



Rewet without regret? Nutrient dynamics in fen peat exposed to different rewetting degrees

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Abstract All over the world, peatlands have been drained, often for agricultural purposes, resulting in CO₂ emissions, soil subsidence and biodiversity loss. To combat these negative effects, drained peatlands are being rewetted, but knowledge of the effects of rewetting on peat biogeochemistry is still incomplete, especially since a variety of rewetting methods and rewetting degrees exists. We conducted a mesocosm experiment in which we exposed 100 intact agricultural fen peat cores (80 cm, 20 cm Ø) to five different water levels (0, 20, 40, 60 cm and variable—surface), two nutrient application levels to mimic continued agricultural use, and two water origins. Over an eight-month period, we harvested above-ground plant biomass five times and sampled pore water at two depths each month. Samples were analysed for nutrients. Our results show increased phosphate and ammonium availability upon fully rewetting (0 cm—surface) and less so under partially rewetted circumstances (20 cm—surface). Above-ground biomass was

strongly affected by nutrient application, especially in the high water level treatments. Vegetation was primarily N-limited, and N in the vegetation decreased with increasing water levels, indicating stronger nitrogen limitation upon rewetting. We conclude that nature restoration under fully rewetted conditions will likely be challenging as a result of the large release of nutrients from the system which may also affect surrounding nature areas. Furthermore, we conclude that partial rewetting combined with low-intensity agricultural use can be a solution to slow down the adverse effects of drainage, although this will lead to decreased agricultural production.

Keywords Internal eutrophication · Mesocosm · Nitrogen · Phosphorus · Potassium · Wetlands

Introduction

Wetlands around the globe are threatened by anthropogenic influences, most notably reclamation for agriculture and agricultural intensification (Joosten and Clarke 2002). This is also the case in the Western Peat District in the Netherlands, where the groundwater table has artificially been kept low to allow using the meadows for dairy farming. This lowered groundwater table has led to desiccation and oxidation of the peat, resulting in soil subsidence and substantial CO₂ emissions (Erkens et al. 2016). Further, the combination of water table drawdown, high nutrient

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inputs through the addition of manure and artificial fertilizer, and sowing fast-growing grass cultivars to boost agricultural production, has changed the peat meadow grasslands into highly productive, but near-monoculture fields. Consequently, plant species that used to thrive under wet and relatively low nutrient conditions have become more rare as they are out-competed by fast-growing species (Vermeer and Berendse 1983). To combat the negative effects of drainage, different rewetting measures are currently being explored and implemented, including passive rewetting, restoring seepage conditions and sub-surface irrigation (Van den Born et al. 2016).

Sub-surface irrigation is currently seen as a promising approach to elevate the groundwater table. With this technique, surface water either passively flows or is actively pumped into submerged drains into the parcels (Van den Akker et al. 2008; Van den Born et al. 2016). This results in a more stable groundwater table throughout the year, but it is particularly aimed at increasing the groundwater table during summer (Van den Born et al. 2016). Sub-surface irrigation can be combined with varying land uses such as intensive dairy farming, low-intensity agriculture, semi-natural grasslands, paludiculture (farming on moist/wet soils) and nature restoration. This broad applicability implies that the extent by which the groundwater level is raised can be fine-tuned to the intended land use. Currently, sub-surface irrigation is mostly brought into practice in combination with continued, but often less intensive, agricultural use, rather than complete restoration of natural ecosystems on former agricultural land. The intended land use also has consequences for nutrient input into the system, which decreases when agricultural practices become less intensive. Besides the water table and nutrient addition, an additional source of variation in the system is the source of the supplemented water. Most rewetting projects use surface water, which usually differs in chemical composition from groundwater.

A common problem resulting from rewetting former agricultural fields is internal eutrophication, i.e. the release of nutrients stored in the system, leading to higher nutrient availability and productivity increase (Smolders et al. 2006; Zak and Gelbrecht 2007). Particularly problematic is the mobilization of phosphate (PO_4^{3-}) from iron-phosphate complexes. As a consequence of the application of manure and artificial fertilizer, phosphorus (P) has

