use ('legacy nutrient stock'), pore water was extracted as described above during every field campaign from the centre of the *Sphagnum* production fields, i.e. at 5 m from the ditch, at 0.06 (see above), 0.25, 0.50 and 1.00 m depth, as described above using ceramic cups. To determine pore water CH_4 concentrations, as a proxy for in-situ CH_4 production and its potential release, additional pore water samples were collected in gastight evacuated 12 mL glass exetainers (Labco, Lampeter, UK) containing 0.1 mL of 65% nitric acid (HNO_3) for sample preservation, using similar ceramic cups as used for pore water collection.

2.6. Soil and biomass sampling

To determine the supply of nutrients from the legacy stock, soil samples were taken in each transect and at each sampling date in production fields (at 5 m distance to the ditch), ditches and levees. In S2011, *Sphagnum* biomass accumulated on top of the old peat surface was first removed and collected from a 10 cm^2 area. In both S2011 and S2016, uncompressed peat cores were then obtained from the peat surface to 50 cm depth using a chamber corer (Eijkelkamp Agrisearch Equipment, the Netherlands) with a diameter of 5 cm and a length of 50 cm. The cores were divided in three parts (0–10 cm, 10–30 cm and 30–50 cm depth) and soil samples were stored at 4 °C until processing.

To determine bioavailable nutrients, extractions were carried out using 17.5 g of fresh soil and 50 mL of 0.2 M sodium chloride (NaCl). After 120 min of incubation on a shaker at 105 rpm, pH was determined and fluid was extracted using rhizon samplers and glass bottles under vacuum. After extraction and measurement of pH (see method below), samples were split up into two 10 mL subsamples and stored at −20 °C and, after adding 0.1 mL of 65% HNO_3, at 4 °C, until further analysis. Subsamples of fresh soil were dried at 70 °C for 48 h to determine dry weight and bulk density.

Ditch sediment was collected in March and November 2018, using a piston sampler (Eijkelkamp Agrisearch Equipment, the Netherlands) to extract the upper 4–8 cm of sludge. After storage at 4 °C, water extractions similar to NaCl extractions but with 50 mL Milli-Q water were carried out to estimate potential leaching of nutrients from sediment to ditch water.

In November 2018, we collected soil samples from the levees from 0–10, 10–50 and 50–90 cm depth at 5 m distance from the ditch at each transect, using an Edelman and a chamber corer (Eijkelkamp Agrisearch Equipment, the Netherlands). We furthermore collected well-mixed levee soil samples from the upper 10 cm at 1.0, 3.0 and 5.0 m from the ditch. Water extractions were carried out as described above.

2.7. Chemical analyses

Within one day after sampling, pH and alkalinity of the pore water and surface water samples were determined using an Ag/AgCl electrode (Orion Research, Beverly, MA, USA) and a TIM 840 Titration Manager (Radiometer Analytical SAS, Villeurbanne, France). Total inorganic carbon (TIC - HCO_3^- and CO_2) was measured using an infrared carbon analyser (IRGA; ABB Analytical, Frankfurt, Germany), followed by pH-based calculation of CO_2 and HCO_3^- concentrations (van Bergen et al., 2020). Next, all samples were divided and i) stored at 4 °C in vials (10 mL) containing 0.1 mL of 65% nitric acid (HNO_3) (ISO 17294-2, 2016) or ii) frozen and stored at −6 °C (10 mL) until further analysis.

Ammonium (NH_4^+), nitrate (NO_3^-), phosphate (PO_4^{3-}) and chloride (Cl^-) concentrations of pore water, surface water and extraction subsamples stored at −20 °C were determined by colorimetric methods (Auto Analyser III, Bran and Luebbe GmbH, Norderstedt, Germany), and Sodium (Na) concentrations using flame photometry (FLM3 Flame Photometer, Radiometer, Copenhagen, Denmark). In NaCl extractions, Na and Cl^- were not measured. In the acidified subsamples, K, and P were measured using inductively coupled plasma optical emission spectrometry (ICP-OES) (Thermo Fischer Scientific, Bremen, Germany).

Pore water CH_4 was measured in the headspace of the exetainers using an HP 5890 gas chromatograph equipped with a Porapak Q column (80/100 mesh) and a flame ionization detector (GC-FID, Hewlett Packard, Palo Alto, CA, USA). The original concentrations in the pore water were calculated using Henry's law (Sander 2015).

Total N in dry soil and plant material (3 mg of each biomass fraction, i.e. *Sphagnum* capitula or other *Sphagnum* biomass, brownmosses or vascular plants) was determined using an elemental CNS analyser (Vario MICRO cube; Elementar Analysensysteme, Langenselbold, Germany). Total P and total K were determined by ICP-OES after adding 4 mL nitric acid (HNO_3) (65%), 1 mL hydrogen peroxide (H_2O_2) (30%) and 95 mL Milli-Q water to 200 mg dried plant material in Teflon vessels, followed by heating in a microwave oven (EthosD, Milestone, Sorisole Lombardy, Italy). Elemental content was determined by ICP-OES (see above).

2.8. Quantification of nutrient fluxes

To study nutrient sources and sinks of the two areas, we quantified N, P and K contents of plant biomass, peat soils and irrigation water. Total stocks of nutrients in the various biomass fractions (*Sphagnum* capitula, other *Sphagnum* biomass, brownmosses, vascular plants) in November 2018 were calculated as:

$$S_{bm} = \frac{C_{bm} * M_{bm}}{A} * 10 \tag{1}$$

where S_{BM} is the total stock of nutrients in a biomass fraction (kg ha^{-1}), C_{bm} is the concentration of a nutrient in the biomass fraction (g g^{-1}), M_{bm} is the dry weight of the biomass fraction within the sample (g) and A is the area of the sample (0.0081 m^2).

Sequestration rates in the *Sphagnum* were then calculated as:

$$R_{Sph} = (S_{cap} + S_{bulk})/Age_{site} \tag{2}$$

where R_{Sph} is the sequestration rate (kg ha^{-1} yr^{-1}), S_{cap} is the total amount of nutrients stored in the *Sphagnum* capitula (kg ha^{-1}), S_{bulk} is the total amount of nutrients stored in the remaining *Sphagnum* living and dead biomass (kg ha^{-1}) and Age_{site} is the age of the site from installation to November 2018 (yr).

