RESEARCH ARTICLE

# Nutrient dynamics of 12 *Sphagnum* species during establishment on a rewetted bog

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**ABSTRACT**

- Peatland degradation through drainage and peat extraction have detrimental environmental and societal consequences. Rewetting is an option to restore lost ecosystem functions, such as carbon storage, biodiversity and nutrient sequestration. Peat mosses (*Sphagnum*) are the most important peat-forming species in bogs. Most *Sphagnum* species occur in nutrient-poor habitats; however, high growth rates have been reported in artificial nutrient-rich conditions with optimal water supply.

- Here, we demonstrate the differences in nutrient dynamics of 12 *Sphagnum* species during their establishment in a 1-year field experiment at a *Sphagnum* paludiculture area in Germany. The 12 species are categorized into three groups (slower-, medium- and fast-growing). Establishment of peat mosses is facilitated by constant supply of nutrient-rich, low pH, and low alkalinity surface water.

- Our study shows that slower-growing species (*S. papillosum*, *S. magellancium*, *S. fuscum*, *S. rubellum*, *S. austinii*; often forming hummocks) displayed signs of nutrient imbalance. These species accumulated higher amounts of N, P, K and Ca in their capitula, and had an elevated stem N:K quotient (>3). Additionally, this group sequestered less C and K per $m^2$ than the fast and medium-growing species (*S. denticulatum*, *S. fallax*, *S. riparium*, *S. fimbriatum*, *S. squarrosum*, *S. palustre*, *S. centrale*). Lower lawn thickness may have amplified negative effects of flooding in the slower-growing species.

- We conclude that nutrient dynamics and carbon/nutrient sequestration rates are species-specific. For bog restoration, generating ecosystem services or choosing suitable donor material for *Sphagnum* paludiculture, it is crucial to consider their compatibility with prevailing environmental conditions.

## INTRODUCTION

Intact peatlands provide valuable ecosystem services as the world's carbon (C) densest ecosystem (Temmink *et al.* 2022), hydrological buffers, and by supporting unique biodiversity (Joosten *et al.* 2012; Minayeva *et al.* 2017). However, draining peatlands to facilitate agriculture and forestry has been shifting peatlands into substantial sources of carbon (Leifeld & Menichetti 2018), leading to land subsidence, eutrophication and biodiversity loss (Renger *et al.* 2002; Joosten *et al.* 2012). Specifically, temperate and boreal bogs (ombrotrophic, mainly rainwater-fed) are important peatland types that are shaped by *Sphagnum* (peat moss) (Sjörs 1950; Rydin & Jeglum 2013; Temmink *et al.* 2022). Bringing the groundwater level back to the near-surface level (rewetting) is an effective long-term mitigation option (Günther *et al.* 2020). Paludiculture, the productive use of wet and rewetted peat soils, both preserves the peat

and allows farming practices after rewetting (Wichtmann *et al.* 2016). For example, the production of *Sphagnum* biomass as a sustainable alternative for horticultural growing media (*Sphagnum* paludiculture), regains lost ecosystem services, including water retention, biodiversity and nutrient sequestration (Temmink *et al.* 2017; Gaudig *et al.* 2018; Vroom *et al.* 2020).

Nevertheless, rewetting alone does not guarantee successful *Sphagnum* establishment and growth, as it also depends on available diaspores, water levels and nutrients: essential elements that sustain life and plant growth (Temmink *et al.* 2017; Gaudig *et al.* 2018; Brown *et al.* 2022). *Sphagnum* thrives at water levels a few centimetres below the *Sphagnum* surface, with a low pH, bicarbonate ($HCO_3^-$) concentration and optimal nutrient stoichiometry (Gaudig *et al.* 2020; Koks *et al.* 2022). While naturally occurring in nutrient-poor environments, *Sphagnum* can still be negatively affected by an

unbalanced supply of macronutrients, namely nitrogen (N), phosphorus (P) and potassium (K), during their establishment and in the long term (Chapin *et al.* 1986). Nutrient deficiency occurs when plants are not receiving sufficient nutrients, while toxicity occurs when an element is in excess of the plant's needs and decreases growth or quality (Chapin *et al.* 1986; Wilson 1993). Under natural bog conditions, N and/or P are typically limiting nutrients for *Sphagnum* (Bragazza *et al.* 2004; Fritz *et al.* 2012). When the balance is disturbed and there is an excessive amount of available N, it can become toxic to *Sphagnum*, as the N surplus cannot be used by the increased growth (Limpens *et al.* 2003). The excess N leaches through the upper moss layer, which provides a competitive edge to vascular plants, leading them to overgrow and outcompete the *Sphagnum* (Limpens *et al.* 2003; Tomassen *et al.* 2003). Evidence suggests that some *Sphagnum* species can thrive under high N when the nutrient NPK stoichiometry is optimal, *i.e.* there is also a sufficient supply of P and K (Temmink *et al.* 2017; Gaudig *et al.* 2020). In optimal nutrient conditions, the N:K (quotient between N and K) in *Sphagnum* capitula should remain well below 3, and N:P (quotient between N and P) below 30 (Bragazza *et al.* 2004). Species-specific stoichiometric thresholds are yet to be developed. However, nutrient stoichiometry is not only dependent on the availability of nutrients, but also on the capacity of uptake by *Sphagnum* (Clymo 1963; Soudzilovskaia *et al.* 2010; Fritz *et al.* 2014). *Sphagnum* cell walls have a high cation exchange capacity (CEC), taking up nutrient cations (*e.g.* $NH_4^+$, $K^+$, $Mg^{2+}$, $Ca^{2+}$) in exchange for protons (Rice 2009). Ombrotrophic *Sphagnum* species are better adapted to low-alkaline and cation-poor conditions compared to minerotrophic (groundwater-fed) species (Koks *et al.* 2022). Therefore, they are more likely to take up cations from ion-rich irrigation water until they reach saturation due to a higher risk of nutrient shortage (Spearing 1972).

So far, long-term studies on nutrient dynamics in *Sphagnum* paludiculture have focused on nutrient uptake, transfer, and spatial and temporal cycling within the moss and in the ecosystem (Temmink *et al.* 2017; Vroom *et al.* 2020). However, these studies focused only on a few *Sphagnum* species, while a wide variety of *Sphagnum* mosses occur in natural peatlands, differing in traits and environmental requirements (Daniels & Eddy 1985; Michaelis 2019). To explore species-specific biomass yields, Prager *et al.* (2023) conducted a multi-species study and found that *S. denticulatum* > *S. fallax* > *S. riparium* > *S. fimbriatum* > *S. squarrosum* produced high amounts (mean >4,200 kg·ha$^{-1}$·year$^{-1}$) of dry mass in the establishment phase under optimal water and nutrient conditions. However, it is still unknown how species differ in their nutrient stoichiometry and sequestration during the establishment phase (*i.e.* the first year after introduction).