accumulated in the top layers of degraded peatlands, where it often is bound to redox-sensitive compounds, mostly iron (Fe) fractions (Richardson 1985). As the redox potential decreases upon rewetting, part of this P becomes mobilized (Caraco et al. 1989). Surface water often contains more SO_4^{2-} than groundwater; therefore, using surface water for rewetting may enhance internal P-eutrophication, i.e. rendering unavailable P to available forms (Geurts et al. 2008). Earlier experience with rewetting formerly drained peatlands has shown that internal P-eutrophication is one of the main factors that prevented the re-establishment of the desired wetland plant species after rewetting (e.g. Van Dijk et al. 2007; Klimkowska et al. 2019; Kreyling et al. 2021). In addition to PO_4^{3-} , increased ammonium (NH_4^+) concentrations have also been observed upon rewetting (Zak and Gelbrecht 2007), which is the result of a lack of nitrification in the anaerobic part of the soil and nitrate (NO_3^-) reduction in the top layer (Burgin and Hamilton 2007). Last, potassium (K) is a very mobile element that is easily leached and that has been observed to increase after rewetting due to the input of K-rich water (Koerselman et al. 1993), thus also contributing to K-release and increased K-availability.

Current societal challenges related to reducing greenhouse gas emissions, increasing carbon sequestration and safeguarding water quality have accelerated the need to rewet large areas of drained peatlands. Given the vast areas that need to be rewetted to meet climate goals as well as the often disappointing results in restoring biodiversity after rewetting due to internal eutrophication, it is currently being explored if rewetting can be combined with continued agricultural activities. With new rewetting techniques already being implemented on a rather large scale with hitherto uncertain effects on nutrient dynamics and plant growth, gaining a better understanding of the biogeochemical response to these rewetting techniques has become critical for the successful implementation of rewetting measures.

Here, we present the results of a full-factorial mesocosm study in which we exposed agricultural fen peat cores to different water levels, water origins and nutrient application levels. By doing so, we mimicked the effects of various new water management strategies in peat meadows. The objective of our study was to test how these factors influence nutrient dynamics

in the peat, nutrient availability to plants and the associated above-ground plant biomass production.

Methods

Site description and peat core collection

In February 2021, we collected 100 peat cores (80 cm, 20 cm Ø) in the peat meadow area Zegveld Polder (52° 08' 40.2" N 4° 50' 08.0" E). Peat formation in this area occurred under minerotrophic conditions. The peat substrate consists mainly of root and leaf remnants of reed and tall sedges, and wood remnants of alder and willow. The sampling location has been in agricultural use as grass production for dairy farming since the Middle Ages. Current vegetation consists of productive grass species and is dominated by *Lolium perenne*, *Poa spec.*, and *Holcus lanatus*. The area is fed by a mixture of rainwater, minerotrophic groundwater and surface water. In summer, desiccation of the meadows is prevented by pumping surface water into the polder that partly originates from the river Rhine. The groundwater table is as high as 10 cm below the surface in winter and drops to an average of 70 cm below the peat surface during the driest summer months.

The peat cores were extracted close to each other, in three parallel rows of 30–35 cores each (total plot of 10×2 m). We put a sharpened PVC pipe on the sward after which we used a knife to cut into the sward around the PVC pipe. Next, we carefully hammered the PVC pipe into the soil for about 30 cm. The remaining 50 cm was pushed into the soil with a crane. When all the peat cores were in the soil, we dug a trench along the peat cores to help us lift the peat cores out of the soil. Afterwards, we moved the peat cores horizontally and while still submerged in the water we closed them with a bottom lid to prevent any peat from falling out of the PVC pipe. The 100 peat cores were then transported to the botanical garden of Utrecht University and immediately put in the different treatment tanks.

We took peat samples two weeks following peat core collection in order to assess the field conditions as the peat cores were taken during a period of frost. Soil samples were taken in the field at depths of 0–10 cm and 35–45 cm below the sward, six samples at each depth. These samples were analysed for

organic matter and moisture content and total nutrient concentrations (Table 1). Total C and N was determined using a CN-analyser (NA1500, Fisons Instruments). All other elements were analysed with inductively coupled plasma-optical emission spectrometry (ICP-OES) (Avio 500, Perkin-Elmer) after 'aqua regia' destruction. The pH was measured after mixing 10 g fresh-weight soil with 25 ml of 1M KCl. Moisture content was determined by freeze drying a fresh-weight soil subsample of about 15 g for 48 h and measuring weight loss. These dried samples were then used to determine organic matter content as loss on ignition by heating them to 550 °C.

