# Topsoil removal for *Sphagnum* establishment on rewetted agricultural bogs

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**Abstract** Rewetting drained agricultural peatlands aids in restoring their original ecosystem functions, including carbon storage and sustaining unique biodiversity. 30–60 cm of topsoil removal (TSR) before rewetting for *Sphagnum* establishment is a common practice to reduce nutrient concentrations and greenhouse gas emissions, and increase water conductivity. However, the topsoil is carbon-dense and preservation in situ would be favorable from a climate-mitigation perspective. The effect of reduced TSR on *Sphagnum* establishment and nutrient dynamics on degraded and rewetted raised bogs remains to be elucidated. We conducted a two-year field experiment under *Sphagnum* paludiculture management with three TSR depths: no-removal (TSR0), 5–10 cm (TSR5), and 30 cm (TSR30) removal. We tested the effects of TSR on *Sphagnum* establishment and performance, nutrient dynamics, and hotspot methane emissions. After two years, TSR5 produced similar *Sphagnum* biomass as TSR30, while vascular plant biomass was highest in TSR0. All capitula nitrogen (N > 12 mg/g) indicated N-saturation. Phosphorus (P) was not limiting (N/P < 30), but a potential potassium (K) limitation was observed in year one (N/K > 3). In TSR0, ammonium concentrations were > 150 μmol/l in year one, but decreased by 80% in year two. P-concentrations remained high (*c.* 100 μmol/l) at TSR0 and TSR5, and remained low at TSR30. TSR30 and TSR5 reduced hotspot methane emissions relative to TSR0. We conclude that all TSR practices

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have their own advantages and disadvantages with respect to *Sphagnum* growth, nutrient availability and vegetation development. While TSR5 may be the most suitable for paludiculture, its applicability for restoration purposes remains to be elucidated. Setting prioritized targets when selecting the optimal TSR with peatland rewetting is pivotal.

**Keywords** *Sphagnum* paludiculture · Bog restoration · Sustainable land use · Nutrient dynamics · Peat

## Introduction

Peatlands are unique ecosystems, because they cover only 3% of Earth's surface and store almost a third of terrestrial carbon, making them the carbon-densest ecosystem worldwide (Gorham 1991; Leifeld & Menichetti 2018; Scharlemann et al. 2014; Temmink et al. 2022). Despite this importance, approximately half of the peatlands in Europe and more than half in Southeast Asia have been drained to be used for agricultural purposes, turning them from carbon sinks into major sources of carbon dioxide ($CO_2$) through accelerated peat oxidation (Bonn et al. 2016; Fluet-Chouinard et al. 2023; Hooijer et al. 2010). Peatland drainage further leads to severe and long-term land subsidence and increased flood risk in coastal areas, susceptibility to peat fires, and loss of unique biodiversity (Page & Baird 2016; Renger et al. 2002; Tapio-Biström et al. 2012).

To mitigate these adverse effects, rewetting is a long-term option to restore the carbon storage function of peatlands, stop land subsidence, bring back the water retention capacity and restore lost biodiversity (Günther et al. 2020; Joosten et al. 2017; Nugent et al. 2018; Temmink et al. 2023a). Furthermore, rewetting rapidly reduces $CO_2$ emissions and can lead to the return of the carbon sequestration function of the peatland on the long-term (Günther et al. 2020; Zerbe et al. 2013). However, rewetted formerly intensively-drained peatlands that were in agricultural use can be susceptible to nutrient mobilization (especially phosphorus and nitrogen) and high methane ($CH_4$) emissions (Harpenslager et al. 2015; Hemes et al. 2018; Zak & Gelbrecht 2007). In addition, in bogs—peatlands predominantly fed by precipitation (Joosten et al. 2017)—high nutrient levels typically favor more common and fast-growing plants, as they easily outcompete peatland-specific species, such as *Sphagnum* (Barkman 1992; Grünig 1994). As such, the natural development of peatland-specific vegetation is a slow process, especially if no other management measures are taken, such as reprofiling and/or removal of the existing vegetation (Kreyling et al. 2021; Mackin et al. 2017).

To promote fast establishment of a *Sphagnum* lawn in paludiculture (sustainable agriculture and forestry on rewetted peatlands) or to facilitate rapid establishment of target species in bog restoration, it is common practice to remove 30 to 60 cm top peat layer before rewetting (Allison & Ausden 2004; Gaudig et al. 2018; Harpenslager et al. 2015; Quadra et al. 2023). Topsoil removal (TSR) aims to level the surface and remove the degraded, rooted, low water-conducting and nutrient-rich grass sod layer (~10 cm) (Allison & Ausden 2004; Gaudig et al. 2018; Harpenslager et al. 2015; Quadra et al. 2023). Moreover, TSR strives to create better hydraulic conductivity of the peat surface by exposing the underlying peat that is generally less decomposed, as maintaining the water table level constantly a few centimeters below *Sphagnum* surface—which is important for *Sphagnum* paludiculture (Brust et al. 2018). TSR also removes the nutrient-rich top layer, which creates more suitable (i.e., nutrient-poor(er)) growth conditions for *Sphagnum* and reduces the potential for internal eutrophication and downstream nutrient pollution (Allison & Ausden 2004; Quadra et al. 2023; Zak & Gelbrecht 2007). Quadra et al. (2023) showed that the removal of 20 cm of topsoil results in 25% reduction of pore water phosphorus (P) on intensively managed agricultural peatlands. Temmink et al. (2023a) showed in a *Sphagnum* paludiculture that the nutrient legacy decreased over 10 years with depth, particularly the concentrations of ammonium ($NH_4^+$).

*Sphagnum* naturally thrives in acidic and oligotrophic conditions and their reintroduction on eutrophic and more alkaline peat often leads them to be outcompeted by vascular plants (Bergen et al. 2020; Gunnarsson & Rydin 2000; Heijmans et al. 2002). Under eutrophic conditions, the balance of macronutrients, particularly nitrogen (N), P and potassium (K), can be easily disrupted, especially due to substantially high N availability (Bragazza et al. 2004; Temmink et al. 2017; Vroom et al. 2020; Temmink et al. 2023a). For instance, *Sphagnum*

growth can be hindered by excess of N, leading to saturation or reduced N-uptake efficiency (Limpens et al. 2011). However, recent research demonstrated that *Sphagnum* can thrive under high N conditions when there is sufficient P and K available, i.e. optimal NPK stoichiometry (e.g. Gaudig et al. (2020), Käärmelahti et al. (2023) and Temmink et al. (2017)). Bragazza et al. (2004) suggested that a N/K and N/P quotient in *Sphagnum* capitula below 3 and between 15 and 30, respectively, are optimal for *Sphagnum* growth.

Under N-rich conditions, vascular plants gain a competitive edge over mosses, because they can utilize N that leeches through the upper moss layer for their growth (Lamers et al. 2000; Limpens et al. 2003; Tomassen et al. 2003). If vascular plants are too abundant, they often reduce *Sphagnum* growth through water and nutrient consumption, litterfall and shading (Limpens et al. 2003, 2011; Malmer et al. 1994). Specifically, shading of more than 50% of *Sphagnum* by plants already negatively affects their growth (Clymo & Hayward 1982). At the same time, however, a small amount of vascular plants can be beneficial to *Sphagnum* growth, because shading creates an improved microclimate with less evaporation and more constant temperature, and the plants themselves provide a structuring effect that stimulates vertical moss growth (Pouliot et al. 2011). In the shade, *Sphagnum* cells have a higher water content that has been linked to greener plants (Breemen 1995), with better photosynthetic function, especially during drought periods (Laing et al. 2014). Furthermore, high abundance of vascular plants has also been linked to longer *Sphagnum* shoots (higher lawn), as taller *Sphagnum* are exposed to more light (Pouliot et al. 2011). In addition, *Sphagnum* cover indicates the success of a *Sphagnum* lawn; once green *Sphagnum* covers more than 90% of the surface, the productivity of a *Sphagnum* paludiculture greatly increases (Gaudig et al. 2017).