Therefore, we studied species-specific optimal nutrient stoichiometry and sequestration rates in the establishment phase of a new *Sphagnum* paludiculture, with nutrient-rich conditions and constantly high watertables. Specifically, we aim to evaluate (1) whether the growth rate of selected *Sphagnum* species can be explained by nutrient stoichiometry in the capitulum, and (2) whether the nutrient stoichiometry can be linked to nutrient uptake and carbon sequestration. To tackle this, we performed a field experiment in a *Sphagnum* paludiculture field in NW Germany using 12 model species representative of a large ecological range (ombrotrophic to minerotrophic) and

growth potential (Prager *et al.* 2023). The species were grouped in fast-, medium- and slower-growing groups. We hypothesised that (i) the faster-growing (fast- and medium-growing) *Sphagnum* species would adapt to the available nutrient pool by maintaining a nutrient balance, which enhances their carbon and nutrient sequestration; and (ii) the slower-growing species would be unable to adapt to the available nutrient pool, leading to nutrient imbalance and lower carbon and nutrient sequestration. Slow growth may increase the exposure to flooding during rain events and deteriorate growth conditions for hummock species.

## MATERIAL AND METHODS

### Study site and experimental setup

The studied *Sphagnum* paludiculture area is located in Hankhauser Moor, NW Germany (53°15.80′ N, 08°16.05′ E; Fig. 1). The bog, with a 2.0–2.5-m thick peat layer overlaying sand, has been drained (without extracting the peat) and used as an agricultural grassland for six decades, until land use was changed to paludiculture. To study differences in nutrient stoichiometry and sequestration for the 12 selected *Sphagnum* species (Table 1), a new experimental field was established in 2019. To acquire optimal *Sphagnum* paludiculture conditions (Gaudig *et al.* 2018), a basin of 10 × 50 m was constructed by removing 30 cm of the strongly degraded topsoil (comparable to earlier experimental blocks on this site; Vroom *et al.* 2020) and surrounded by a 0.5-m wide and deep irrigation ditch (Fig. 1). To avoid desiccation and inundation, the ditch is connected to an automatic irrigation system, which maintains the water table at *ca.* 9 cm below the peat surface (Figure S1). The irrigation water originates from the nearby stream 'Schanze'. A total of 12 *Sphagnum* species were selected for the experiment, based on their productivity potential and suitability as raw material for horticultural purposes (Prager *et al.* 2023). In a pre-selection mesocosm experiment, the highest productivities for each species of different origins within Europe had been identified and the most productive 1–3 origins were selected for the field experiment (Prager *et al.* 2023; Table S1). To enable optimal water and nutrient supply, a total of 84 plots of 60 × 60 cm or 45 × 45 cm were established adjacent to the irrigation ditch by spreading *Sphagnum* founder material to 80% cover in September–November 2019 (Fig. 1). Vascular plants were removed four times a year to limit their growth.

### Biomass sampling for nutrient analyses and measuring *Sphagnum* lawn thickness

To analyse nutrient content in the *Sphagnum* capitula (0–1 cm, shoot apex with branches not fully developed; *cf.* Clymo 1973) and stems, *Sphagnum* biomass was sampled from each plot by cutting 15 × 15 cm plugs down to the peat surface (easily recognizable by a much stronger degree of decomposition) 1 year after spreading (September–November 2020; for more details, see Prager *et al.* 2023). The fresh *Sphagnum* biomass was separated into capitula and stems, dried for 48 h at 70 °C, and ground using a centrifugal ball mill (18,000 rpm for 1–2 min; Fritsch pulverisette 14, Idar-Oberstein, Germany) to homogenize each sample.
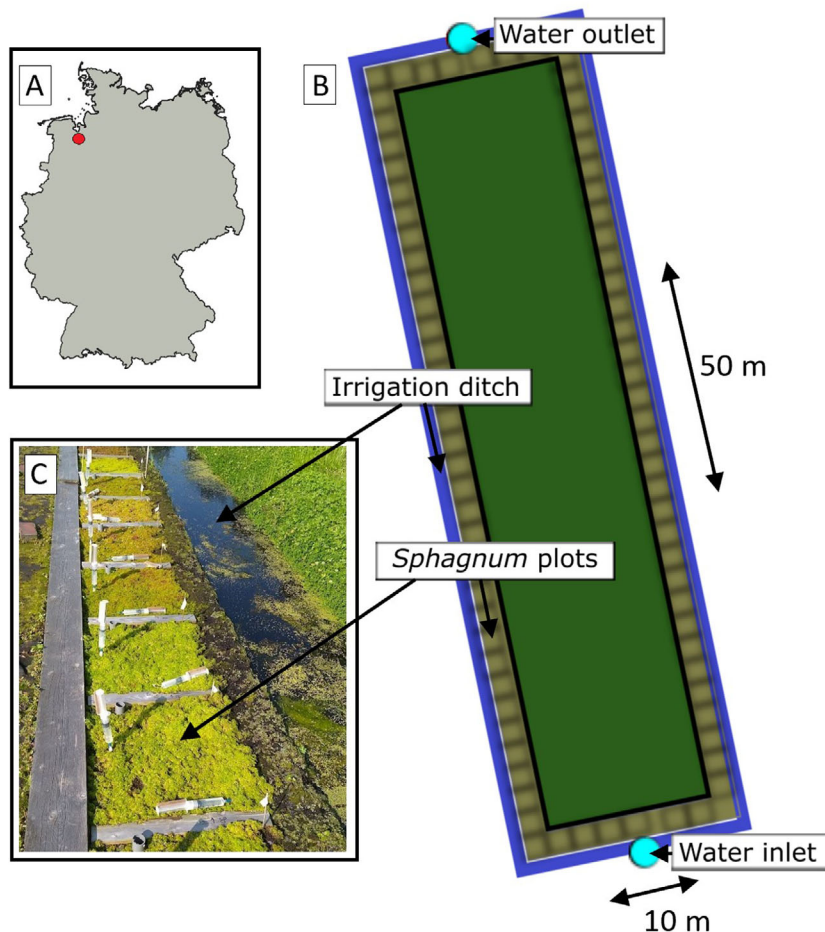
**Fig. 1.** (A) Location of the study site in NW Germany (map source: European Economic Area), (B) set-up of the experimental field and (C) photograph of *Sphagnum* plots 1 year after establishment (photo credit: S.A. Käärmelahti).

**Table 1.** Studied *Sphagnum* species grouped by growth rate (Prager *et al.* 2023) with number of replicates (in brackets).

| fast | medium | slower |
|---|---|---|
| *S. denticulatum* (6) | *S. palustre* (15) | *S. papillosum* (12) |
| *S. fallax* (9) | *S. centrale* (6) | *S. magellancium* (9) |
| *S. riparium* (6) | | *S. fuscum* (2) |
| *S. fimbriatum* (2) | | *S. rubellum* (12) |
| *S. squarrosum* (9) | | *S. austinii* (6) |

*Sphagnum* lawn thickness was recorded in each plot before cutting (at five points in each plot) by measuring the distance between the *Sphagnum* surface and the peat surface below.

### Surface and pore water collection and watertable measurements

We used water sampling methods similar to those in Vroom *et al.* (2020). Surface water in the ditch and stream was sampled each month from September to November 2020. We used vacuum syringes connected to ceramic cups to filter out large and suspended particles. Porewater in the *Sphagnum* layer (*ca.* 2 cm below peat moss surface) and in the peat (0–6 cm below the peat surface) was collected using vacuum syringes attached to a rhizon soil moisture sampler (Rhizosphere Research Products, Wageningen, the Netherlands). Each water sample was divided and stored in (a) a 10-ml tube containing 0.1 ml 65% nitric acid ($HNO_3$) at 4 °C and (b) 10-ml pot at -20 °C. The phreatic watertable was measured in the ditch within a perforated plastic tube every hour using an automatic data logger with automatic compensation for barometric fluctuations (pressure transducer; Hydrotechnik HT Type 575; Figure S1).