Experimental set-up

The experiment took place in the botanical garden of Utrecht University and lasted from 11 February 2021 until 30 October 2021. To mimic the field situation as best as possible, the experiment was conducted in the open air. Tanks (85 cm, 60 cm Ø) to hold the cores were installed in the soil to prevent strong temperature fluctuations in the peat cores. The experimental design consisted of five different water levels, two water origins and two nutrient application levels in a full factorial set-up, which resulted in 20 individual treatments (Table 2). For every treatment, one tank was used with five peat cores (Fig. 1). Small holes (Ø 2–3 mm) were drilled in the PVC cores at eight cm

Table 1 Peat soil characteristics (average±SE) at the peat core sampling location, n=6. All elemental analysis is of the total and the units are in g/kg dry weight

	0–10 cm	35–45 cm
C	286.4±20.3	376.5±22.2
N	22.8±1.5	22.4±1.7
P	1.9±0.08	0.65±0.03
K	6.7±0.1	3.8±0.3
Fe	19.5±0.3	12.5±1.1
Al	31.4±0.7	21.8±1.1
Ca	18.7±0.6	26.0±0.7
Mg	3.9±1.3	3.1±0.1
S	9.5±0.7	19.4±1.6
Fe:P molar ratio	5.8±0.2	10.9±1.1
pH-KCl	5.1	4.6
% organic matter	56.8±4.9	74.3±3.5
% moisture	62.6±1.9	77.9±1.4

Table 2 Factor levels of the mesocosm treatments. A full-factorial design was applied, including five water levels, two water origins and two nutrient application levels, resulting in a total of 20 treatments

Water level (WL)	Water origin (WO)	Nutrient application (NT)
Permanently saturated: 0 cm (WL0)	Groundwater (GW)	Low: 50 kg N/ha (Low)
Constant, High: – 20 cm (WL20)	Surface water (SW)	High: 250 kg N/ha (High)
Constant, Medium: – 40 cm (WL40)		
Constant, Low: – 60 cm (WL60)		
Variable: – 60 cm/– 20 cm (Var)		

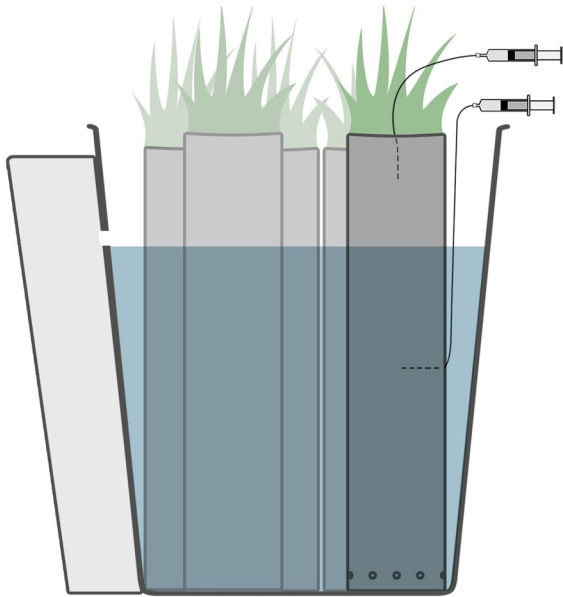


Fig. 1 Experimental set-up. Five peat cores (80 cm, 20 cm Ø) were placed in every tank. Small holes were drilled in the bottom to allow water inflow into the peat core. In every peat core, a Rhizon sampler was installed in the top 10 cm and at 40 cm depth. These Rhizon samplers were then connected to syringes for pore water collection. In total, 20 different treatment tanks were created including five water levels, two water origins and two nutrient application levels

from the bottom with a total of eight per core to allow water exchange between the peat core and the tank.

The five water level treatments included four stable water levels and one variable water level. The four stable water level positions (with water levels of 0, 20, 40 and 60 cm below peat surface) mimicked several rewetting degrees. The variable water level was kept at 20 cm and 60 cm below the peat surface during winter and summer respectively, to mimic the current water management situation in most Dutch peat meadows used for dairy farming. We drilled a 25 mm Ø hole at the desired water level in all tanks to create an overflow for periods of ample rain (Fig. 1). During dry periods,

water levels were kept constant by manually adding water every 2–3 days. The water level in the tanks with a variable water level was kept at 20 cm below peat surface from day 0 to day 102 (24 May 2021). In the summer months, between days 102 and 222 (21 September 2021) of the experiment, the water level was kept at 60 cm below peat surface, and at day 222 the water level was raised to 20 cm below peat surface again until the end of the experiment. Four tanks were created for each of the five water level treatments.