Nutrient input by irrigation water was calculated by multiplying the concentrations of N, P and K in the inlet water with the inflow volume per month from June 2017 until November 2018 (Brust et al., unpublished results). For months in which no water samples were taken (September and December 2017, August 2018) average concentrations of the prior and following month were used. Results for each month were divided by the surface area of the respective production field to estimate the yearly input of N, P and K per hectare. For S2016, a rough yearly budget was made using data from October 2017 until November 2018. Nutrient input and output by irrigation water were calculated as above – the latter by using concentrations at the water outlet and monthly outflow volumes. To estimate the amount of nutrients from sources other than irrigation water, input values were subtracted from the sum of the output and sequestration values.

2.9. Statistical analysis

Statistics were performed using R version 3.5.2 (R Core Team, 2018). Differences in biological (biomass, lawn thickness) and biogeochemical variables (pH, alkalinity, NH_4^+, NO_3^-, P, K, Cl^-) in all transects and depth profiles were tested using general linear models (Pinheiro et al., 2018) followed by analysis of variance (ANOVA). Main effects of site, distance to the ditch, sampling month (if applicable) and their two-way interactions were included in the model. For depth profiles, only the biogeochemical variables were tested (including CH_4) and the main effect of distance to ditch was replaced by depth. Transect and depth profile number were included as a random factor if this decreased Akaike information criterion (AIC) values. Model selection was done by first removing non-significant interactions and then main effects from the model in a backwards stepwise analysis. Residual plots were created for visual assessment of normality and homogeneity. If necessary, data were log transformed to improve normality and homogeneity of residuals. In-text values are averages ± standard errors. Plots were created using ggplot2 (Wickham, 2016).

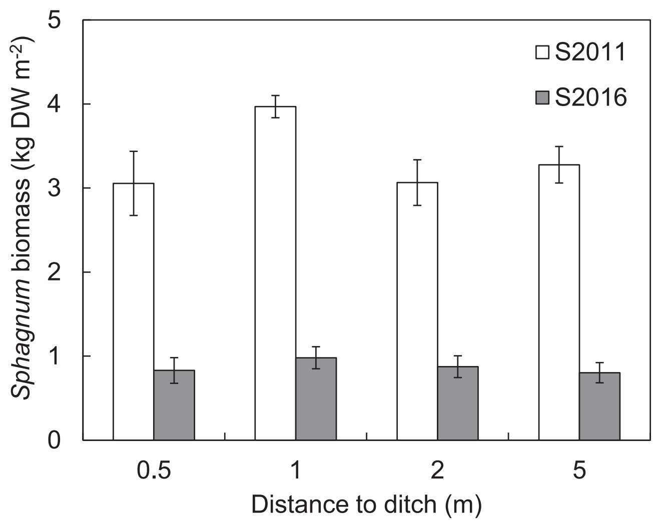

Fig. 2. Mean *Sphagnum* biomass (kg dry weight m^{-2}) at increasing distance to the ditch in November 2018. Error bars represent standard errors (S2011, $n = 6$; S2016, $n = 9$).

3. Results

3.1. Sphagnum biomass accumulation

The older site (S2011) had accumulated the largest *Sphagnum* biomass with the largest lawn thickness. *Sphagnum* dry mass in S2011 reached 3.3 ± 0.2 kg DW m^{-2} in November 2018, which was 3.6 times higher than in S2016 (0.9 ± 0.03 kg DW m^{-2}, $p < .001$; Fig. 2). This is in accordance with the 3.5 times longer growth time in the S2011 site. Resulting dry mass accumulation rates are on average 4.4 and 3.6 ton DW ha^{-1} yr^{-1} in S2011 and S2016, respectively. *Sphagnum* biomass was not affected by the distance to the ditch ($p = .746$). *Sphagnum* lawn thickness was on average 66% higher in S2011 (18.2 ± 0.2 cm) compared to S2016 (11.0 ± 0.3 cm) ($p < .001$) and in S2016 decreased slightly with increasing distance to the ditch (from 11.6 cm at 0.5 m to 9.9 cm at 5 m, $p < .001$). Besides a higher lawn thickness, *Sphagnum* in S2011 had a 2.3 times higher average bulk density than in S2016 (18.5 and 8.0 g DW l^{-1} FW, respectively).

3.2. Ditch water and pore water quality

Pore water alkalinity and P and K concentrations decreased with increasing distance to the ditch, indicating that irrigation water was the main source of these nutrients in the production fields. By contrast, NH_4^+ and NO_3^- were generally low in ditch and pore water.

The pH of the ditch surface water was 5.7 ± 0.1 and 5.5 ± 0.1 in S2011 and S2016, respectively. In the *Sphagnum* lawn, pore water pH was lower, with values ranging from 4 to 4.5 (Figs. 3A, B). In S2011, pH decreased slightly with increasing distance to the ditch ($p = .023$). In November 2018, lawn pH in S2011 dropped to 2.9 ± 0.3 following harvest-related lowering of the water table.

The irrigation ditches contained weakly buffered water (alkalinity <0.5 meq L^{-1}) throughout this study, but alkalinity in the *Sphagnum* lawn already dropped to (near-)zero values within the first 0.5 m distance to the ditch (Fig. S1). HCO_3^- in ditches was 102 ± 30 μmol L^{-1} in S2011 and 139 ± 30 μmol L^{-1} in S016 (Table S1).

The irrigation water in the ditches had chloride (Cl^-) concentrations below 1500 μmol L^{-1} (Fig. 3C, D). During summer, pore water Cl^- concentrations increased in the *Sphagnum* lawn, with concentrations typically becoming higher than those in the ditches, indicative of evapotranspiration. In addition, Cl^- concentrations increased slightly with increasing distance to the ditch ($p = .012$). Porewater Cl^- concentrations showed a drastic increase, up to 3.77 mmol L^{-1} in the centre of the S2011 field in November 2018 after harvest-related lowering of the water table.

Porewater NH_4^+ concentrations were generally low in the lawns (<40 μmol L^{-1}) and increased with increasing distance to the ditch ($p = .001$), particularly at S2016 ($p = .007$) (Fig. 4A, B). At S2011, NH_4^+ concentrations increased in time throughout the lawn ($p < .001$).