### Chemical analyses

Total N and C in the *Sphagnum* capitula and stems were determined from 4–5 mg of each milled biomass fraction using an elemental CNS analyser (Vario Micro cube; Elementar Analysensysteme, Langenselbold, Germany). Total P, K, Mg and Ca were determined by digesting *ca.* 200 mg dried moss material in 4 ml nitric acid ($HNO_3$; 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). Element content was determined using inductively coupled plasma emission spectrophotometry (ICP-OES, Thermo Fischer Scientific, Bremen, Germany).

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, P, Mg and Ca in water samples were measured using inductively coupled plasma optical emission spectrometry (ICP-OES-ARCOS Spectro Analytical; Kleve, Germany). Ammonium ($NH_4^+$), nitrate ($NO_3^-$) and phosphate ($PO_4^{3-}$) concentrations of water samples stored at -20 °C were determined by colorimetric methods (Auto Analyser III, Bran and Luebbe GmbH, Norderstedt, Germany).

## Calculation of nutrient sequestration

Nutrient sequestration of N, P, K, C, Mg and Ca was calculated using the nutrient contents measured and biomass fractions 'capitula' and 'stems' collected after 1 year by Prager *et al.* (2023). Total sequestration for each *Sphagnum* plot was calculated as:

$$S_{tot} = B_A(r_C \times C_C + r_S \times C_S)$$

where $S_{tot}$ is the total sequestration (kg·ha$^{-1}$·year$^{-1}$), $B_A$ is the total accumulated biomass (capitula and stems together; kg·ha$^{-1}$·year$^{-1}$), $r_C$ is the fraction of capitula in the biomass, $C_C$ is the nutrient content in capitula (kg·kg$^{-1}$), $r_S$ is the fraction of stems in the biomass, and $C_S$ is the nutrient content in the stems (kg·kg$^{-1}$).

## Statistical analyses

Statistics were performed using R version 4.1.2 (R Core Team 2021). *Sphagnum* species were divided into three groups based on their growth potential analysed with boosted regression tree modelling using biomass yield data for fast-, medium- and slower-growing groups (Prager *et al.* 2023). Differences in capitula nutrient content (C, N, P, K, Mg, Ca), element quotient capitula:stem (C, N, P, K, Mg, Ca), nutrient quotients in capitula (C:N, N:P, N:K, K:Mg, K:Ca) and sequestration (C, N, P, K, Mg, Ca) between the three groups were evaluated using linear mixed effects models (Pinheiro *et al.* 2021), followed by ANOVA. Land of origin was included as a random factor. When differences were significant, a *post-hoc* test was applied (Tukey multiple comparisons of means) using emmeans (Lenth 2018). Normality and homogeneity were checked visually using residual plots. Non-normally distributed data were log10, square-root or 1/× transformed. Significance was assumed at $P \leq 0.05$. Plots were created using ggplot2 (Wickham 2016).

## RESULTS

### Nutrient concentrations in the water and average watertable

Nutrients in the peat were evenly distributed over all plots. Nutrient concentrations and pH values in the irrigation ditch and stream water were generally higher than in the peat and moss pore water, with the lowest values in the moss layer (Table 2). The stream had the highest nutrient concentration with intermediate levels of alkalinity and pH. Average water table relative to the peat level (±SE) in September 2019–November 2020 was -9.0 ± 0.1 cm (Figure S1).

### *Sphagnum* lawn thickness and nutrient content in *Sphagnum* capitula and stems

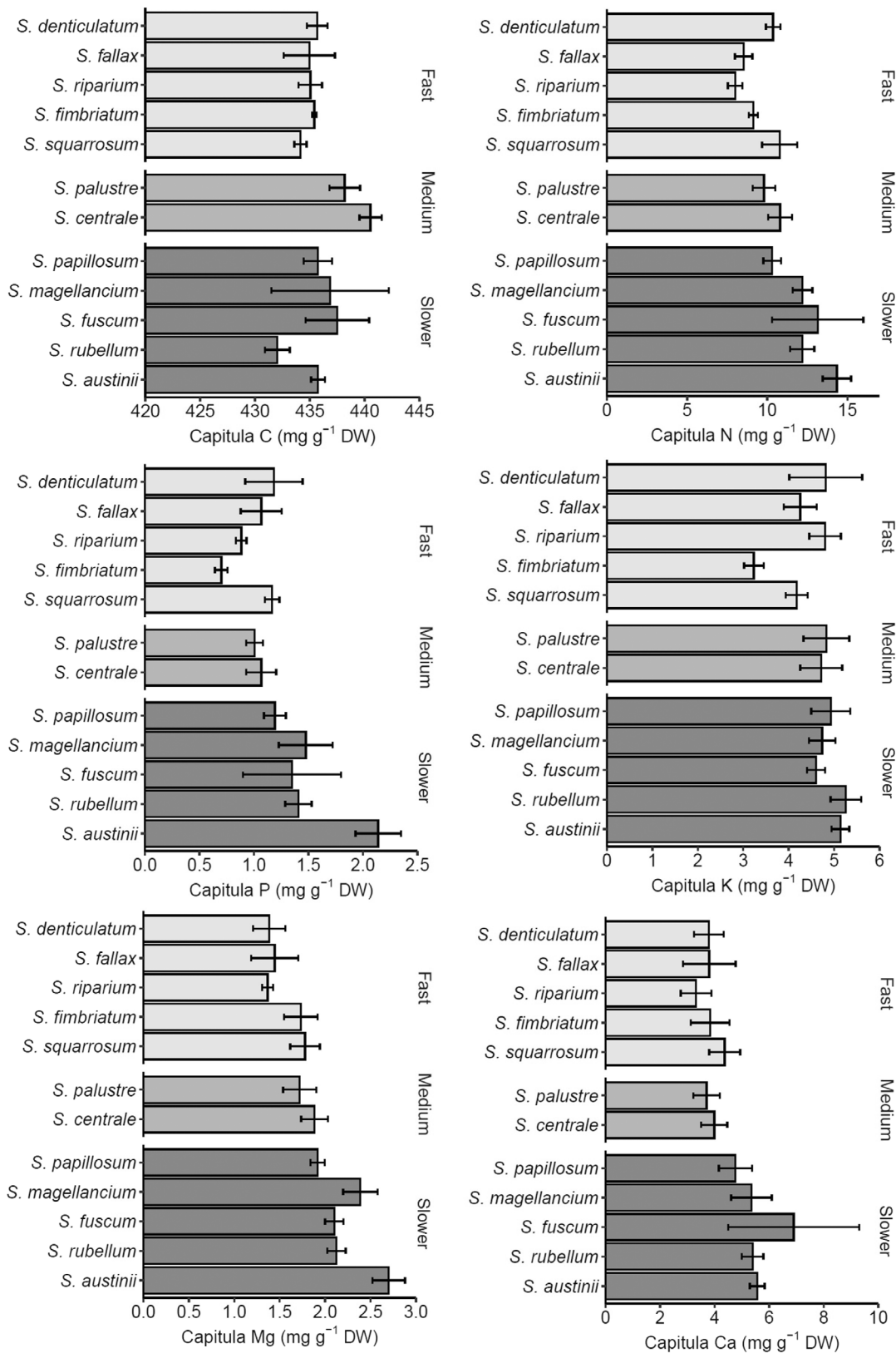The average (±SE) *Sphagnum* lawn thickness 1 year after the experiment's installation, was lower for the slower-growing group (2.8 ± 0.1 cm) than for the medium- (4.4 ± 0.4 cm) and fast-growing (4.7 ± 0.3 cm) groups ($F_{1,2} = 14.7$, $P < 0.0001$; Table S2). Among nutrients, we observed differences between groups for C ($F_{1,2} = 4.3$, $P = 0.02$), N ($F_{1,2} = 4.7$, $P = 0.01$), P ($F_{1,2} = 5.4$, $P = 0.006$), Mg ($F_{1,2} = 7.0$, $P = 0.002$) and Ca ($F_{1,2} = 5.2$, $P = 0.008$) content in the capitula (Fig. 2, Table 3 for descriptive statistics, Table S2 for statistical output). Specifically, the average N, P, Mg and Ca contents of the slower-growing *Sphagnum* group were higher compared to the medium-growing and the fast-growing groups. The maximum N and P values were as high as 17.8 (*S. rubellum*) and 2.8 (*S. austinii*) mg·g$^{-1}$ DW (dry weight) in the capitula, respectively. However, the average N, P, Mg and Ca content did not differ between medium- and fast-growing groups, and the average capitula K content did not differ between any of the groups.