Rewetting nutrient-rich peat dominated by plants adapted to drained conditions will result in easily decomposable roots and plant biomass, fueling $CH_4$ production and emissions (Bridgham & Richardson 1992; Schrier-Uijl et al. 2011). Although TSR has been found to reduce $CH_4$ emissions post-rewetting, it also removes the stored carbon, which greatly affects the carbon budget of the site at high costs (Daun et al. 2023; Huth et al. 2022; Wichmann et al. 2020; Segers

1998). While TSR of 25 cm can lower $CH_4$ emission by 99% (Harpenslager et al. 2015; Quadra et al. 2023), Quadra et al. (2023) found that removing as little as 5 cm already reduced $CH_4$ emissions by 80%. Taking multiple perspectives into account, it seems that less than 30 cm of TSR can be sufficient for better nutrient conditions for *Sphagnum* establishment, while being carbon-conscious when restoring agricultural bogs (Huth et al. 2022; Quadra et al. 2023). However, it remains to be elucidated how TSR affects nutrient availability and the establishment and productivity of *Sphagnum* and vascular plants in nutrient-rich environment.

To unravel the effects of topsoil removal on *Sphagnum* establishment, we studied how different depths of TSR affect nutrient dynamics, *Sphagnum* performance and biomass accumulation under field paludiculture conditions. We aim to determine whether a *Sphagnum* lawn can successfully established with less TSR in relatively nutrient-rich field conditions. Therefore, we applied three levels of TSR (0, 5–10 and 30 cm) in a large-scale (*c.* 3000 $m^2$) two-year field experiment. Next to this, we provide a snapshot of hotspot $CH_4$ fluxes in the different treatments. We examined how less TSR affects nutrient availability, *Sphagnum* nutrient stoichiometry, *Sphagnum* performance, amount of *Sphagnum* and vascular plants, and hotspot $CH_4$ fluxes. We hypothesized that (i) nutrient mobilization will be higher with less topsoil removal; (ii) 5–10 cm topsoil removal already substantially reduces the competition between vascular plants and *Sphagnum*; (iii) 5–10 cm topsoil removal will show a better nutrient stoichiometry for *Sphagnum* establishment and performance compared to no removal; (iv) 5–10 cm topsoil removal is enough to reduce hotspot fluxes of $CH_4$.

## Materials and methods

Study site and experimental setup

Our study site is part of a 17-hectare *Sphagnum* paludiculture study site located in the peatland Hankhauser Moor in NW Germany (53° 15.80′ N, 08° 16.05 ′E, Fig. 1). The bog, with a 2–2.5 m thick peat layer overlaying sand, has been drained and used as an agricultural grassland for six decades until land use changed to paludiculture. In November 2020,
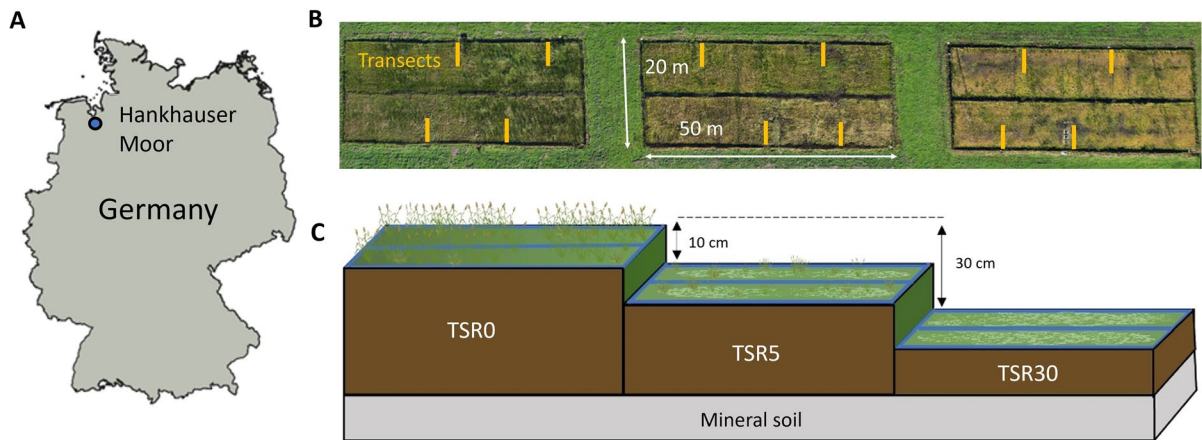
**Fig. 1** **A** The location of the field site in Germany indicated by a blue dot, **B** aerial view of the topsoil removal (TSR) treatments and locations of the sampling transects indicated by yellow lines, and **C** schematic cross-section of the TSR fields. NB: the schematic figure in C is not scaled; the remaining peat thickness is *c.* 2 m. Picture B: R.J.M. Temmink

three fields of 20×50 m were installed by either only milling the surface layer *i.e.* no TSR (named TSR0), or removing the top layer of peat by an excavator in two different depths: 5–10 cm of TSR (named TSR5) and 30 cm of TSR (named TSR30) (Fig. 1). Each field is surrounded by a ring ditch of 0.5×0.5 m (width×depth) and is divided by a ditch in the centre, resulting in two 10×50 m subfields (Fig. 1). A mix of six *Sphagnum* species (*S. papillosum*, *S. cuspidatum*, *S. palustre*, *S. divinum*, *S. medium*, *S. rubellum*, *S. fallax*) or pure *S. fallax* (at the other subfields) was spread over the fields to achieve *c.* 65% initial cover following (Gaudig et al. 2017). Water tables were kept at *c.* 5 cm below the peat moss surface through active water management (i.e., pumping, outlet to prevent flooding, details see Brust et al. 2018). During the growing season, vascular plants were mown 4–6 times (all fields at the same time) a few centimetres above *Sphagnum* surface.

Transect setup and porewater collection

Surface water and porewater samples were collected in four transects from the ditch to the centre of a subfield in each treatment (Fig. 1). At each transect, one ditch surface water sample was collected using a vacuum syringe attached to a ceramic cup sampler (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands; $n=4$ per field). Per transect, four pore-water samples were collected using syringes under

vacuum attached to a rhizon (Rhizosphere Research Products, Wageningen, the Netherlands), placed at 0–10 cm depth relative to the surface. The rhizons were placed at 0.5, 1, 2.5, and 5 m from the ditch ($n=4$ per distance per treatment) following Temmink et al. (2017, 2023a) and Vroom et al. (2020). Water samples were collected five times in 2021 (March, April, June, August, and November) and six times in 2022 (March, May, June, August, September and November). To prevent oxygenation of the samples, syringes were directly closed, stored at 4 °C and processed within two days. Upon processing (see method below) samples were split into two 10 mL subsamples, either stored at −20 °C or after adding 0.1 mL of 65% nitric acid ($HNO_3$) at room temperature, until further chemical analyses.