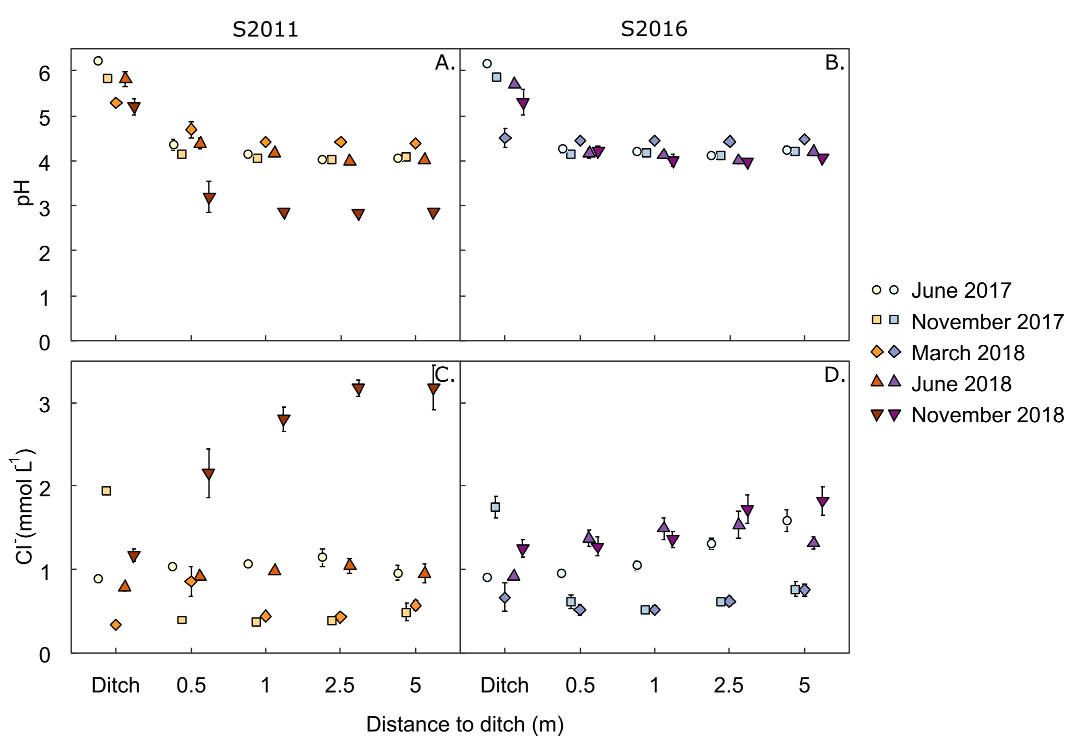

Fig. 3. Development in time of pore water pH (A, B) and Cl^- concentrations (μmol L^{-1}) (C, D) in the upper 10 cm of soil in the production fields at increasing distance to the irrigation ditch. Left hand panels: S2011, right hand panels: S2016. Error bars indicate standard errors ($n = 6$ for S2011; $n = 9$ for S2016 at each sampling date and distance).

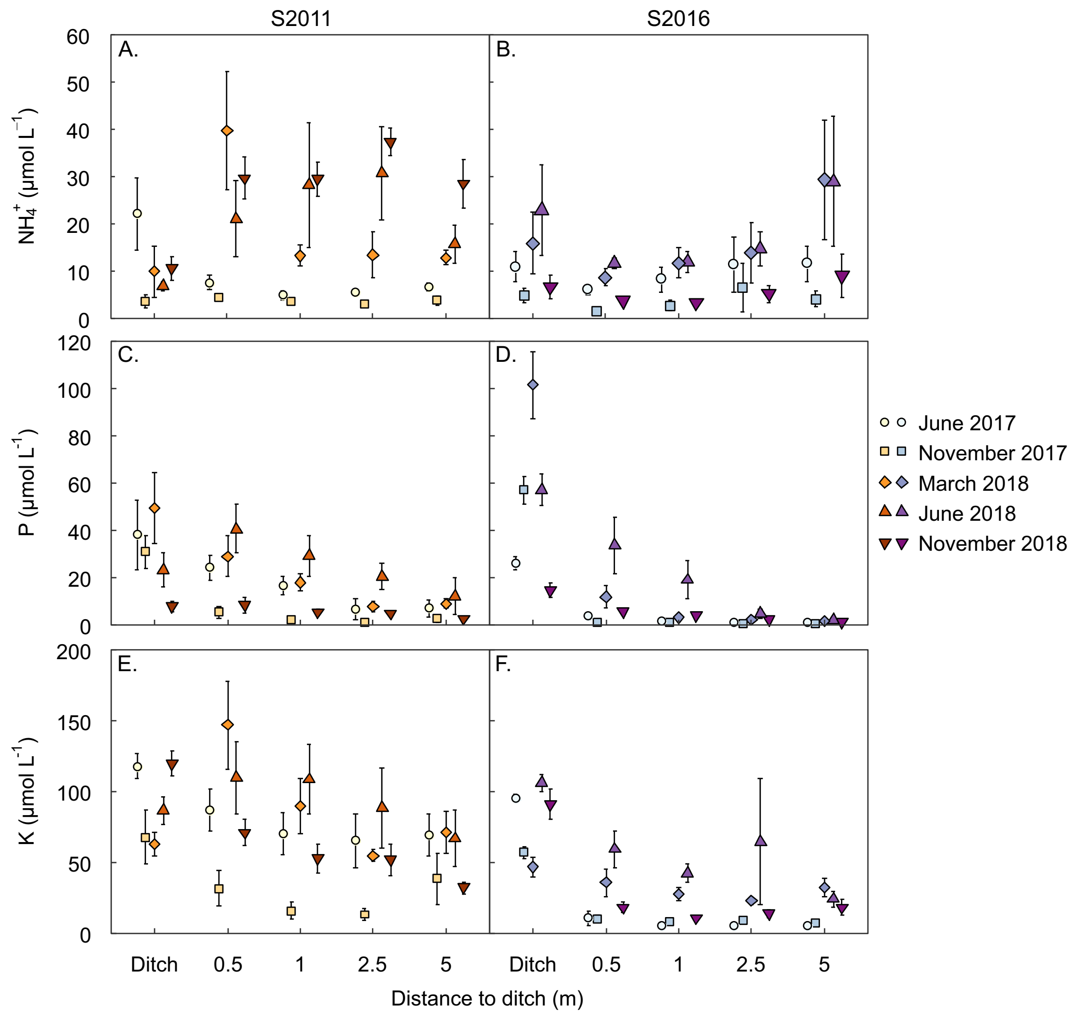

Fig. 4. Development in time of pore water NH_4^+ (A–B), P (C–D) and K (E–F) in the upper 10 cm of soil in the production fields at increasing distance to the irrigation ditch. Left hand panels: S2011, right hand panels: S2016. Error bars indicate standard errors ($n = 6$ for S2011; $n = 9$ for S2016 at each sampling date and distance).