When observing the differences in nutrient content between capitula and stems (capitula:stem element quotient), we found higher content in the capitula for all nutrients except for *Ca*. Additionally, we found a group effect for P, with larger quotients (*e.g.* *S. denticulatum* 1.6 ± 0.4) for the fast-growing group ($F_{1,2} = 3.3$, $P = 0.04$; Tables 3, Table S2); in contrast, Mg values were larger (*e.g.* *S. austinii* 1.7 ± 0.0) for the slower-growing group ($F_{1,2} = 7.1$, $P = 0.001$). The element quotients for N, K, C and Ca did not differ between the three groups.

### Nutrient quotients in *Sphagnum* capitula and stems

Most elemental quotients in capitula differed between groups: C:N ($F_{1,2} = 4.6$, $P = 0.01$), N:K ($F_{1,2} = 4.0$, $P = 0.02$), K:Mg ($F_{1,2} = 8.2$, $P < 0.001$) and K:Ca ($F_{1,2} = 6.3$, $P = 0.003$), but not N:P ($F_{1,2} = 2.0$, $P = 0.1$) (Fig. 3, Table 4 and Table S2). For the

**Table 2.** Nutrient concentrations (µmol·l$^{-1}$), pH and alkalinity (meq·l$^{-1}$) in peat pore water (Peat) from 0 to 6 cm below peat surface, moss pore water (Moss) from *ca.* 2 cm below moss surface, surface water from the irrigation ditch (Ditch) and the stream 'Schanze'.

| | | $NO_3^-$ | $NH_4^+$ | $PO_4^{3-}$ | P | K | Mg | Ca | pH | alk |
|---|---|---|---|---|---|---|---|---|---|---|
| Unit | | µmol·l$^{-1}$ | µmol·l$^{-1}$ | µmol·l$^{-1}$ | µmol·l$^{-1}$ | µmol·l$^{-1}$ | µmol·l$^{-1}$ | µmol·l$^{-1}$ | | meq·l$^{-1}$ |
| Peat | 84 | 1 ± 0 | 27 ± 2 | 11 ± 1 | 12 ± 1 | 39 ± 2 | 114 ± 5 | 139 ± 8 | 4.7 ± 0.03 | NA |
| Moss | 84 | 4 ± 1 | 7 ± 1 | 3 ± 0 | 3 ± 0 | 26 ± 2 | 85 ± 4 | 112 ± 6 | 4.5 ± 0.04 | NA |
| Ditch | 12 | 5 ± 3 | 37 ± 11 | 7 ± 2 | 23 ± 8 | 77 ± 10 | 141 ± 6 | 270 ± 25 | 5.8 ± 0.1 | 0.4 ± 0.1 |
| Stream | 8 | 14 ± 5 | 126 ± 44 | 9 ± 3 | 38 ± 15 | 114 ± 12 | 160 ± 10 | 318 ± 27 | 5.9 ± 0.1 | 0.6 ± 0.1 |

Reported values are mean ± SE (NA, not analysed).

**Fig. 2.** Content of C, N, P, K, Ca and Mg in capitula (mg·g⁻¹ DW) for each species within each growth group (fast-, medium- and slower-growing). Bars are mean ± SE. See Table 1 for replicates and Table S2 for statistical results.

**Table 3.** Nutrient content mg·g$^{-1}$ (capitula), element quotient (concentration of C, N, P, K, Mg and Ca in capitula normalized by stem concentrations; capitula:stem) g·g$^{-1}$ and sequestration kg·ha$^{-1}$·year$^{-1}$ (capitula + stem).

| | Group | C | N | P | K | Mg | Ca |
|---|---|---|---|---|---|---|---|
| Nutrient content (mg·g$^{-1}$) | Fast | 434.9 ± 0.7[a] | 9.4 ± 0.4[a] | 1.1 ± 0.1[a] | 4.3 ± 0.2[a] | 1.5 ± 0.09[a] | 3.9 ± 0.3[a] |
| | Medium | 438.8 ± 1.1[b] | 10.1 ± 0.5[a] | 1.0 ± 0.1[a] | 4.8 ± 0.4[a] | 1.8 ± 0.1[a] | 3.8 ± 0.4[a] |
| | Slower | 434.9 ± 1.1[ab] | 12.0 ± 0.4[b] | 1.5 ± 0.1[b] | 5.0 ± 0.2[a] | 2.2 ± 0.07[b] | 5.3 ± 0.3[b] |
| Element quotient ent (g·g$^{-1}$) | Fast | 1.1 ± 0.0[a] | 1.2 ± 0.1[a] | 1.4 ± 0.1[a] | 1.1 ± 0.1[a] | 1.0 ± 0.0[a] | 0.7 ± 0.0[a] |
| | Medium | 1.1 ± 0.0[a] | 1.0 ± 0.0[a] | 1.3 ± 0.1[ab] | 1.2 ± 0.1[a] | 1.1 ± 0.1[a] | 0.7 ± 0.1[a] |
| | Slower | 1.1 ± 0.0[a] | 1.0 ± 0.0[a] | 1.3 ± 0.1[b] | 1.4 ± 0.1[a] | 1.3 ± 0.0[b] | 0.8 ± 0.0[a] |
| Sequestration (kg·ha$^{-1}$·year$^{-1}$) | Fast | 1540 ± 131[a] | 30.2 ± 2.3[a] | 3.1 ± 0.3[a] | 15.5 ± 1.3[a] | 5.0 ± 0.4[a] | 16.9 ± 1.7[a] |
| | Medium | 1370 ± 172[b] | 29.7 ± 3.5[a] | 2.7 ± 0.4[a] | 13.3 ± 1.5[a] | 4.6 ± 0.5[a] | 14.6 ± 1.5[a] |
| | Slower | 930 ± 80[b] | 25.9 ± 2.1[a] | 2.6 ± 0.3[a] | 8.8 ± 0.7[b] | 3.9 ± 0.3[a] | 12.9 ± 1.6[a] |

Reported values are mean ± SE. Significant differences between groups are indicated by different letters.

slower-growing group, the C:N, K:Mg and K:Ca quotients were lower than for the medium-growing and the fast-growing groups. N:P quotients were statistically similar among all the groups, however, ranging from a minimum value of 4.9 (*S. denticulatum*) up to a maximum of 18.8 (*S. palustre*). The slower-growing group had a higher N:K quotient (2.5 average) than the fast-growing group, while this did not differ from the medium-growing group.