To accomplish the water origin treatments, half of the tanks were filled with surface water and the other half with groundwater (for the chemical composition of the surface water and groundwater, see Table S1). The surface water was pumped from a ditch in the polder where the peat cores originated, and the groundwater was taken from a 12 m deep well in the same polder area. To prevent algae growth in the tanks, we put ball pit balls in the tanks surrounding the peat cores, thereby preventing the sunlight from reaching the water. Furthermore, all water in the tanks was refreshed monthly 4–5 days after pore water collection. To that end, we pumped all water out of the tanks and immediately filled the tanks again with surface water or groundwater which we transported every month from the Zegveld area.

Half of the cores received a high nutrient application of 250 kg N/ha/year, which is comparable to an N input to meadows that are used for intensive dairy farming in the Netherlands (Kleijn et al. 2001). The other half of the cores received a nutrient application of 50 kg N/ha/year, which is representative for maintenance of mesotrophic herb-rich grasslands with low-intensity agriculture (cut once annually and low-intensity grazing; Schippers et al. 2014). Nutrients were manually applied by adding slow-release granules with a N:P:K of 16:5:12 (Osmocote flower, slow-release 2–3 months), which resembled an N fertilization of 250 and 50 kg N/ha/year in total. Granules were added on day 51, 133 and 201 of the experiment.

In every peat core, we installed 10 cm Rhizon pore water samplers (pore size 0.12–0.18 μm , Rhizosphere Research Products, the Netherlands) at two depths (Fig. 1). One Rhizon sampler was installed vertically in the top 10 cm of the peat core. The other Rhizon sampler was inserted horizontally at 40 cm in the soil. To install the Rhizon sampler at the lower depth, we drilled a small hole in every PVC column. This hole was sealed after insertion of the Rhizon and we allowed the cores to stabilize for 27 days before the first pore water samples were taken.

Data collection and chemical analyses

The experiment started with the collection of peat cores on 11 February 2021 (day 0). Pore water samples were taken on day 27, 60, 95, 124, 158, 193 and 249 at both depths. To sample pore water, syringes (20 ml) were connected to the Rhizons and put under vacuum the day before pore water collection. On day 124 and 158 no pore water samples were taken in the top soil layer of the WL60 and variable WL treatments, as the peat cores in these treatments were too desiccated to allow pore water sampling. Pore water samples were divided into three different subsamples and were stored in Greiner tubes. The first subsample was used to measure electric conductivity (EC) and pH (3110 portable meter, xylem analytics), and alkalinity using a Hach field test (Hach, model AL-AP), all within two hours of sampling. The remainder of this subsample was used to measure NH_4^+ colorimetrically using the indophenol blue method (Koreleff 1976), and to determine SO_4^{2-} and Cl^- concentrations using Ion Chromatography (930 Compact IC Flex, Metrohm). The second subsample of 3 ml was acidified by adding 30 μl HNO_3 (68%) immediately after sampling and was used to measure PO_4^{3-} colorimetrically using the molybdenum blue method (Murphy and Riley 1962). After this, the remainder of subsample two was 5 \times diluted and Al, Ca, Fe, K, Mg, Na, and P were analysed with ICP-OES (Avio 500, Perkin-Elmer). A last subsample of 3 ml was frozen until further analysis on a Discrete Analyser (Gallery, Thermo Scientific) to measure NO_x .

Above-ground biomass was clipped five times during the growing season (April–October), on day 78, 126, 167, 201 and 245 of the experiment. Dry weight was measured after drying the plant material for 48 h at 70 °C. We further analysed the dried samples of harvest 1, 3 and 5 for total C, N, P and K contents. Prior to

chemical analysis, the material was first clipped using a Fritsch Cutting Mill Pulverisette 15. The clipped material was then pulverized using a Herzog HP-Ma automatic pulverizer. C and N content was determined using a CN-analyser (NA1500, Fisons Instruments) and P and K content was determined using total reflection X-ray fluorescence (S2 Picofox, Bruker).

Nutrient limitation

Ratios of nutrient concentrations in the plant tissue are often used as an indicator of nutrient limitation (e.g. Wassen et al. 1995; Van de Riet et al. 2010). Here, we follow the critical values of nutrient ratios as described by Olde Venterink et al. (2003) with critical ratios of N:P = 14.5, N:K = 2.1, and K:P = 3.4. For nitrogen, N:P ratios < 14.5 and N:K values < 2.1 indicate N limitation. Phosphorus limitation is indicated by N:P ratios > 14.5 and K:P ratios > 3.4. For potassium, N:K values > 2.1 and K:P values < 3.4 indicate K limitation. However, critical values should be considered as general rules of thumb and are not suited to very precisely define a switch from one nutrient being limited to the other as values around the critical ratio may indicate co-limitation. According to Güsewell (2004), co-limitation is thought to occur for N:P ratios between 14 and 16.