Porewater NO_3^- concentrations in ditches and lawns were negligible (<20 μmol L^{-1}) (Fig. S2). NH_4^+ concentrations in ditch surface water decreased from 36.8 ± 6.8 μmol L^{-1} at the inlet to 12.1 ± 1.8 μmol L^{-1} at the outlet ($p < .001$).

Ditch water appeared to be a prominent source of P in the production fields, as shown by concentrations in ditches being generally higher than lawn concentrations (Fig. 4C, D). Concentrations in the lawn pore water were higher in S2011 compared to S2016 ($p < .001$). P concentrations in the pore water decreased with increasing distance to the ditch ($p < .001$), from 29.8 ± 5.1 (ditch) to 7.5 ± 1.8 μmol L^{-1} (5 m from ditch) in S2011 (75% decrease) and from 51.3 ± 5.6 to 1.2 ± 0.1 μmol L^{-1} in S2016 (98% decrease), with steepest P gradients in sampling months June and March. Ditch surface water P concentrations did not change with increasing distance to the inlet ($p = .06$).

K showed similar patterns to P, with higher concentrations in the ditches than in the lawns (Fig. 4E, F). Pore water K concentrations were higher in S2011 (71.5 ± 4.0 μmol L^{-1}) than in S2016 (33.8 ± 2.8 μmol L^{-1}, $p < .001$). Similar to P, pore water K concentrations decreased with increasing distance to the ditch, on average over all sampling dates from 90.8 ± 6.6 (ditch) to 55.4 ± 7.1 μmol L^{-1} (5 m from ditch) in S2011 and from 79.1 ± 4.5 to 17.5 ± 2.5 μmol L^{-1} in S2016 (average ± SE, $p = .037$). Contrary to P, ditch surface water K concentrations decreased with increasing distance to the inlet ($p < .001$): from 78.3 ± 9.7 μmol L^{-1} at the inlet to 55.2 ± 14.8 μmol L^{-1} at the outlet.

3.3. Water quality in peat depth profiles

Pore water NH_4^+ concentrations at 0.06 m depth remained low (<40 μmol L^{-1}) throughout the entire period at both sites (Fig. 5A, B), while concentrations in deeper layers in S2016 were considerably higher than in S2011 ($p < .001$). In S2016 however, a decrease over time was observed ($p = .002$), most prominently at 0.5 m depth (54% decrease on average). NO_3^- concentrations were negligible (2.4 μmol L^{-1} on average (Fig. S3). In comparison, pore water P concentrations (14.9 ± 1.3 μmol L^{-1}) did not change over time ($p = .097$), but P levels increased with depth in S2016 ($p < .001$) (Fig. 5C, D). Pore water K concentrations increased with depth in S2016 ($p < .001$), while concentrations were similar throughout depth in S2011 (Fig. 5E, F). K concentrations at 0.06 and 0.25 m depth were on average twice as high in S2011 than in S2016. CH_4 was absent from pore water at 0.06 m depth in S2011, and CH_4 concentrations were lower than in S2016 ($p < .001$) (Fig. 5G, H). CH_4 concentrations increased with depth in both sites ($p < .001$), and in S2016, CH_4 concentrations decreased over time ($p = .001$).

3.4. Nutrient storage in the sphagnum biomass

Both sites accumulated high amounts of N, P and K in the newly formed biomass since their installation (Table 1). *Sphagnum* biomass