In the case of stems, there were differences in C:N ($F_{1,2}$ = 5.1, $P = 0.008$), N:K ($F_{1,2} = 15.5$, $P < 0.001$) and K:Mg ($F_{1,2}$ = 9.3, $P < 0.001$) quotients between the groups. Stems in the slower-growing group had lower C:N and K:Mg quotients and higher N:K ratio than the fast- and medium-growing groups (Table 4 and Table S2). The N:P quotients in the stems were higher and K:Ca ratios lower than in the capitula.

### Carbon and nutrient sequestration

The amounts of sequestered C and nutrients differed between the groups only for C ($F_{1,2} = 5.0$, $P = 0.009$) and K ($F_{1,2} = 7.8$, $P < 0.001$; Fig. 4, Table 3 and Table S2). The slower-growing group sequestered less C and K than the fast-growing group, but a similar amount of C compared to the medium-growing group. *Sphagnum* species sequestering the most C (1.8 ± 0.2 and 1.7 ± 0.3 t·ha$^{-1}$·year$^{-1}$), N (33.4 ± 5.7 and 31.9 ± 4.6 kg·ha$^{-1}$·year$^{-1}$) and P (4.0 ± 0.9 and 3.4 ± 0.6 kg·ha$^{-1}$·year$^{-1}$), on average, were *S. denticulatum* and *S. fallax* from the fast-growing group. *S. denticulatum* also sequestered the most K (18.9 ± 2.9 kg·ha$^{-1}$·year$^{-1}$) together with with fast-growing *S. riparium* (17.0 ± 1.1 kg·ha$^{-1}$·year$^{-1}$) and *S. fallax* (16.4 ± 2.9 kg·ha$^{-1}$·year$^{-1}$).

### DISCUSSION

#### Nutrient availability and nutrient dynamics in *Sphagnum*

Nutrient dynamics of 12 *Sphagnum* species, categorized into three groups, slower- (*S. papillosum*, *S. magellancium*, *S. fuscum*, *S. rubellum*, *S. austinii*), medium- (*S. palustre*, *S. centrale*) and fast-growing (*S. denticulatum*, *S. fallax*, *S. riparium*, *S. fimbriatum*, *S. squarrosum*), were examined under similar nutrient-rich and constantly wet field conditions. Generally, the species categorized as fast-growing are better adapted to these minerotrophic conditions, whereas the slower-growing species, mostly ombrotrophic bog species occupying

hummocks and dry lawns, do not usually grow under such nutrient-rich conditions (Sjörs 1950; Daniels & Eddy 1985; Lamers *et al.* 1999; Rydin & Jeglum 2013). Our results reveal that 1 year after installation, the slower-growing group displayed signs of nutrient imbalance. Specifically, the slower-growing *Sphagnum* species had the lowest capitula C:N, K:Mg and K:Ca quotients, highest stem N:K quotient and the highest concentrations of N, P, Mg and *Ca*. Furthermore, the fast-growing group accumulated less of these nutrients and had higher capitula quotients. Based on the capitula nutrient quotients of N:P and N:K, there is no evidence of P or K limitation in these groups (Bragazza *et al.* 2004). Interestingly, stem N:K quotient in the fast-growing group stayed well below 3, whereas the slower-growing group exceeded this threshold, suggesting first signs of K deficiency among the slower-growing sphagna (Hoosbeek *et al.* 2002; Bragazza *et al.* 2004).