Biomass, cover and lawn height analyses

Sampling of *Sphagnum* and vascular plants for nutrient analyses and biomass of 2021 (one year after installation) followed methods published previously (Temmink et al. 2017; Vroom et al. 2020), where the samples were collected using quadrats of 10 by 10 cm. The samples were collected from the *Sphagnum* lawn down to the old initial peat surface, which was easily recognized by a much stronger degree of decomposition. These samples were collected at each transect at 0.5 and 5 m from the ditch in August 2021 and November 2022 for nutrient analyses and

November 2021 for biomass. In November 2022, 10 additional biomass samples of 15 by 15 cm per treatment field were collected randomly (Hurlbert 1984) to be analysed for final biomass accumulation two years after installation. The amount of initial *Sphagnum* founder material was determined right after installation in November 2020 using similar random sampling method with 20 samples for each treatment.

For nutrient analyses, vascular plants, *Sphagnum* capitula and stems, and *Sphagnum* founder material were processed separately. All biomass fractions were weighed (fresh weight), dried for 72 h at 70 °C and weighed again (dry weight). Dried *Sphagnum* samples were homogenized at 18,000 rounds per minute for 2 min using 5 mm bullets (bullet grinder Mixer Mill MM 400, Retsch, Haan, Germany). Biomass samples were stored in dry conditions until chemical analyses.

*Sphagnum* (total and green) and vascular plant cover was monitored visually four times during the experiment: October–November 2020, May 2021, April 2022 and November 2022 using the scale of Londo (1976) at 20 randomly located plots (25×25 cm) per treatment (*cf.* Hurlbert 1984). Additionally, the *Sphagnum* lawn height was recorded at five points per plot.

### Greenness index analysis

For *Sphagnum* greenness analyses, 10×10 samples were collected in June 2022 at the transects (see method for biomass sampling) from which three representative shoots were selected by hand and photographed on a white background, in a standardized manner. Subsequently, colour analyses of the *Sphagnum* shoots were performed with the image analysis software ImageJ (Schneider et al. 2012). Specifically, the capitula from each of the shoots was selected by drawing an elliptical shape around it, and the analyses were performed with the Colour Histogram command (three measurements per *Sphagnum* sample). The greenness index of the samples was calculated from the green, red and blue light values of the output, following the formula:

$$\text{Greenness index (mean)} = (2 \times \text{green}) - (\text{red} + \text{blue})$$

The higher the greenness index the greener the plant (high chlorophyll content), which is an indication of better photosynthetic function, and thus growth performance.

### Chemical analyses

Water pH and alkalinity were determined the day after sampling using an Ag/AgCl electrode (Orion Research, Beverly, MA, USA) and a TIM 840 Titration Manager (Radiometer Analytical SAS, Villeurbanne, France). Concentrations of K and P in the water samples preserved with acid were measured using inductively coupled plasma optical emission spectrometry (ICP-OES ARCOS Spectro Analytical; Kleve, Germany). Ammonium ($NH_4^+$) concentrations of water samples stored at $-20$ °C were determined by colorimetric methods following NEN protocols (NEN-EN-ISO 13395:1997; NEN-EN-ISO 11732:2005) adapted to the Seal Auto Analyzer System (SEAL Analytical Ltd., Norderstedt, Germany).

Total N and C in the *Sphagnum* capitula were determined from 4–5 mg of each milled biomass fraction with an elemental CNS analyser (Vario MICRO cube; Elementar Analysensysteme, Langenselbold, Germany). Total P and K were determined by digesting c. 200 mg dried moss material in 4 mL of $HNO_3$ (65%) and 1 mL hydrogen peroxide ($H_2O_2$; 30%) in Teflon vessels, followed by heating in a microwave oven (EthosD, Milestone, Sorisole Lombardy, Italy). Elemental content was determined by inductively coupled plasma optical emission spectrophotometry (ICP-OES, Thermo Fischer Scientific, Bremen, Germany).

### Methane flux measurements

$CH_4$ fluxes were measured three times (once in May and twice in June) during 2022 from partly flooded parts of the field. As Daun et al. (in preparation) already conducted a GHG study on relatively dry fixed sublocations on these fields for annual GHG budget calculations, we selected wetter subsites to study $CH_4$ dynamics on potential emission hotspots. With this we want to highlight the need for measurements with better spatial resolution, as the fluxes during these peak moments can be quite substantial. Gas measurements were carried out using an automatic chamber system with three PVC

chambers per field (volume of 60 L, area of 0.1 m$^2$), which were connected to a Li-COR Trace Gas Analyzer (LI-7810, LI-COR Corporate, Nebraska, USA). The automated system was developed by the Technocentrum at Radboud University in the Netherlands. The chambers have a built-in fan to allow constant airflow. The measurements lasted for 180 s per chamber, with 30 s of flushing time. In total, all treatments had 32 measurements (daytime only). Simultaneously with the gas measurements, the air temperature was logged using a HOBO logger (Onset Computer Corporation, Bourne, MA, USA). CH$_4$ fluxes (mg/m$^2$/d) were calculated following previous publications (Almeida et al. 2016; Paranaíba et al. 2020; Quadra et al. 2023). Briefly, the calculation considers the slope of the relationship between the gas over time; the volume and area of the chamber; atmospheric pressure and air temperature; the gas constant; and the molecular weight of CH$_4$ (16 g/mole).

## Statistical analyses

Statistical analyses were performed using R version 4.1.2 (R Core Team 2021). The effect of TSR and time (factors) on NH$_4^+$, P, K concentrations in porewater; plant biomass; *Sphagnum* lawn height N, P and K concentrations in *Sphagnum* biomass; C/N, N/P and N/K quotients; N, P and K capitula/ stem nutrient allocation; green *Sphagnum* cover; *Sphagnum* lawn height; greenness index and CH$_4$ fluxes (variables) were tested using linear mixed-effects models (lme) or generalized least squares (gls), from package 'nlme' (Pinheiro et al. 2023). Main effects of treatment, year and their interaction were included in the model. Model selection was done by first removing non-significant interactions and then main effects from the model in a backwards stepwise analysis. Normality and homogeneity of the residuals were visually assed for the best fitting model (Zuur et al. 2009). Non-normally distributed data were log10 or square root transformed (Table S1). *Sphagnum* biomass, cover and lawn height were tested only from November 2022. Distance from the irrigation ditch was included as a random effect and, in case of porewater concentrations, sampling time was included as a nested random effect. When differences were significant, a post-hoc test was applied (Tukey multiple comparisons of means) using 'emmeans' (Lenth 2018). Significance was assumed at $p \leq 0.05$. Plots were created using ggplot2 (Wickham 2009). All results are shown with their standard error of the arithmetic mean ($\pm$ SE).

## Results

### Biomass and *Sphagnum* greenness

The initial amount of the spread *Sphagnum* founder material in November 2020 was $77.4 \pm 8.8$ g DW/ m$^2$ (average $\pm$ SE, Fig. 2). *Sphagnum* biomass increased in all treatments from 2021 to 2022 ($p < 0.05$, Table S1, Fig. 2). The average *Sphagnum* biomass productivity two years after installation (November 2022) was highest at TSR5 and TSR30 with $740 \pm 120$ and $740 \pm 78$ g DW/m$^2$, respectively ($p > 0.05$, Table S1). TSR0 had nearly six times lower *Sphagnum* biomass than TS5 and TS30 with $130 \pm 110$ g DW/m$^2$ (Fig. 2). TSR0 had the highest percentage (70%) of plots without any *Sphagnum* biomass. In contrast, vascular plant biomass of $770 \pm 120$ g DW/m$^2$ was the highest at TSR0 compared to the other fields with $330 \pm 71$ at TSR5 and $110 \pm 25$ g DW/m$^2$ at TSR30 ($p < 0.05$, Table S1, Fig. 2). The greenness index in *Sphagnum* capitula was the highest at TSR0 ($31 \pm 2.4$) and lowest at TSR5 ($21 \pm 1.9$; Fig. 2).