Data analysis

All statistical analyses were conducted in R version 4.1.2 (R Core Team 2021). Differences in pore water and vegetation response variables between treatments were tested using a linear mixed-effect model with restricted maximum likelihood (REML) estimation (Bates et al. 2015). In our model, we treated the factors “water level”, “nutrient application”, “water origin” and “sampling month” as fixed effects. We included the main effects and two-way interactions of these four factors in the model. Moreover, we included peat core numbers as a random effect. From this model, an ANOVA test was retrieved using the lmerTest package in R (Kuznetsova et al. 2022). Normality and homogeneity were visually assessed using residual plots. Data were log-transformed if this resulted in a better residual plot. We used the emmeans package with multivariate t distribution adjustment to perform a post-hoc multiple comparisons test (Russell et al. 2023).

Results

Nutrient availability in pore water

The results of a selection of pore water variables related to nutrient dynamics are presented in Table 3. Figure 2 shows the effect of water level on the nutrient availability in the pore water at the two different sampling depths. As water origin and nutrient application had no significant effect on nutrient availability in the pore water, we pooled all nutrient and water origin treatments in Fig. 2.

Nitrogen

Overall, NH_4^+ concentrations were highest under saturated water levels (WL0). In the top soil layer (0–10 cm) this was most visible in the summer months, during which NH_4^+ concentrations increased significantly in the WL0 treatment

(Fig. 2a; Table S3). The NH_4^+ concentrations in the other water table treatments did not differ from each other in the top soil layer (Table S4). At 40 cm depth, the NH_4^+ concentrations were higher in the two wettest treatments (WL0 and WL20) compared to the two driest treatments (Fig. 2b, Table S5). After the water level was decreased in the variable water level treatment, the NH_4^+ concentrations dropped from ca. 4.5 mg/l to ca. 1 mg/l (Fig. 2b). These values correspond to the values measured in the water table treatments WL20 and WL60 respectively. At 40 cm depth, NH_4^+ concentrations were higher in the high nutrient treatments in the WL20 treatment and almost ($p=0.061$) in the WL0 treatment (Table S6). At both depths, there was no significant main effect of nutrient application (Table 3; Fig. S1a, b) or water origin (Table 3; Fig. S2a, b) on NH_4^+ concentrations.

In the top soil layer, NO_x concentrations were highest in the lowest water level treatment (WL60) during

Table 3 Results of linear mixed-effect model on the effects of sampling month (SM), water level (WL), nutrient application (NT), and water origin (WO), and their two-way interactions on the main pore water and vegetation variables

	Depth (cm)	SM	WL	NT	WO	WL*SM	WL*NT	WL*WO	NT*SM	WO*SM	NT*WO
Pore water variables											
NH_4^+	0–10	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s
	40	***	***	n.s	n.s	***	*	n.s	n.s	n.s	n.s
NO_x	0–10	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s
	40	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s
PO_4^{3-}	0–10	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s
	40	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s
K_{tot}	0–10	***	**	n.s	n.s	***	*	n.s	n.s	n.s	n.s
	40	***	***	n.s	n.s	***	*	n.s	n.s	n.s	n.s
Fe_{tot}	0–10	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s
	40	***	***	n.s	n.s	***	n.s	n.s	**	n.s	n.s
SO_4^{2-}	0–10	***	***	**	n.s	***	n.s	n.s	n.s	n.s	n.s
	40	***	***	n.s	n.s	***	n.s	n.s	n.s	n.s	*
Vegetation variables											
Above-ground biomass		***	***	***	n.s	***	**	n.s	***	n.s	n.s
N (mg/g DW)		***	***	*	n.s	***	n.s	n.s	*	n.s	n.s
P (mg/g DW)		***	**	n.s	n.s	***	n.s	n.s	*	n.s	n.s
K (mg/g DW)		***	n.s	n.s	n.s	*	n.s	n.s	n.s	n.s	n.s
N:P		***	***	n.s	n.s	***	n.s	n.s	**	n.s	n.s
N:K		***	***	*	n.s	***	n.s	n.s	***	n.s	n.s
K:P		***	*	n.s	n.s	***	n.s	n.s	n.s	n.s	n.s