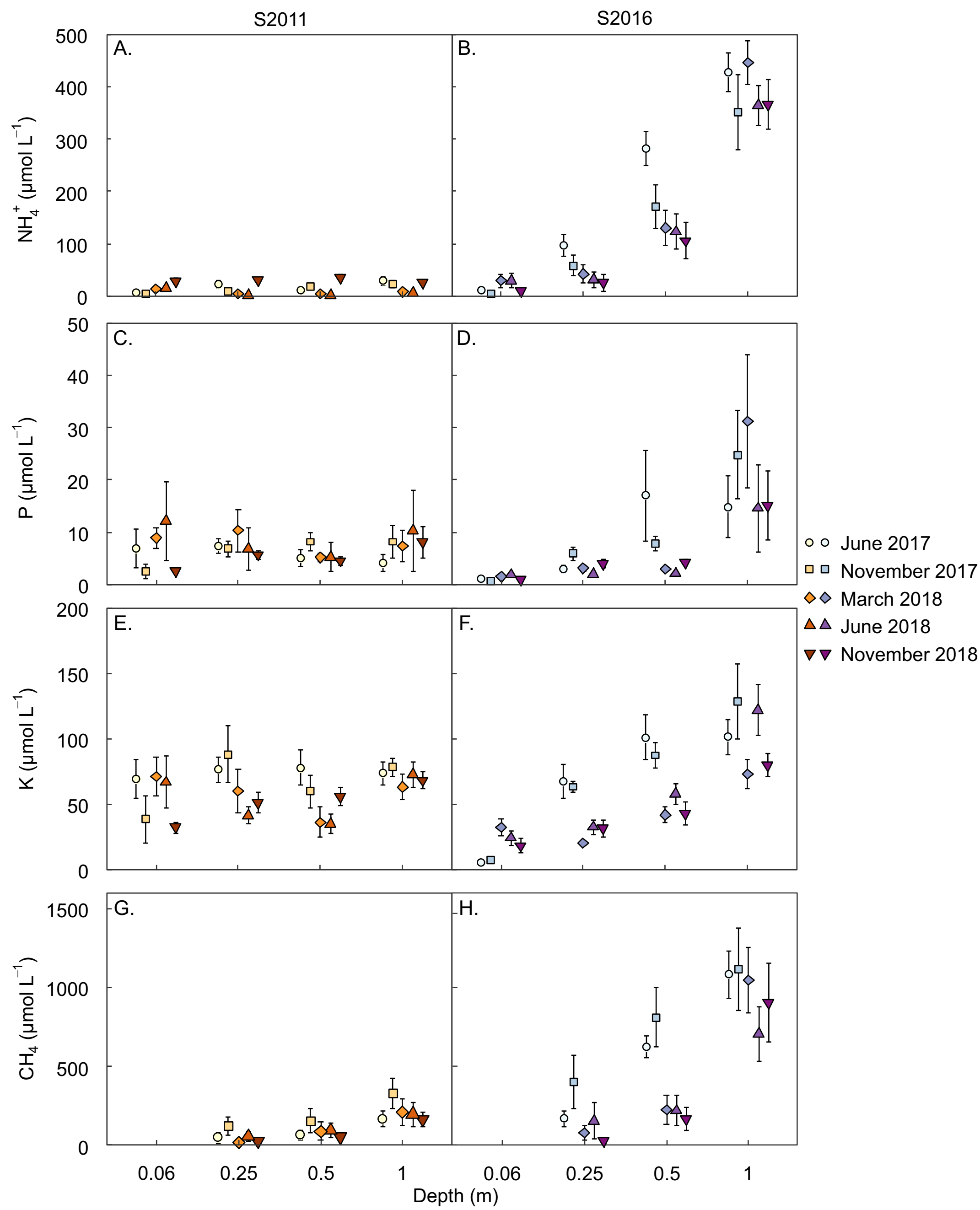

Fig. 5. Development in time of pore water NH_4^+ (A–B), P (C–D), K (E–F) and CH_4 (G–H) at 0.06, 0.25, 0.5 and 1 m depth in the centre of the production fields. Left hand panels: S2011, right hand panels: S2016. CH_4 concentrations were not measured at 0.06 m depth. Error bars indicate standard errors ($n = 6$ for S2011; $n = 9$ for S2016 at each sampling date and depth).

in S2011 had higher concentrations of N and P than in S2016. Average sequestration rates in total *Sphagnum* biomass were similar for both sites, except the lower K sequestration rate in S2011. This hints at K saturation in this site, which is further supported by an accumulation of K in the *Sphagnum* biomass, indicated by a very low N:K ratio compared to underlying peat soil and living *Sphagnum* capitula. The entire lawn biomass (i.e. *Sphagnum*, other mosses and higher plants) sequestered 46.0 ± 2.3 kg N, 3.9 ± 0.4 kg P and 9.8 ± 0.7 kg K ha^{-1} yr^{-1} in S2011 and 47.4 ± 3.2 kg N, 4.9 ± 0.9 kg P and 16.1 ± 1.2 kg K ha^{-1} yr^{-1} in S2016.

Table 1
Nutrient storage in plant biomass at the differently aged Sphagnum farming sites (averages ± standard errors, $n = 30$ in S2011 and $n = 45$ for S2016).

Site		N	P	K
S2011	Total amount in total *Sphagnum* biomass (kg) at 0.815 ha accumulated over 7.5 years	226.9 ± 11.2	17.2 ± 1.2	38.4 ± 2.8
	Sequestration rate in total *Sphagnum* biomass (kg ha^{-1} yr^{-1})	36.3 ± 1.8	2.8 ± 0.2	6.2 ± 0.5
	Sequestration rate in entire plant biomass (kg $ha^{-1}yr^{-1}$)	46.0 ± 2.3	3.9 ± 0.3	9.8 ± 0.7
S2016	Total amount in *Sphagnum* biomass (kg) at 2.8 ha accumulated over 2.5 years	239.1 ± 19.2	24.8 ± 2.5	82.9 ± 6.0
	Sequestration rate in total *Sphagnum* biomass (kg ha^{-1} yr^{-1})	35.3 ± 2.8	3.7 ± 0.4	12.3 ± 0.9
	Sequestration rate in entire plant biomass (kg ha^{-1} yr^{-1})	47.4 ± 3.2	4.9 ± 0.5	16.1 ± 1.2

3.5. Nutrients in irrigation water, ditch sediment and levees

In S2011, inflow of canal water for irrigation took place from March till August 2017 and from February through November in 2018. For S2011, estimated resulting nutrient inflows were 0.46 kg N, 0.56 kg P and 4.04 kg K ha^{-1} in 2017 (June–December), and 7.0 kg N, 4.87 kg P and 22.30 kg K ha^{-1} in 2018 (January–November). For S2016, estimated nutrient inflows were 0.84 kg N, 1.14 kg P and 7.41 kg K ha^{-1} in 2017 (June–December) and 3.91 kg N, 3.31 kg P and 15.84 K kg ha^{-1} in 2018 (January–November). Outflows from S2016 were lower than inflows for total N (N_{tot}), but higher for P and K. The resulting nutrient budget suggests substantial nutrient inputs from sources other than irrigation water (Table 2). Next to irrigation water, ditch sediment and levee soil had high concentrations of NH_4^+, P and K in both sites, but concentrations were lower in S2011. NH_4^+ in the levees is highest in the deepest layer (50–90 cm), whereas P and K are similar at all depths.

4. Discussion

Drainage of peatlands for agriculture and forestry strongly affects the climate and environmental quality globally. Paludiculture, as an alternative land use option after rewetting, stops peat losses and reduces GHG emissions, while allowing the cultivation of biomass for food, fodder, fibres and fuel to continue (Wichtmann et al., 2016). We here demonstrated that Sphagnum farming enables considerable yields, nutrient sequestration, and reduction of soil nutrient stocks. Irrigation with ditch water provided a homogeneous and sufficient supply of water and nutrients to the entire production field. Nutrients that had accumulated in the soil during former drainage-based agriculture dramatically declined after rewetting.