### *Sphagnum* cover and lawn height

Total *Sphagnum* cover increased at TSR5 and TSR30 since installation, but decreased at TSR0 (Fig. 3). In November 2022, two years after the installation, green *Sphagnum* cover at TSR5 and TSR30 plots was similarly high (TSR5 $83 \pm 4.4\%$; TSR30 $89 \pm 3.1\%$), but much lower at TSR0 ($10 \pm 5.1\%$; $p < 0.05$, Fig. 3). At TSR0, green *Sphagnum* cover decreased during the first spring (May 2021) to $12 \pm 3.5\%$ and remained low until November 2022, whereas the vascular plant cover increased to $64 \pm 4.7\%$ (Fig. 3). *Sphagnum* lawn was higher at TSR5 in November 2022 with $15 \pm 0.9$ cm and at TSR0 with $12 \pm 1.0$ cm than at TSR30 with $8.0 \pm 0.6$ cm ($p < 0.05$, Table S1, Fig. 3).
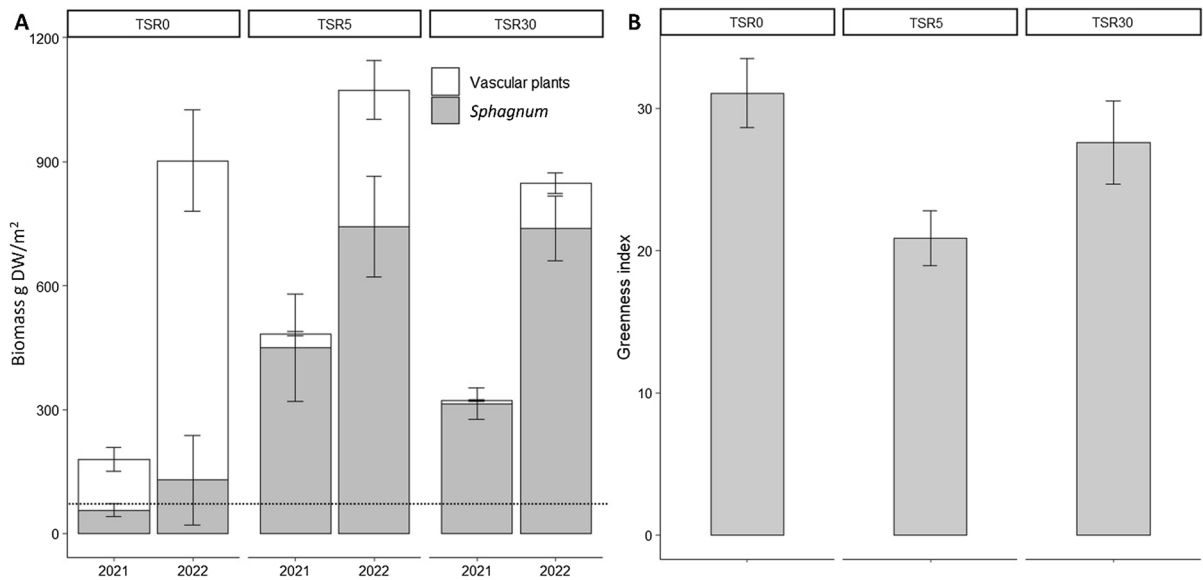
**Fig. 2 A** *Sphagnum* (grey) and vascular plant (white) biomass (g DW/m$^2$) in November 2021 ($n=8$) and 2022 ($n=10$), the dashed horizontal line represents the average amount of *Sphagnum* founder material (g DW/m$^2$) spread for installation, sampled in November 2020. **B** Greenness index in *Sphagnum* capitula in June 2022 ($n=8$). Bars represent means with ±standard error (SE)

### Elemental contents and quotients in *Sphagnum*

*Sphagnum* capitula and stem N content were highest at TSR0 in 2021 with $16 \pm 1.6$ mg/g, but lower and similar to the other treatments in 2022 with $14 \pm 0.7$ mg/g ($p < 0.05$, Fig. 4, Table S1). Surprisingly, these N capitula concentrations were moderate, despite considerable $NH_4^+$ porewater concentrations (see 3.3), high atmospheric N deposition (21 kg ha$^{-1}$ year$^{-1}$; UBA 2023) and limited biomass accumulation (Fig. 2, 4, 5). Capitula K content was highest at TSR0 in both years, and decreased by 40% between 2021 and 2022 at TSR0 from $8.3 \pm 0.6$ to $4.9 \pm 0.6$ mg/g and increased by 160% at TSR30 from $1.8 \pm 0.2$ to $4.7 \pm 0.4$ mg/g ($p < 0.05$, Fig. 4, Table S1). The same trend was observed for K content in the stems, although they were lower than capitula content and the increase was not significant at TSR30 (Fig. 3, Table S1). P content both in capitula and stems decreased from 2021 to 2022 in all treatments ($p < 0.05$), but were similar between the treatments (average of all treatments 2021: $2.7 \pm 0.3$ and 2022: $1.3 \pm 0.1$ mg/g; Fig. 4, Table S1).