The capitula N:P quotients were generally low and similar among all three groups. Nearly all capitula N:P quotients were close to or below 10 (group means 8.9–10.3) which Aerts *et al.* (1992) considered as a threshold for N limitation. P-rich irrigation water potentially lowered N:P quotients below 10, despite elevated N availability (atmospheric, irrigation). Mean capitula N content was found to be below saturation for the fast- and medium-growing groups, being between 9.4–10.1 mg·g$^{-1}$, but approaching saturation for the slower-growing group, at 12 mg·g$^{-1}$ (Table 3; Lamers *et al.* 2000), thus preventing growth limitation by N. Bragazza *et al.* (2004) reported a change in *Sphagnum* plants from being N-limited at atmospheric deposition >10 kg·N·ha$^{-1}$·year$^{-1}$, which corresponds to an N content of 9.5–13.6 mg·g$^{-1}$ in hummock and lawn species in peatlands of Europe. As in our study we have similar N content and higher deposition (23 kg·N·ha$^{-1}$·year$^{-1}$; UBA 2016), as well as extra load from irrigation water (see Temmink *et al.* 2017; Vroom *et al.* 2020), we exclude a growth limitation by N. The differences in N content may be explained by the higher growth rate (Prager *et al.* 2023), which, consequently, may have led to growth dilution of the nutrient content (Jarrell & Beverly 1981; Fritz *et al.* 2014; Krebs *et al.* 2018) as well as different species-specific metabolic adaptations to high N supply (*cf.* Bragazza *et al.* 2005; Gaudig *et al.* 2020). High N content (>20 mg·g$^{-1}$) can be toxic and hinder *Sphagnum* growth (Granath *et al.* 2009; Fritz *et al.* 2012; Gaudig *et al.* 2020), but no toxic N concentrations (>20 mg·g$^{-1}$) were exceeded for any of the three groups or for individual species (with one exception: 1 × *S. rubellum* stem: 20.1 mg·N·g$^{-1}$) in this study. We
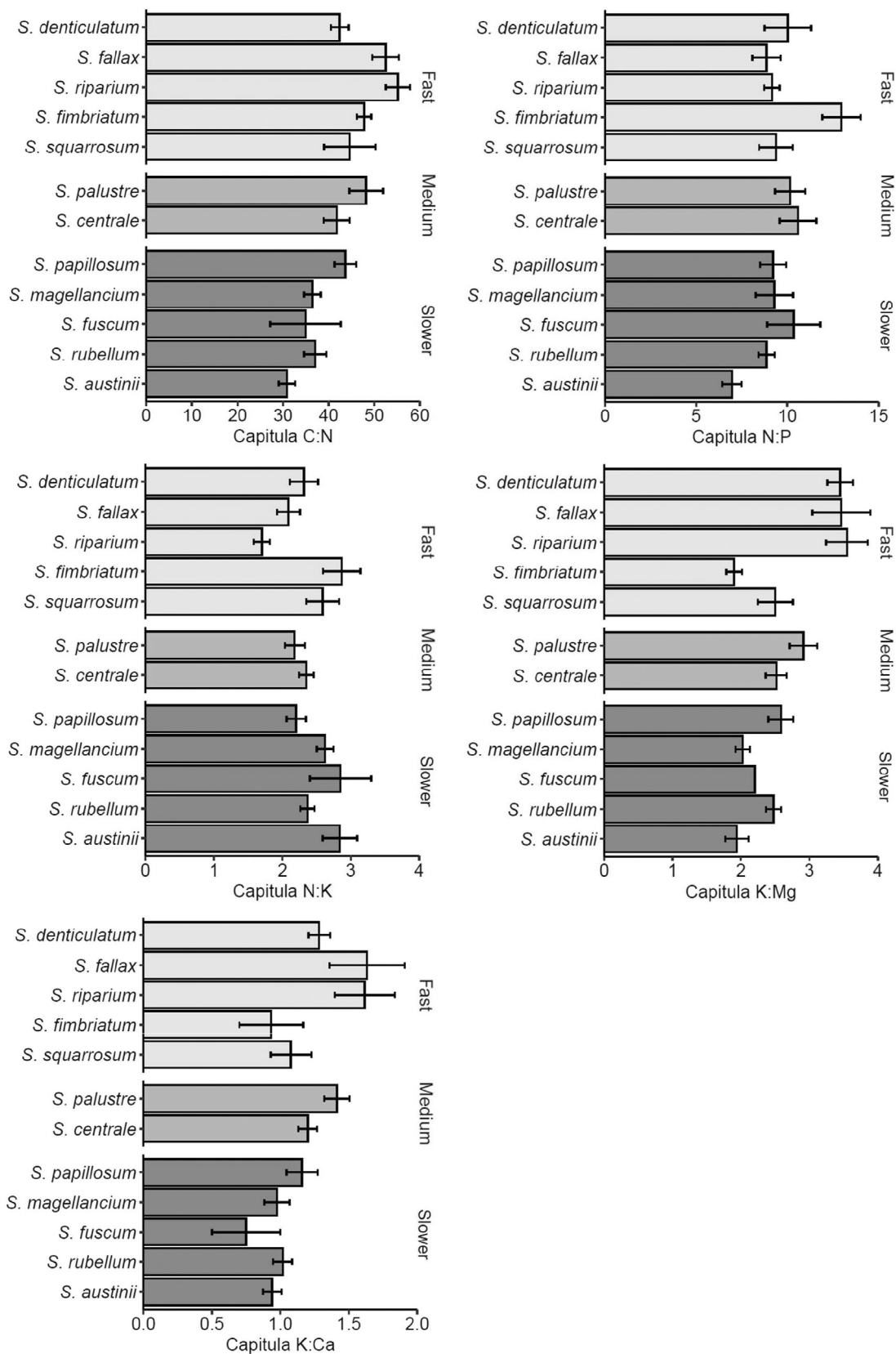
**Fig. 3.** Nutrient quotients C:N, N:P, N:K, K:Mg and K:Ca in capitula for each species within each growth group. Bars are mean ± SE. See Table 1 for replicates and Table S2 for statistical results.

**Table 4.** Capitulum and stem C:N, N:P, N:K, K:Mg and K:Ca ratios (g g$^{-1}$) for each group.

| | Group | C:N | N:P | N:K | K:Mg | K:Ca |
|---|---|---|---|---|---|---|
| Capitula (g g$^{-1}$) | Fast | 48.6 ± 2.0[a] | 9.6 ± 0.4[a] | 2.3 ± 0.1[a] | 3.1 ± 0.2[a] | 1.4 ± 0.1[a] |
| | Medium | 46.4 ± 2.8[a] | 10.3 ± 0.6[a] | 2.2 ± 0.08[ab] | 2.8 ± 0.2[a] | 1.4 ± 0.07[a] |
| | Slower | 38.1 ± 1.3[b] | 8.9 ± 0.4[a] | 2.5 ± 0.1[b] | 2.3 ± 0.08[b] | 1.0 ± 0.05[b] |
| Stem (g g$^{-1}$) | Fast | 52.7 ± 3.0[a] | 11.4 ± 0.5[a] | 2.1 ± 0.1[a] | 3.0 ± 0.2[a] | 0.9 ± 0.1[a] |
| | Medium | 44.8 ± 3.9[a] | 12.9 ± 0.9[a] | 2.4 ± 0.1[a] | 2.8 ± 0.1[a] | 0.8 ± 0.1[a] |
| | Slower | 35.1 ± 1.5[b] | 11.3 ± 0.5[a] | 3.4 ± 0.2[b] | 2.3 ± 0.1[b] | 0.7 ± 0.1[a] |

Reported values are mean ± SE. Significant differences between groups are indicated by different letters.

speculate that dilution by fast C accumulation (*e.g.* growth) prevented N accumulation in capitula beyond toxic levels as even the slower-growing group showed vigorous growth.

When focusing on P and K stoichiometry, the N:P and N:K quotients in our experiment were much lower compared to values found at high N deposition sites (up to 20 kg·N·ha$^{-1}$·year$^{-1}$; Bragazza *et al.* 2004). Specifically, the quotients in our study ranged from 1.2 to 3.6 for N:K and 4.9 to 18.9 for N:P, while those of Bragazza *et al.* (2004) were as high as 3.0–4.7 and 26.5–39.2, respectively. That study also showed generally lower N:K quotients in lawns than in hummocks (purely ombrotrophic) under high N stress levels. As P limitation occurs at N:P > 30 and K limitation at N:K > 3 (Bragazza *et al.* 2004), our data highlight that P and K were not limiting or co-limiting. Here, we argue that this can be explained by their sufficient supply from irrigation water and the agricultural legacy (Temmink *et al.* 2017; Vroom *et al.* 2020; Table 2). In contrast, high stem N:K quotients (>3), together with substantially lower (*ca.* 40% difference) K sequestration rates of the slower-growing group may indicate the start of K (co-) limitation (Hoosbeek *et al.* 2002), increasing the risk of K deficiency in the following growing seasons. Moreover, in previous studies on this *Sphagnum* paludiculture site in the peatland Hankhauser Moor, low quotients of N:P (mean 11.2) and N:K (mean 2.4) for *S. palustre*, *S. papillosum* and *S. fallax* were observed after 3 years (Temmink *et al.* 2017) and 2.5–7.5 years (Vroom *et al.* 2020) after installation. In contrast, the capitula P (mean 1.0–1.5 mg·g$^{-1}$; Table 3) and K content (mean 4.3–5.0 mg·g$^{-1}$) were lower in the present study (1 year after installation). While nutrient limitation seemed to be absent, we can conclude that slower-growing species sequestered C and K at lower rates than the faster-growing species. Lower lawn thickness of the slower-growing species may have increased their susceptibility to flooding over time, *e.g.* after rainfall, compared to medium- and fast-growing species. Moreover, slower-growing species like *S. fuscum*, *S. rubellum*, *S. austinii* and *S. papillosum* may exhibit intrinsically low growth rates (*cf.* Gunnarsson 2005).