4.1. Sphagnum yields and C sequestration

Our field study demonstrated that *Sphagnum* biomass production (on average 4.4 ton DW ha^{-1} yr^{-1} in S2011 and 3.3 ton DW ha^{-1} yr^{-1} in S2016) was distributed homogeneously at both sites, independent of the distance to the irrigation ditch. The combination of sufficient water supply, adequate lateral infiltration, and an appropriate quality (low alkalinity and sufficient P and K) of the irrigation water allowed considerable *Sphagnum* growth (Temmink et al., 2017; Wichmann et al., 2014). Growth rates were comparable to natural bog systems with mean dry mass productivities of ca. 4 ton ha^{-1} yr^{-1} for *S. fallax* (Gunnarsson, 2005), 4.7 ton ha^{-1} yr^{-1} for *S. palustre* (Krebs et al., 2016) and 2.3 ton ha^{-1} yr^{-1} for *S. papillosum* (Krebs et al., 2016). Water levels close to the capitula provided optimal moisture levels for photosynthesis causing high C accumulation rates (Robroek et al., 2009; Schouwenaars and Gosen, 2007). These *Sphagnum* growth rates are favourable for the climate, because - although this C stock is planned to be harvested, used and oxidized – the newly grown *Sphagnum* biomass is a renewable resource and will be used to substitute fossil peat, while rewetting simultaneously stops the mineralisation of the underlying peat.

Our irrigation water was low in alkalinity and HCO_3^- (<0.5 meq L^{-1} and 18–488 μmol HCO_3^- L^{-1}), and *Sphagnum* appeared to be successful in compensating this alkalinity through acidification (cf. Clymo, 1963; Soudzilovskaia et al., 2010), which was illustrated by the fact that all HCO_3^- had already disappeared from the *Sphagnum* lawn within the first 0.5 m from the irrigation ditch.

4.2. Nutrient sequestration in Sphagnum farming

Nutrients in the Sphagnum farming site came from multiple sources: irrigation water, atmospheric deposition, and soils within the site. N concentrations were rather low in the water of the irrigation ditches and the canal 'Schanze' (the origin of the irrigation water). These low NO_3^- concentrations may be attributed to rapid denitrification in the ditches and *Sphagnum* lawn (Novak et al., 2019; Veraart et al., 2011). We therefore assume that the N sequestered in the biomass primarily originated from wet and dry atmospheric deposition (17–25 kg N ha^{-1} yr^{-1}; UBA, 2016; University of Rostock, unpublished data). Such a high N load could be detrimental to *Sphagnum* growth, but the high concentrations of P and K (>8 μmol P and >90 μmol K L^{-1}) in the irrigation water apparently balanced the high N inputs. These nutrients originated in part from the canal 'Schanze', but the nutrient budget suggests a substantial additional within-site source of K and especially P. Erosion from the levees, constructed from the removed agricultural top soils, could

Table 2
Average concentrations ± standard errors of NH_4^+, P and K in different fractions of S2011 and S2016, sampled in November 2018 and the nutrient budget estimation for S2016. N_{tot} represents the sum of NH_4^+ and NO_3^- in water samples and extractions, and total N in biomass samples. The balance for S2016 was calculated by subtracting the irrigation inflow from the sum of irrigation outflow and *Sphagnum* sequestration. FW: fresh weight. N/A: not applicable. Biomass and peat pore water: $n = 30$ and $n = 45$ for S2011 and S2016, respectively; ditch water and sediment, and peat and levee soil: $n = 6$ and $n = 9$ for S2011 and S2016, respectively; for canal surface water and canal pore water single values are given ($n = 2$).

Fraction	Sample type	Unit	S2011			S2016		
			N_{tot}	P	K	N_{tot}	P	K
Sphagnum capitula	Biomass	μmol L^{-1} FW	14,548 ± 608	589 ± 45	1362 ± 112	7707 ± 479	437 ± 34	1299 ± 73
Other *Sphagnum* biomass	Biomass	μmol L^{-1} FW	13,796 ± 685	466 ± 28	821 ± 49	7660 ± 435	334 ± 23	930 ± 62
Total lawn vegetation	Biomass	μmol L^{-1} FW	13,860 ± 755	523 ± 41	1056 ± 81	7829 ± 452	343 ± 26	894 ± 43
Ditch surface water	Water	μmol L^{-1}	11 ± 6	8 ± 2	120 ± 9	4 ± 1	15 ± 3	91 ± 11
Ditch pore water	Water	μmol L^{-1}	228 ± 93	73 ± 27	118 ± 3	221 ± 151	121 ± 50	103 ± 12
Ditch sediment	Milli-Q extraction	μmol L^{-1}	329 ± 39	47 ± 27	158 ± 12	262 ± 49	72 ± 89	160 ± 13
Peat pore water 6 cm	Water	μmol L^{-1}	32 ± 2	5 ± 2	52 ± 10	5 ± 1	3 ± 1	15 ± 4
Peat pore water 25 cm	Water	μmol L^{-1}	39 ± 4	6 ± 1	51 ± 8	26 ± 16	4 ± 1	31 ± 7
Peat pore water 50 cm	Water	μmol L^{-1}	45 ± 5	4 ± 1	56 ± 7	106 ± 35	4 ± 1	43 ± 9
Peat pore water 100 cm	Water	μmol L^{-1}	30 ± 4	8 ± 3	68 ± 6	367 ± 46	15 ± 7	80 ± 9
Sphagnum biomass	NaCl extraction	μmol L^{-1} FW	14 ± 5	7 ± 3	192 ± 27	N/A	N/A	N/A
Peat soil 0–10 cm	NaCl extraction	μmol L^{-1} FW	15 ± 3	6 ± 1	75 ± 16	27 ± 5	3 ± 1	135 ± 33
Peat soil 10–30 cm	NaCl extraction	μmol L^{-1} FW	12 ± 1	4 ± 1	48 ± 7	98 ± 34	4 ± 2	132 ± 41
Peat soil 30–50 cm	NaCl extraction	μmol L^{-1} FW	19 ± 3	4 ± 1	47 ± 10	205 ± 59	4 ± 1	144 ± 19
Levee soil 0–10 cm	Milli-Q extraction	μmol L^{-1} FW	486 ± 165	162 ± 35	270 ± 49	374 ± 141	306 ± 36	264 ± 77
Levee soil 10–50 cm	Milli-Q extraction	μmol L^{-1} FW	288 ± 106	54 ± 12	71 ± 21	497 ± 201	256 ± 45	203 ± 88
Levee soil 50–90 cm	Milli-Q extraction	μmol L^{-1} FW	852 ± 139	116 ± 24	110 ± 23	652 ± 157	292 ± 38	189 ± 27
Canal surface water	Water	μmol L^{-1}	51; 109	4; 3	103; 109	N/A	N/A	N/A
Canal pore water	Water	μmol L^{-1}	139; 242	54; 97	104; 119	N/A	N/A	N/A
Irrigation inflow	Water	kg ha^{-1} yr^{-1}				3.91	3.31	15.84
Lawn vegetation sequestration	Biomass	kg ha^{-1} yr^{-1}				47.40	4.90	16.10
Irrigation outflow	Water	kg ha^{-1} yr^{-1}				2.58	10.14	4.25
Balance (non-irrigation input)		kg ha^{-1} yr^{-1}				46.08	11.73	4.51