C/N quotients in capitula and stems followed an opposite pattern than N content, being the lowest at TSR0 with $28 \pm 2.3$ in 2021, but higher and similar to others with $32 \pm 1.5$ in 2022 (Fig. 4, Table S1). The mean C/N capitula quotient at TSR30 decreased by 30% from with $46 \pm 2.9$ in 2021 to $31 \pm 1.2$ in 2022 ($p < 0.05$, Fig. 4, Table S1). N/P quotients in both capitula and stems were generally low at all treatments but increased considerably at both TSR0 from $6.8 \pm 0.9$ to $15 \pm 1.7$ and TSR30 from $5.2 \pm 0.6$ to $15 \pm 2.2$ between 2021 and 2022. In 2022, N/P quotients were the lowest at TSR5 with $9.2 \pm 0.4$ (Fig. 4, Table S1). Both capitula and stem N/K quotients in 2021 were higher at TSR30 with $5.7 \pm 0.6$ compared to TSR5 with $3.0 \pm 0.4$ and TSR0 with $2.0 \pm 0.3$. All capitula N/K quotients were higher than 3 and similar between treatments in 2022 (average of all $3.3 \pm 0.1$; Fig. 4, Table S1). Capitula N/K quotient at TSR0 increased and in TSR30 decreased from 2021 to 2022, opposite from the trend for K contents ($p < 0.05$, Fig. 4, Table S1). N/K quotients in the stems were higher than in capitula in all treatments ranging from $3.8 \pm 0.3$ at TSR5 to $4.9 \pm 0.6$ in 2022 (Fig. 4). N and P were mostly equally distributed between capitula and stem (quotient close to 1), but K capitula/stem quotient increased from 2021 to 2022, ranging from $1.5 \pm 0.1$ in TSR30 to $1.6 \pm 0.1$ in TSR0 and TSR5 in 2022.
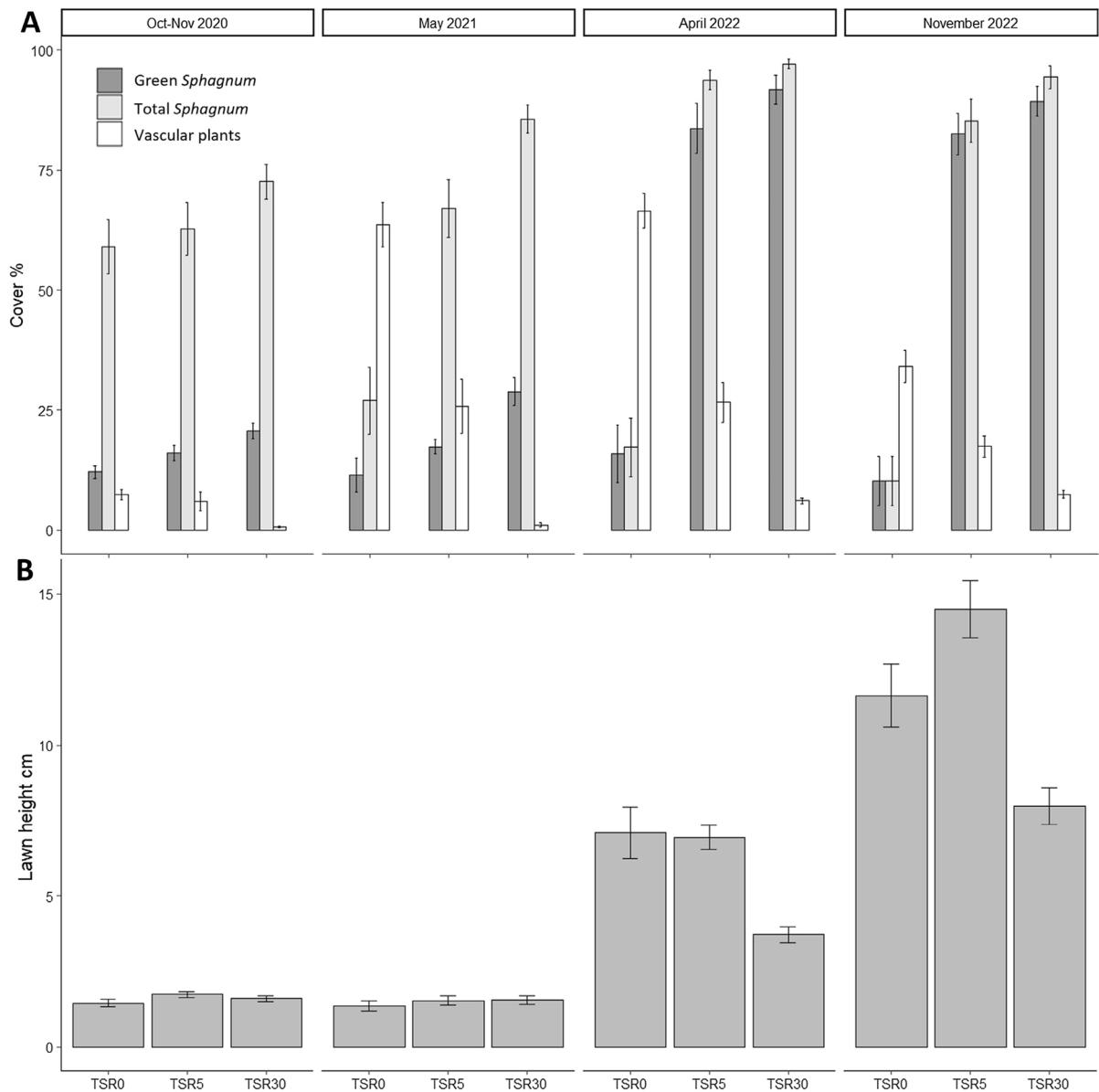
**Fig. 3** **A** Total and green *Sphagnum* cover, vascular plant cover % ($n = 20$), and **B** *Sphagnum* lawn height cm (n = 100) from four sampling times from October 2020 to November 2022. Bars represent means ± standard error (SE)

### Surface and porewater nutrient concentrations

Topsoil removal resulted in lower nutrient concentrations in the porewater. Specifically, in the first year the average $NH_4^+$, P and K concentrations were highest at TSR0 with values of $160 \pm 27$, $500 \pm 52$ and $110 \pm 13$ µmol/l, respectively (Fig. 5). The average porewater P concentrations were approximately four times lower at TSR5 with