Interestingly, we found high capitula Ca and/or Mg contents, especially among the slower-growing species. This may be explained by the higher cation exchange capacity of species growing naturally more distant from the influence of cation-rich water (Spearing 1972; Vicherová *et al.* 2017), which applies to species of the slower-growing group. Also, the slower growth might lead to a higher accumulation of nutrients in the capitula (Figs 2 and 3). Laekemariam *et al.* (2018) found that if Ca and/or Mg dominate the cation exchange over K in agricultural soils, this may reduce K availability and potentially result in K deficiency for plants, because the divalent Mg and Ca are more

easily absorbed by plants as opposed to monovalent K$^+$ (Breuer & Melzer 1990). In addition, for *Sphagnum* the affinity of K$^+$ to the cell wall exchanger can be enhanced by a low content of competing polyvalents and low pH (Hájek & Adamec 2009). For this reason, K content does not solely depend on the K availability, but also depends on the relative amounts of other cations. The surface water and pore water concentrations of Mg and Ca were higher at our field site (Table 2) compared to bogs and were comparable to poor fens and minerotrophic fens (Horton *et al.* 1979; Hájek *et al.* 2006; Hájková & Hájek 2007). As such, the slower-growing group (corresponding to hummock/bog species) are not well adapted to such conditions, as opposed to most of the fast-growing species, which occur under more minerotrophic conditions (Daniels & Eddy 1985; Wojtuń 1994). Consequently, the high Mg and Ca concentrations might have reduced C and nutrient sequestration through reduced K uptake of the slower-growing group (Rice 2009). Yet, the importance of this mechanism for different *Sphagnum* moss species remains to be determined in more detail. Nevertheless, the slower-growing species (typically non-calcitolerant bog species) did not show dramatic signs of nutrient imbalance/toxicity in this study. However, C sequestration rates in *Sphagnum* biomass of the slower-growing group were still substantial compared to those of Gunnarsson (2005). It cannot be ruled out that the peat mosses were flooded by slightly alkaline and mineral-rich water during rain events. Alkaline flooding, which occurs rarely at this experimental site (Vroom *et al.* 2020), is more likely to occur in natural conditions (Granath *et al.* 2010; Vicherová *et al.* 2017). This might have severe consequences for the slower-growing group, being less likely to 'out-grow' negative effects of flooding (Lamers *et al.* 1999; Granath *et al.* 2010; Harpenslager *et al.* 2015; Koks *et al.* 2022).

Among groups, we did not observe large differences in nutrient translocation (nutrient cycling within the moss) from stem to capitula (capitula:stem quotient; Table 3). This is an expected result in a nutrient-rich environment, as translocation from the old tissues to younger tissues is more likely to take place when nutrient availability is low (Vitousek 1982; Bridgham *et al.* 1995). However, the fast-growing group displayed higher P translocation to the capitula compared to the slower-growing group (except for *S. austinii*, which had a very high mean quotient of 1.9), most likely induced by a higher requirement to sustain growth. Overall, P quotients were much closer to those of natural unfertilized sites than those of N and K, which were much closer to the results acquired from N and/or P fertilized experiments with a higher supply in N and P (Fritz *et al.* 2012). Even though no group effect on the capitula:stem K quotients was observed, there was a substantial difference
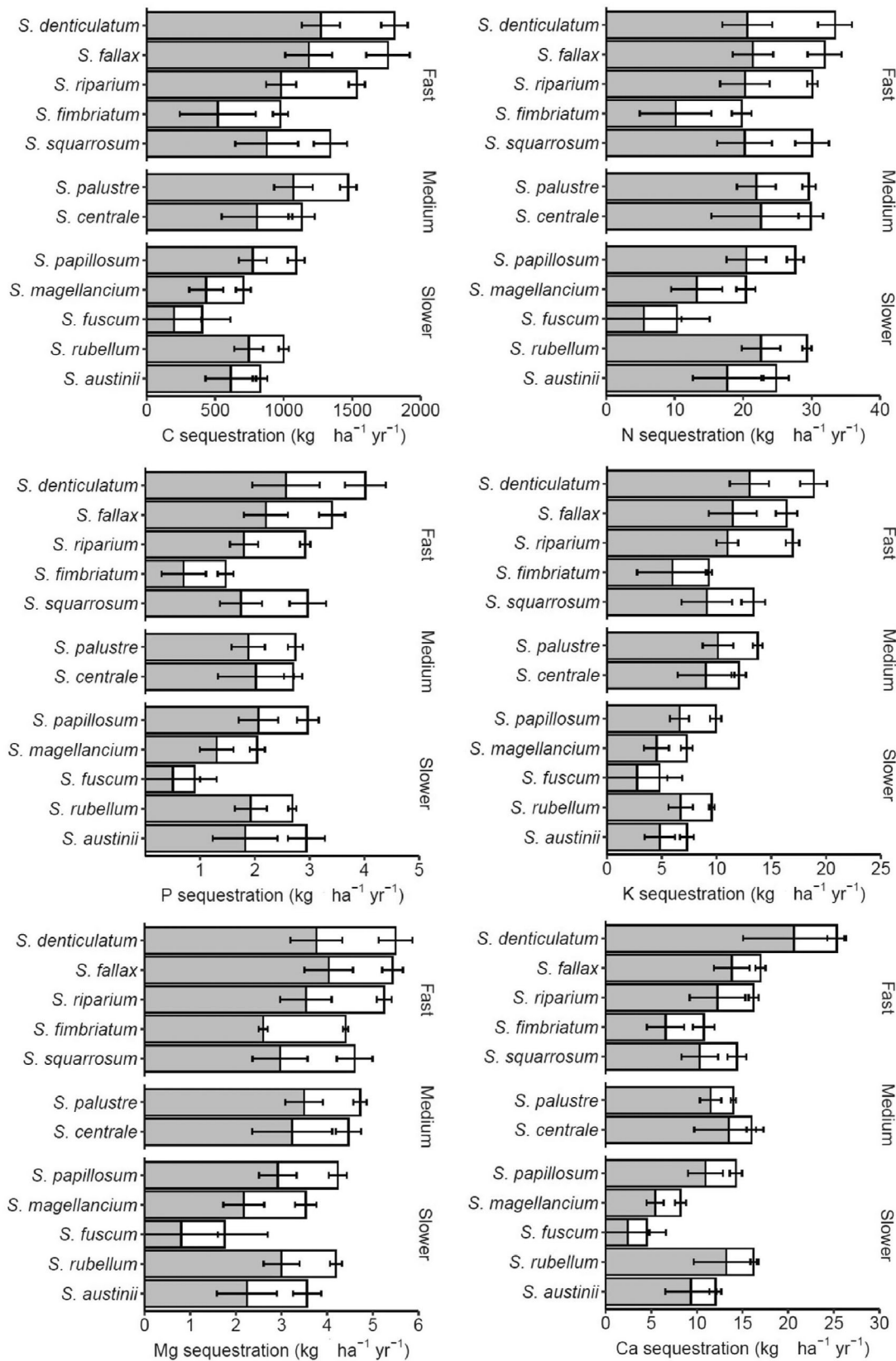
**Fig. 4.** Nutrient sequestration of C, N, P, K, Mg and Ca·kg·ha$^{-1}$·year$^{-1}$ in capitula (white) and stems (grey) for each species within each growth group. Bars are mean ± SE. Statistics were performed on total sequestration (capitula + stems). See Table 1 for replicates and Table S2 for statistical results.

between mean N:K ratios in capitula (2.5) and stems (3.4) in the slower-growing group, indicating differing K economics, possibly linked to the high capitula:stem Mg quotients within this group. However, further research should provide more insight into the co-uptake and ion translocation mechanisms within *Sphagnum*.