have led to mobilization and subsequent release of nutrients to the ditch water. Moreover, dredged material from ditches and mown plants removed from the production fields were periodically deposited on the levees, accelerating nutrient cycling between levees and ditch water (Gaudig et al., 2018; Temmink et al., 2017). Fortunately, the high nutrient concentrations are present in non-toxic ratios that allow lasting *Sphagnum* growth and high yields (Fritz et al., 2012; Temmink et al., 2017). Although we observed well-growing *Sphagnum* in connection with high and stoichiometrically balanced nutrient levels, they may still lead to problems for Sphagnum farming. High nutrient levels promote the growth of more competitive vascular plants and more eutrophic mosses, outcompeting *Sphagnum* spp. for light (Harpole and Tilman, 2007; Limpens et al., 2004; Tomassen et al., 2003). Consequently, frequent mowing and proper management of the water table are essential to prevent unwanted competition of vascular plants at the cost of *Sphagnum* growth (Gaudig et al., 2018, 2014).

The *Sphagnum* vegetation has the potential to sequester high quantities of nutrients either in plant biomass or in the soil matrix, preventing them from leaching back into the ditches. S2011 and S2016 sequestered 46 and 47 kg N, 4 and 5 kg P and 10 and 16 kg K ha^{-1} $^{-}yr^{-1}$, respectively - values similar to those found by Temmink et al. (2017) for the preceding years. However, lower P and K sequestration rates as well as higher pore water P and K concentrations in S2011 could indicate saturation in this site, which can, however, be countered by periodic harvesting the *Sphagnum* biomass.

Porewater depth gradients clearly demonstrated that N, P, K, and CH_4 concentrations substantially declined within the first year after installation in the newer site (S2016), whereas in the older site (S2011) concentrations were low already. Interestingly, CH_4 pools, also at larger depths (>50 cm), were very low in S2011, highlighting the importance of young, easily decomposable C to produce substrates (incl. acetate, hydrogen, and CO_2) for CH_4 formation (Clymo and Bryant, 2008). Low nutrient concentrations in S2011 indicate that the decline in soil pore water concentrations will likely continue in S2016. The decrease in nutrient concentrations at larger depths shows the great potential of Sphagnum farming for soil recovery.

4.3. Further optimization of Sphagnum farming design

Although our results clearly highlight that Sphagnum farming has great potential for land rehabilitation, it is important to note that various elements in the design can be improved. Although the rather small outflow volume of irrigation water (Brust et al., 2018) illustrates an optimal water use efficiency, helophyte filters could further improve the quality of both the outflowing and the inflowing water, decreasing downstream pollution and on-site nutrient loads. The nutrient input from the levees into the ditches raises the question whether the levees and causeways are required to manage the *Sphagnum* production fields or whether specialized machinery could be capable of driving directly on the fields without damaging the moss layer. Alternatively, levees could be constructed from other materials. The fate of the top soil is an important consideration, especially in terms of GHG emissions. Smolders et al. (2019) recently introduced the ‘topping up’ concept: the removal of topsoil from one place to raise the surface in another place. Although topping up allows to raise the overall water levels (with a reduction of GHG emissions and soil subsidence as a consequence) and to locally continue conventional drainage-based agriculture, the concept – similarly to the Hankhausen Sphagnum farm -