$97 \pm 9.5$ µmol/l and virtually absent at TSR30 with $3.6 \pm 0.4$ µmol/l in both years. Mean $NH_4^+$, P and K concentrations were also higher at TSR5 than at TSR30 in both years, except for $NH_4^+$ in 2021 ($p < 0.05$, Table S2). There was a decrease in $NH_4^+$ and K concentrations between the years within TSR0 ($p < 0.05$, Table S2). Specifically, $NH_4^+$ concentrations decreased largely from $160 \pm 27$ in 2021 to $25 \pm 1.2$ µmol/l in 2022 ($p < 0.05$, Table S2,
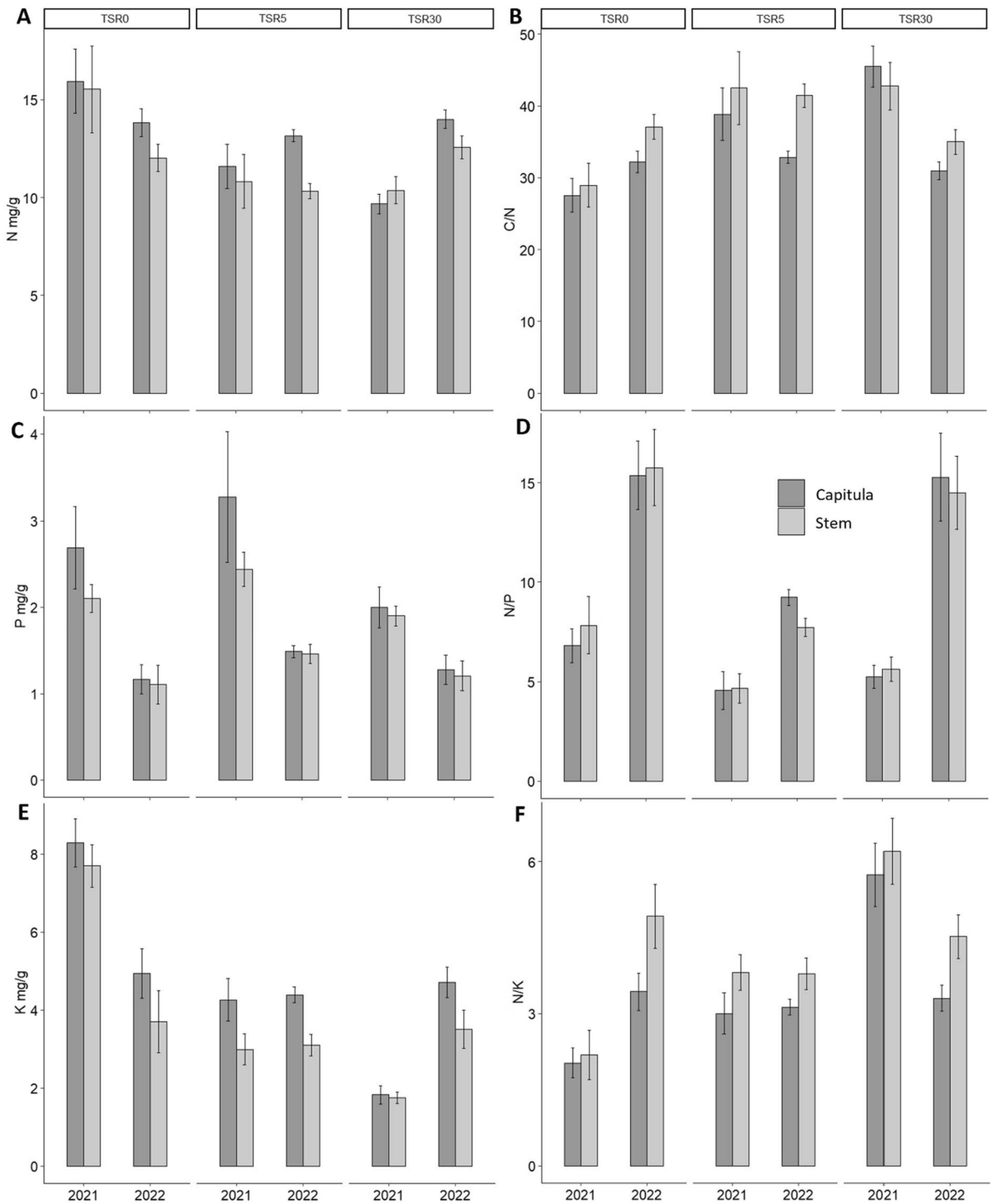
**Fig. 4** Elemental contents (mg/g) of A) nitrogen (N), C) phosphorus (P) and E) potassium (K), and B) C/N, D) N/P and F) N/K quotients in *Sphagnum* capitula and stems between treatments in August 2021 ($n = 8$) and November 2022 ($n = 24$). Bars represent means with $\pm$ standard error (SE)
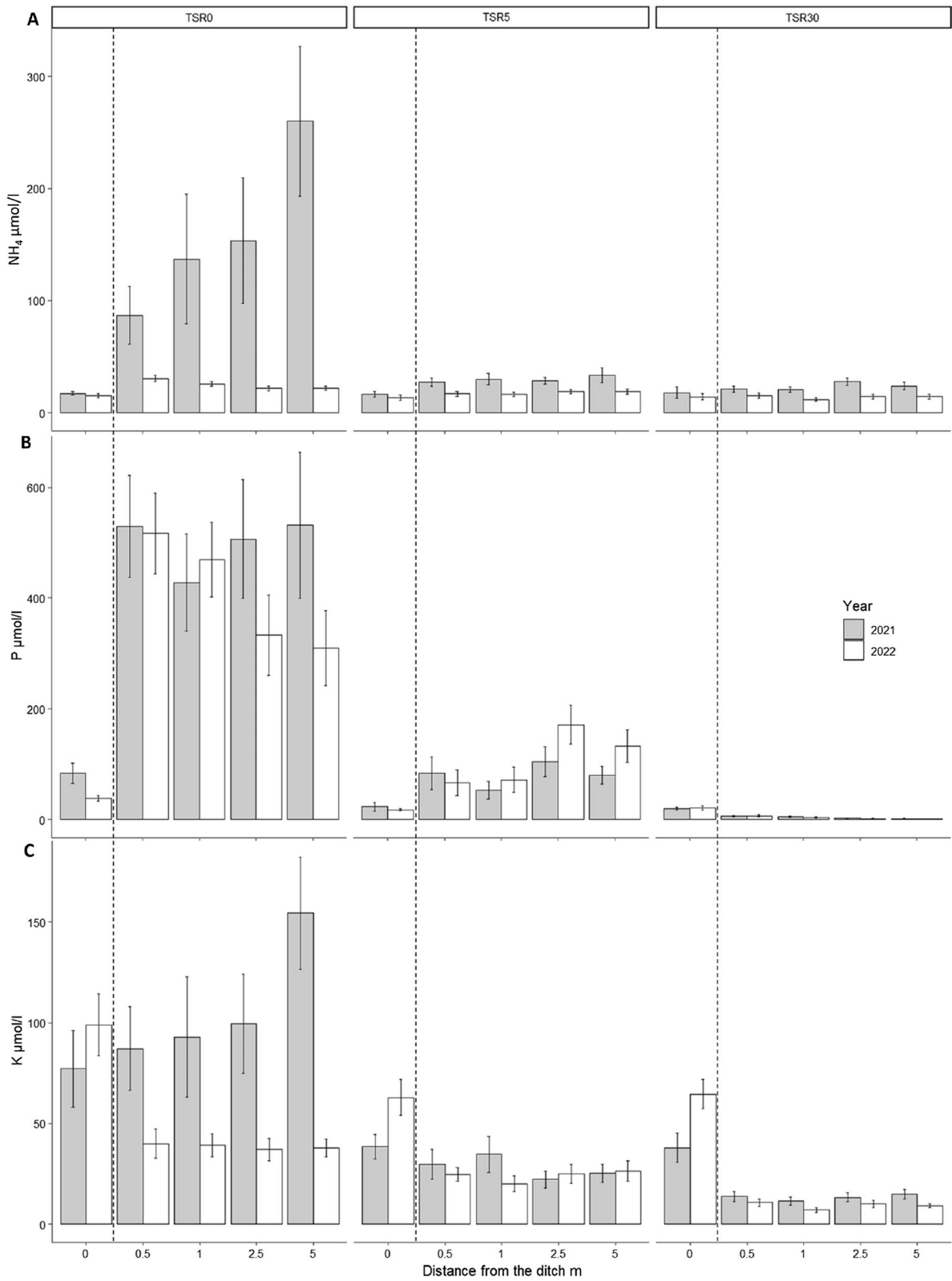
◄**Fig. 5** Ammonium ($NH_4^+$), phosphorus (P) and potassium (K) concentrations (µmol/l) in the porewater at different distances (m) from the irrigation ditch (0 represents ditch surface water, which was excluded from the model) in 2021 ($n = 20$) and 2022 ($n = 24$). Bars represent means ± standard error (SE). The vertical dotted line separates the ditch surface water and the porewater in the field

Fig. 5). Similarly, K concentrations in TSR0 decreased from $110 \pm 13$ in 2021 to $39 \pm 2.9$ µmol/l in 2022 ($p < 0.05$, Table S2). P porewater concentrations did not differ between years within any of the treatments ($p > 0.05$, Table S2).

The irrigation water could generally be characterized with low pH ($5.4 \pm 0.1$) and very low alkalinity ($0.33 \pm 0.03$ meq/l). $NH_4^+$ concentrations in the surface water of the irrigation ditches were similar between treatments ($16 \pm 1.2$ µmol/l, $p > 0.05$, Table S2). However, on average over the two-year period, P and K concentrations in the ditches were higher at TSR0 than at TSR5 and TSR30. The mean surface water K concentration of $89 \pm 12.0$ µmol/l and P concentration of $58 \pm 9.3$ µmol/l at TSR0 were 1.7 and 2.9 times higher (respectively, $p < 0.05$, Table S2) than in the other treatments with near-detectable concentrations of P. Ditches were influenced by activities outside of the treatment fields which limits the information value of a direct comparison.

## Hotspot methane fluxes

Spring/summer daytime $CH_4$ fluxes from partly flooded lawns increased from spring to summer, with average (per treatment) fluxes ranging from $1.5 \pm 0.6$ to $18 \pm 7.7$ mg/m²/day in early May, $12 \pm 3.6$ to $110 \pm 22$ mg/m²/day in early June, and $3.4 \pm 0.3$ to $190 \pm 40$ mg/m²/day in mid-June (Fig. 6). We measured a reduction in $CH_4$ emissions in TSR5 and TSR30 compared to TSR0 at the days with highest fluxes, in mid-June ($p < 0.05$, Fig. 6, Table S2).