### Carbon and nutrient sequestration

The sequestration rates of C and nutrients of peat mosses during the establishment phase were generally high at this site, despite differences in nutrient dynamics between the groups. For instance, Turunen *et al.* (2004) recorded an average recent accumulation rate of 18 kg·N·ha$^{-1}$·year$^{-1}$ on 23 ombrotrophic bogs in eastern Canada, where N deposition range was 3–8 kg·N·ha$^{-1}$·year$^{-1}$. This discrepancy may be explained by N$_2$ fixation by symbiotic microorganisms in the peat and mosses (Vile *et al.* 2014; van den Elzen *et al.* 2018). Lateral influx of ammonium from ditch water is an alternative explanation (Table 2). All species-specific N sequestration rates in our study displayed higher N accumulation than the above example, except for *S. fuscum* (mean 10.3 kg·N·ha$^{-1}$·year$^{-1}$), ranging from 19.7 (*S. fimbriatum*) to 33.4 (*S. denticulatum*) kg·N·ha$^{-1}$·year$^{-1}$, on average, in the establishment phase. In addition, *S. magellanicum* in our experiment sequestered 10 times more N (22.3 kg·N·ha$^{-1}$·year$^{-1}$) on average than in natural bogs in Patagonia (2.2 kg·N·ha$^{-1}$·year$^{-1}$; Fritz *et al.* 2012). Such differences may be explained by the higher nutrient load, nutrient availability and biomass growth. For example, N deposition was below 2 kg·N·ha$^{-1}$·year$^{-1}$ in Patagonia (Fritz *et al.* 2012), while it was 23 kg·N·ha$^{-1}$·year$^{-1}$ at our study site (UBA 2016). Furthermore, *Sphagnum* mosses at our site were influenced by nutrient-rich irrigation water (in terms of N, P and K) which yielded high loads (Vroom *et al.* 2020; Temmink *et al.* 2017; Table 2). This difference is amplified on peat moss lawns of between 3 and 7.5 years old, which showed double N sequestration rates in previous analyses (34–47 kg·N·ha$^{-1}$·year$^{-1}$; Temmink *et al.* 2017; Vroom *et al.* 2020). In addition, the amounts of sequestered P and K in our experiment were similar (3 kg·P, 12 kg·K·ha$^{-1}$·year$^{-1}$, on average) to their studies (4–5 kg·P and 10–17 kg·K·ha$^{-1}$·year$^{-1}$). These early-stage findings are promising as the sequestration is likely to increase due to a higher productivity when the *Sphagnum* lawn becomes fully established.

The mosses in the fast-growing group, especially *S. denticulatum* and *S. fallax*, could reach higher mean C sequestration rates (1,810 and 1,760 kg·C·ha$^{-1}$·year$^{-1}$, respectively) than the average recent sequestration rates on natural eastern Canadian bogs, ranging from 400 to 1,170 kg·C·ha$^{-1}$·year$^{-1}$ (Turunen *et al.* 2004), as well as long term (past 10 to 125 years) sequestration rates of 1,200 kg·C·ha$^{-1}$·year$^{-1}$ reported by Temmink *et al.* (2022). The average C sequestration rate of the slower-growing group, 930 kg·C·ha$^{-1}$·year$^{-1}$, remains in the upper range of sequestration rates of Canadian natural bogs. The lower sequestration rates of the slower-growing species are directly linked to slower growth as a consequence of poorer adaptation to nutrient-rich conditions and, possibly, conditons being too wet, thus reducing the diffusion of CO$_2$ for photosynthesis (Rydin & McDonald 1985; Rice & Giles 1996; Hájek & Beckett 2008). However, we would like to highlight the fact that even these less adapted species were able to sequester a considerable amount of C in their establishment phase. Yet, it is important to consider that, in the case of

paludiculture, part of the sequestered nutrients and C will be harvested and, consequently, part of the sequestered C will most likely oxidize in the long term (Gaudig *et al.* 2018). Nevertheless, this harvested *Sphagnum* biomass will be used as a substitute for fossil peat products, which will lead to C offset in the long term (Gaudig *et al.* 2018; Günther *et al.* 2020). On the other hand, when *Sphagnum* is grown for restoration purposes without biomass harvest, optimal water management, coupled with optimal nutrient stoichiometry of the irrigation water, can yield high-end C sequestration and storage as well.

### Conclusions and implications

Overall, we conclude that nutrient supply is sufficient to prevent major nutrient imbalances for the 12 tested *Sphagnum* species, but optimal nutrient stoichiometry needs to be tested to determine optimal levels and supply of N, P and K for each species. Furthermore, we conclude that nutrient sequestration rates were high and species-/group-specific, specifically as the slower-growing group sequestered less C and K than the fast-growing group. In this light, it is vital to consider species-specific nutrient dynamics and C sequestration rates when selecting species for *Sphagnum* paludiculture and bog restoration. As such, the selection of *Sphagnum* species can (1) determine whether or to what extent a *Sphagnum* lawn can act as a nutrient/C sink, and (2) influence *Sphagnum* biomass yield, which in turn can prevent accumulation of excess, and thus toxic, N. Future research should focus on longer-term C and nutrient sequestration (C, N, P, K), performance of *Sphagnum* species under different environmental conditions, such as drought, and larger-scale tests for the most promising species. At a more fundamental level, the mechanisms and reasons why these species exhibit different intrinsic C uptake rates and nutrient dynamics (uptake, transfer and cycling) remain to be fully elucidated.

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## AUTHOR CONTRIBUTIONS

S.A.K. and R.J.M.T wrote the original draft and all authors contributed to the subsequent drafts. S.A.K., R.J.M.T., G.vD., A.P., Mi.K., G.G., A.H.W.K., W.L., Ma.K., C.J.H.P. and C.F. contributed to the methodology. S.A.K., A.H.W.K. and W.L. analysed the data. R.J.E.V. visualized the data. All authors contributed to carrying out the field experiment and/or sample analyses. K.G. was responsible for the field maintenance and C.J.H.P. led and organized the laboratory work. A.P., G.G., Mi.K. and Ma.K. were responsible of project administration and mainly supervised set-up and performance of the Sphagnum paludiculture field trial.

## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data available via Archiving and Networked Services (DANS) EASY: https://doi.org/10.17026/dans-zy5-9598.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Supporting information.

**Figure S1.** Water table below peat surface (cm) for the study period (daily mean of hourly measurements), measured in the ditch with automatic data logger (pressure transducer, Hydrotechnik HT Type 575).

**Table S1.** Groups, species with the number of replicates, lands of origin, dates of establishment, (pore)water collection and biomass sampling.

**Table S2.** ANOVA outputs of nutrient contents, capitula:stem element quotients and sequestration rates per nutrient, nutrient quotients (capitula and stem separately) and lawn height between groups.

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