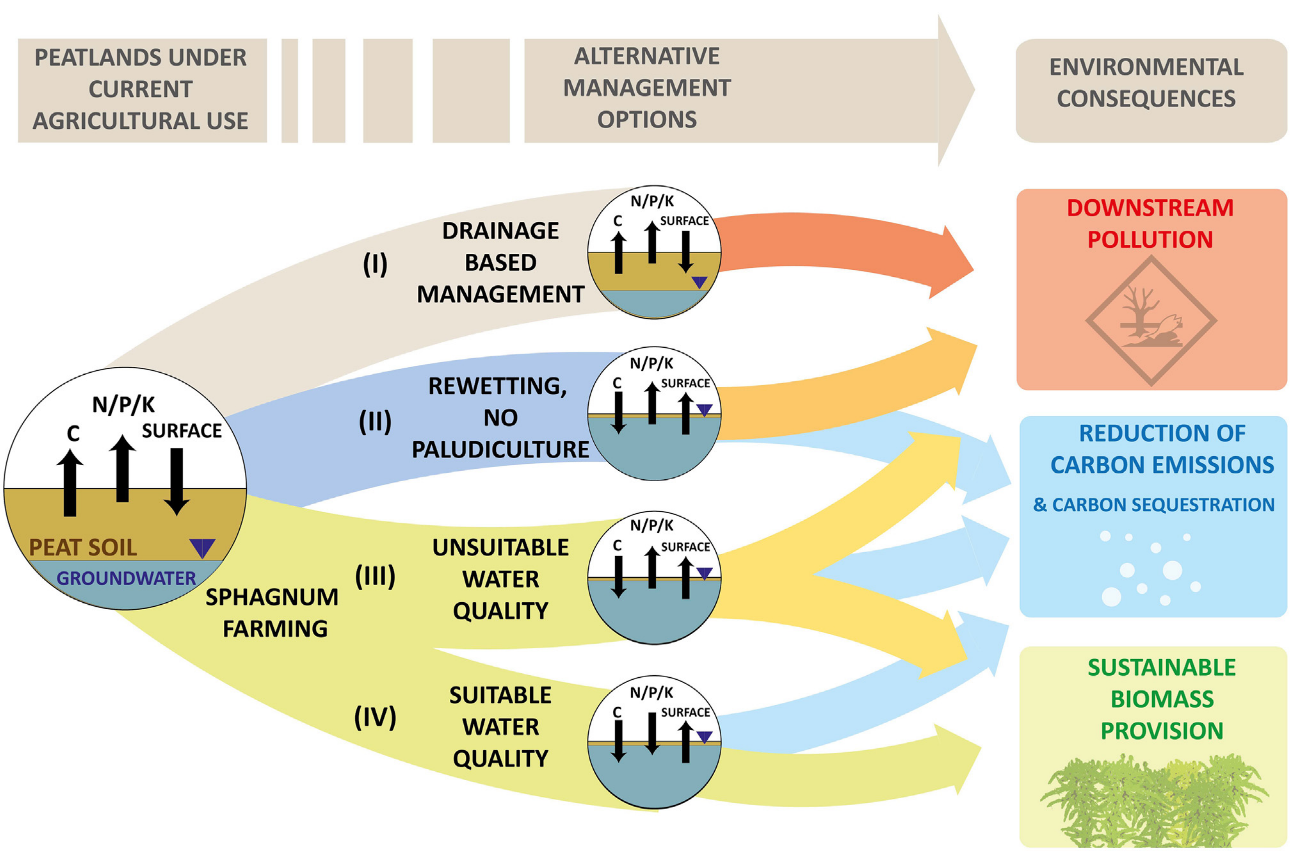

Fig. 6. Indicative environmental effects of alternative types of land use on drained agriculturally used bogs. I) Continuation of the current drained situation with continuing surface height loss, GHG emissions and downstream pollution from peat oxidation and fertilizer use (grey), II) Rewetting without paludiculture (blue) and III) Rewetting with paludiculture, i.c. Sphagnum farming (green), with supply of IIIa) ‘unsuitable’ or IIIb) ‘suitable’ water. By effective rewetting, peat C is conserved and ‘new’ peat may even be sequestered. Sphagnum farming provides sustainable biomass yields and reduces (IIIa) or prevents (IIIb) downstream pollution by sequestering nutrients and by denitrification. Blue triangles indicate the groundwater tables.

does not allow the complete stop of subsidence and CO_2-emissions from the 'topped-up' areas, as is implicitly required by the Paris Agreement (IPCC, 2018). Lastly, the current design of the Sphagnum farming site heavily relies on irrigation ditches (Brust et al., 2018; Gaudig et al., 2018, 2014). Ditches are a major source of CH_4 (Günther et al., 2017; Kosten et al., 2019; Schrier-Uijl et al., 2011, 2010) and the overall GHG balance of a Sphagnum farming site could greatly benefit from the reduction of this source. The surface area ratio of ditches and fields could be lowered if this does not affect *Sphagnum* growth. Alternatively, water could be supplied in a different way, for instance via irrigation/drainage pipes.

4.4. Sphagnum farming as an alternative for drainage-based agriculture on peat soils

Recent studies have summarized the impact of various forms of land-use on the environment, including GHG emissions and eutrophication (Clark and Tilman, 2017; Clark et al., 2019). To minimize these impacts, we must develop and implement novel types of land use.

The prevention of nutrient runoff from agriculture is of vital importance to avoid downstream pollution. The observed soil remediation and nutrient sequestration show the great potential of Sphagnum farming in reducing downstream pollution, hereby restoring an original ecosystem service of natural peatlands. Yet, we obviously cannot expect that water quality is adequate everywhere to cultivate *Sphagnum*. A clear example are the extensive peatlands in the western part of the Netherlands, which have a well-maintained water infrastructure, but surface water that is particularly rich in HCO_3^-, with concentrations reaching 4–5 mmol HCO_3^- L^{-1} or even higher (van de Riet et al., 2018; Van Diggelen et al., 2018). Here, pre-treatment of the irrigation water would be required to lower alkalinity and nutrient levels (cf. García et al., 2010).

Peatlands drained for agriculture and forestry are currently responsible for huge GHG emissions from a rather small area. With respect to reducing GHG emissions, the improved management of peat soils (incl. rewetting of drained peatlands) is considered as one of the most promising options ("Project Drawdown", 2019). Although ditches used in Sphagnum farming may continue to emit CH_4, the long-term warming effect will be strongly reduced compared to continued CO_2 emissions from drained peatlands (Günther et al., 2020). Rapidly depleted soil CH_4 stocks and low GHG emissions from *Sphagnum* lawns (Günther et al., 2017) further advocate the positive climate impact of Sphagnum farming as a land-use alternative.

4.5. Conclusion

In a broader perspective, the global degradation of peatlands critically requires sustainable solutions for landscape-scale restoration. Novel land-use options such as Sphagnum farming and other forms of paludiculture, which prevent peat degradation while still ensuring production, are vital alternatives to drainage-based farming to tackle this global challenge (Fig. 6). We argue that Sphagnum farming on formerly drained and agriculturally used peatlands may offer a viable approach for large scale and sustainable biomass production while preserving the peat, reducing GHG emissions, and preventing downstream pollution.

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CRediT authorship contribution statement

Renske J.E. Vroom: Investigation, Data curation, Writing - original draft, Visualization, Methodology.**Ralph J.M. Temmink:**Investigation, Data curation, Writing - original draft, Visualization, Methodology.**Gijs van Dijk:**Investigation, Resources, Writing - original draft, Visualization, Methodology.**Hans Joosten:**Writing - review & editing, Supervision. **Leon P.M. Lamers:**Writing - review & editing, Supervision.**Alfons J.P. Smolders:**Writing - review & editing, Supervision.**Matthias Krebs:** Writing - review & editing, Project administration.**Greta Gaudig:**Writing - review & editing, Project administration.**Christian Fritz:**Conceptualization, Methodology, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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