## Discussion

Our experiment revealed that topsoil removal affects *Sphagnum* establishment and nutrient content in *Sphagnum* and porewater nutrient concentrations. Specifically, *Sphagnum* establishment was rapid and its growth was the highest at both TSR5 and TSR30

with near-optimal nutrient supply. Nutrient availability was the highest at TSR0, which promoted the growth of vascular plants. On the other hand, removing 30 cm of topsoil possibly removed too many nutrients, which reduced the growth of vascular plants, but also reduced *Sphagnum* growth. Lastly, we found first indications that TSR5 slightly reduced hotspot $CH_4$ emissions, but this warrants frequent monitoring of carbon fluxes spanning two years or longer (Huth et al. 2020).

### Biomass

5–10 cm topsoil removal seems to have promoted balanced nutrient stoichiometry in *Sphagnum*, and led to substantial *Sphagnum* biomass (*c.* 740 g DW/m²) in only two years after establishment, which is in line with our hypothesis. Biomass at TSR5 was similar to TSR30, which is the current common practice on this site (Wichmann et al. 2017). Vroom et al. (2020) reported *Sphagnum* biomass of *c.* 900 g DW/m² after 2.5 years of *Sphagnum* cultivation with 30 cm topsoil removal on this site, which is similar yearly growth as in our study for both TSR5 and TSR30. Interestingly, the TSR0 field did still produce *Sphagnum* biomass—though nearly six times less than the other treatments—with *c.* 11% green *Sphagnum* cover remaining after two years. Vascular plants dominated TSR0, however, this field produced healthy green (high greenness index) *Sphagnum* biomass with no clear signs of macronutrient limitation. However, without the regular mowing of the vascular plants it is likely that *Sphagnum* would have completely lost the competition for light as *Sphagnum* growth is reduced when shading exceeds 50% (Clymo & Hayward 1982). As the N deposition on this site is already very high (21 kg ha⁻¹ year⁻¹; UBA 2023)—more than twice as high as the critical load threshold defined by Bragazza et al. (2004) for natural bogs—the competitive equilibrium has already shifted to be more beneficial to vascular plants. Since not all N can be taken up by the mosses, it can leach through the moss layer and can become available for vascular plants (Lamers et al. 2000).

After two years of growth, we observed the greatest *Sphagnum* lawn height at TSR0 and TSR5. At higher N availability (also combined with high P), length growth of *Sphagnum* might be promoted to compete with vascular plants, while growing in

**Fig. 6** Spring/summer daytime methane (CH$_4$) fluxes (mg/m$^2$/day) on May 3rd ($n=4$), June 2nd ($n=8$) and June 16th ($n=20$) in 2022 in partly flooded lawns (not spatially representative) at all treatments. Bars represent means ± standard error (SE)
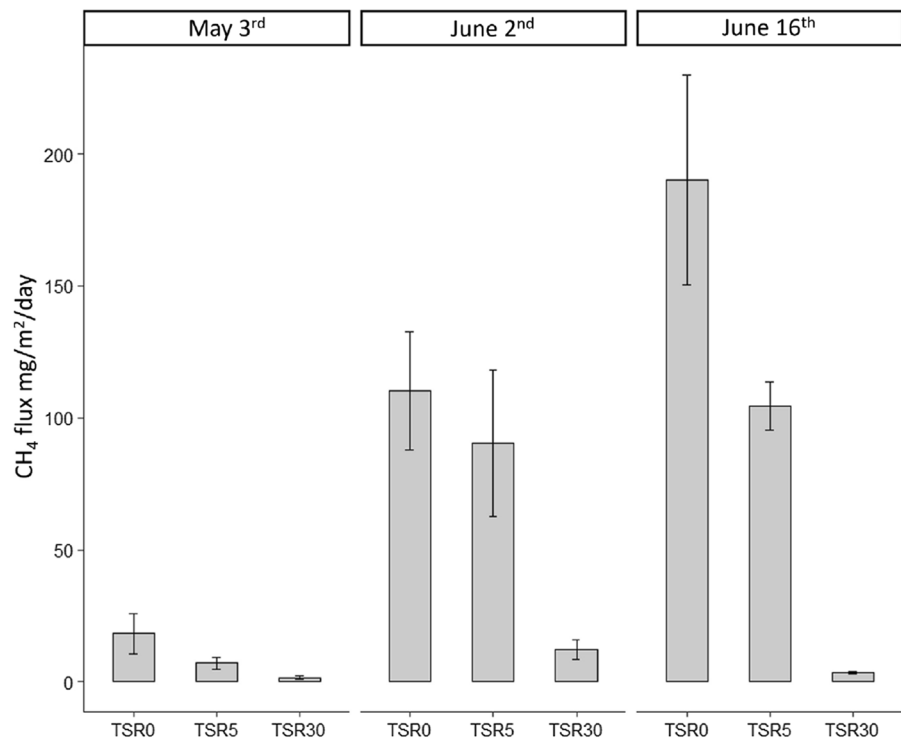


less dense (Fritz et al. 2014; Bengtsson et al. 2021), although some reported results show that increased N availability does not change length growth (e.g., Li et al. 2018). Still, it is possible that the higher N concentrations at TSR5 relative to TSR30, and the lower cover of vascular plants (and, thus, less competition for resources) relative to TSR0, yet enough vascular plants to provide structuring effect (Malmer et al. 1994), might have created the most favorable conditions for *Sphagnum* growth. Length increment does reflect the ability to reach light, which is crucial for *Sphagnum* to compete with vascular plants (Bengtsson et al. 2021; Li et al. 2018). That was the case in an experiment carried out by Ma et al. (2015), where shading had no effect on overall biomass production, but caused an increase in length in all studied *Sphagnum* species. This might partly explain the higher lawn at TSR5 and TSR0.

To support *Sphagnum* growth and generate good quality biomass under nutrient-rich conditions in *Sphagnum* paludiculture, it is crucial to manage vascular plants and water level (Gaudig et al. 2017, 2018; Wichmann et al. 2017). For restoration, after an initial intervention, the area would (nearly) not be managed and left to develop naturally. After two years of regular mowing, peat moss growth was comparable in TSR5 and TSR30, not forgetting that *Sphagnum* biomass did also increase in TSR0. However, the long-term development of peat moss growth on natural succession (without mowing and water management) still needs to be investigated for all of these TSR depths.

Nutrient stoichiometry

Despite the high N input, *Sphagnum* did not display clear signs of nutrient imbalance or toxicity in *Sphagnum* paludiculture setting with vascular plant management. This could explain their successful establishment and rapid growth, especially at TSR5. The mean *Sphagnum* capitula N concentrations remained moderate though saturated (> 12 mg/g, Lamers et al. 2000) within all treatments. Only in 2021 at TSR0,

capitula N concentration was slightly more elevated (> 15 mg/g), which van der Heijden et al. (2000) proposed to indicate N pollution stress. This treatment also had highest C/N quotients (more N relative to C than in TSR5 and TSR30). The higher concentration of N in the first year could be explained by higher porewater $NH_4^+$ concentrations and limited biomass accumulation (Figs. 2, 5). Interestingly, in 2022 mean N concentrations in the *Sphagnum* capitula at TSR0 were lower (13–14 mg/g) and similar to the other treatments in 2022, after two years of growth, comparable to those reported by Temmink et al. (2017) and Käärmelahti et al. (2023) from this same site. If environmental N load is increasing gradually, it has been shown that *Sphagnum* can adapt to this by decreasing N uptake efficiency and so avoid N toxicity (Fritz et al. 2014). However, the moderate capitula N contents and absence of N toxicity is most likely explained by sufficient supply of other macronutrients, namely P and K (Chapin et al. 1986).

Capitula N/P quotients remained low in all the treatments indicating no evident P limitation in any of the treatments. Capitula N/P quotient was the lowest at TSR5 (< 10) implying high uptake of P at medium to high N concentrations (optimal ratio of these nutrients) (Arróniz-Crespo et al. 2008; Granath et al. 2009, 2012). On the other hand, N/K quotients in the capitula were high (5.7) at TSR30 in 2021. This is clearly above capitula N/K quotient of 3, which Bragazza et al. (2004) proposed as a threshold for K limitation. The high N/K quotient in TSR30 indicates suboptimal potassium supply directly after installation. In 2022, in all treatments capitula N/K quotients decreased but remained elevated (N/K > 3) potentially reducing growth in high N environments. Moreover, in the stems, especially at TSR0 and TSR30, N/K quotients were well above 3 (4.5 and 4.9, respectively) suggesting a lower relative amount of K in the stems. This is supported by high capitula/stem K quotients in 2022, suggesting a translocation of K from the stems to capitula in order to have enough K to sustain growth probably supplied by the irrigation water (Bridgham et al. 1995; Vitousek 1982). Further research is necessary to find out whether clear K-limitation would occur in a longer term and if the topsoil removal of 30 cm could affect *Sphagnum* growth due to limited supply of K. In addition, nutrient addition experiments would be needed to quantify the effect of potassium on *Sphagnum* establishment and growth under high supply of N and P. Furthermore, it remains to be elucidated what would be the effects on *Sphagnum* stoichiometry without vascular plant management.

Nutrients in the porewater

We show that TSR prior to rewetting is very effective in reducing N, P and K and thereby potentially preventing leaching of these nutrients. Removing 5–10 cm of topsoil already reduced $NH_4^+$ and K porewater concentrations after two years (73% and 64% decrease, respectively). However, relatively high porewater P concentrations ($97 \pm 10$ µmol/l) remained at TSR5, indicating fairly large P leaching potential. These results are in line with Quadra et al. (2023), who also found 54–76% reduction in porewater $NH_4^+$ concentrations with as little as 5 cm of topsoil removal, but it required 25 cm of TSR to reduce most of the stored P in Dutch peat soils drained for agriculture. Interestingly, in TSR0 a substantial decrease of $NH_4^+$ was observed from 2021 to 2022, where the average $NH_4^+$ concentrations were more than six times lower in the second year, suggesting efficient uptake by vascular plants. However, longer term monitoring would reveal whether the P mobilization reduces overtime.

Topsoil removal is a potent method to remove nutrients, but does not allow the removal of selective nutrients. Even though it may be necessary to remove excess N and P, this may lead to the loss of K, which is essential for *Sphagnum* growth and even more so for vascular plants, in particular with excess availability of N. However, as *Sphagnum* can thrive with lower K availability than most vascular plants, it can succeed better with low K-availability (Bragazza et al. 2004; Wassen et al. 2020). Especially mowing and removing the mowed biomass has been linked to reduced K availability (Koerselman et al. 1990). It is important to take into account that the removed topsoil is not completely removed from the system, but used for the construction of causeways next to the fields, allowing possible leaching of the nutrients into the water of the irrigation ditch. However, the ditch water concentrations of $NH_4^+$ and P were similar between the treatments, and K concentrations were only higher in the irrigation ditch of TSR0.

Porewater K concentrations at TSR30 in 2022 ($9 \pm 1$ µmol/l) were lower than in previous studies

with a similar amount of topsoil removal from this site after one year (39±2 µmol/l, Käärmelahti et al. 2023) and 2.5 years (15±4 µmol/l; Vroom et al. 2020) of *Sphagnum* cultivation. At TSR5, K concentrations of 2022 were higher (24±2 µmol/l), indicating higher availability of potassium. It is likely that the topsoil removal together with wetter year of 2021 (less K in the irrigation water due to dilution) caused K-limitation at TSR30 during the first year. In the long term, K availability in the irrigation water and weather conditions are crucial to predict potential nutrient shortages. For example, Temmink et al. (2023a) showed that K concentrations in *Sphagnum* lawns gradually increased over 5 years. Overall, low porewater K concentration together with the higher stem N/K ratios at TSR30 at the end of the experiment indicate potential K limitation during the 2-year establishment period.

### Hotspot methane fluxes

In line with previous studies, we also found that TSR reduced $CH_4$ fluxes, even during hotspot moments in wetter parts of the field, with very low fluxes at TSR30 (i.e., Daun et al. 2023; Huth et al. 2020, 2022; Quadra et al. 2023). Our results are a pilot in the site to investigate the magnitude of $CH_4$ fluxes under different TSR in a field scale experiment in partly flooded sublocations on the fields. Our data is limited, disregarding winter- and night time measurements, being unrealistic to draw robust conclusions or reliable annual estimates. However, this data does still provide a snapshot to $CH_4$ fluxes on this site in favourable conditions for $CH_4$ emissions (i.e., warmer periods under wet conditions). Within the scope of the present work, we showed that TSR reduced $CH_4$ fluxes during these hotspots and hot moments, either visually observable (early May/June) or statistically significant (mid-June). For future studies and greenhouse gas budget calculations, it is important to consider the wintertime fluxes, as well as oxidation potential of the removed peat (Daun et al. in preparation). For instance, Daun et al. (2023) found that topsoil-made causeways were the major source of $CO_2$ at this site. Although TSR30 reduced $CH_4$ fluxes the most, for climate mitigation the TSR5 treatment may be a preferred option, because it minimizes carbon export through TSR.

### Conclusions and implications

Our study shows the effects of TSR on nutrient dynamics, nutrient stoichiometry and *Sphagnum* performance on rewetted agricultural peatland under *Sphagnum* paludiculture management for two years directly after installation in the establishment phase. In terms of *Sphagnum* paludiculture with continuous management of water and vascular plants, 5–10 cm of TSR is likely to be the best cost–benefit option considering *Sphagnum* productivity and yields. However, in case of reduced or discontinuous management for bog restoration, *Sphagnum* establishment should be tested in the absence of vascular plant (and water) management and in the long term to verify whether *Sphagnum* is able to outcompete vascular plants. In addition, further long-term studies to monitor the greenhouse gas emissions with reduced amount of TSR are needed.

In a broader context, the worldwide decline of peatlands is causing adverse environmental effects such as loss of unique biodiversity, land subsidence, downstream pollution and long-term high greenhouse gas emissions. This highlights the urgent need for extensive restoration efforts to reinstate essential peatland functions on rewetted peatlands through bog restoration or *Sphagnum* paludiculture (i.e. wetscapes; Temmink et al. 2023b). Removing less topsoil could lower the threshold to establish *Sphagnum* paludiculture in terms of costs and labor intensity, which, in turn, can contribute significantly to the goals of the Paris Agreement and the UN Decade on Ecosystem Restoration. Productive use of wetlands could efficiently enhance the ecological functioning of peatlands while reducing the challenges associated with more extensive restoration efforts.

**Declarations**

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