DW dry weight

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

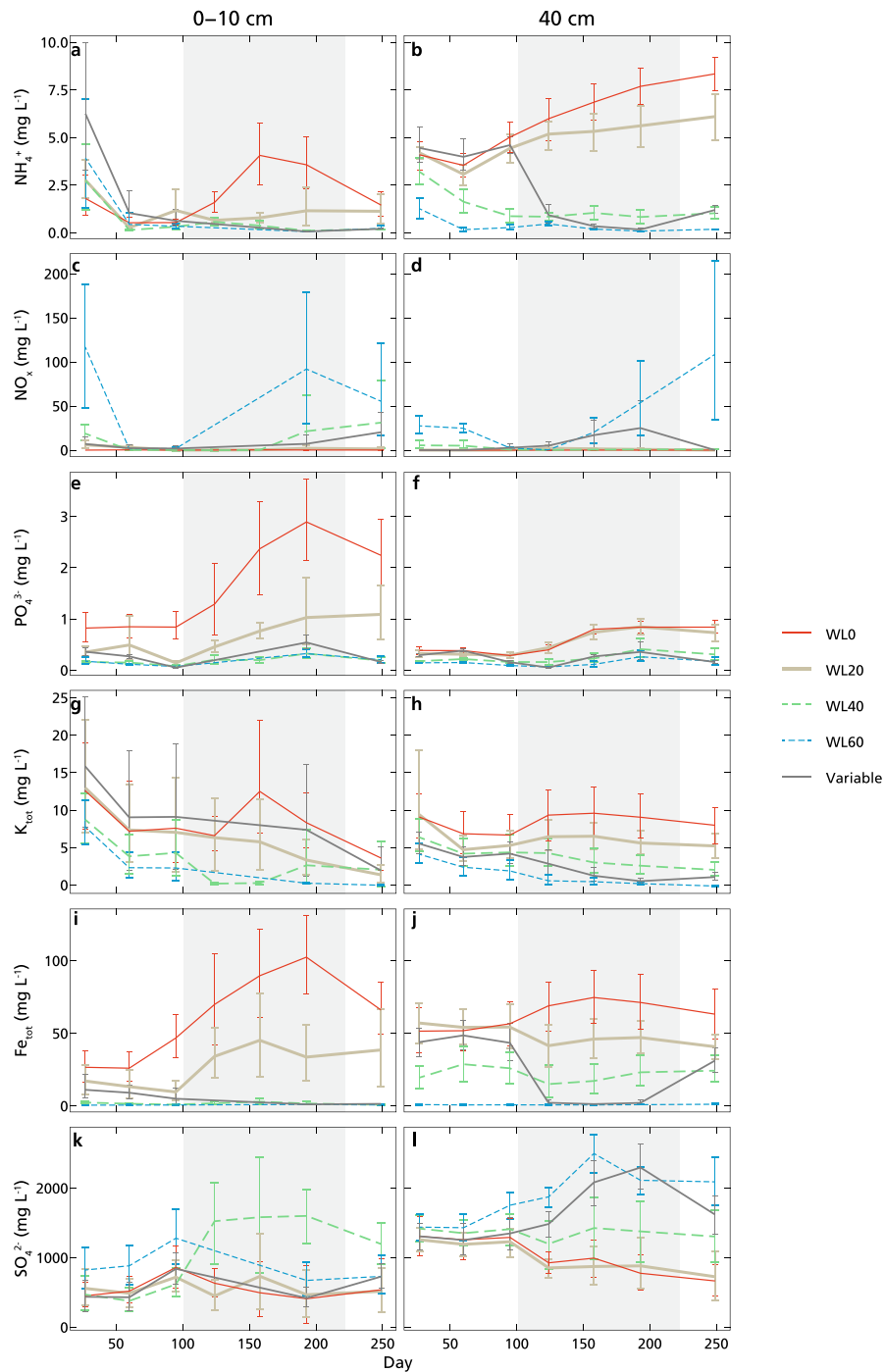


Fig. 2 Pore water variables over time in the different water table (WL) treatments (different line colours) at 0–10 cm depth (left panels) and 40 cm depth (right panels). The nutrient application treatments and water origin treatments are pooled (n was mostly between 15 and 20, with some exceptions, depending on the number of missing data points). Concentrations

(mg/l) are expressed as total mass of the ion. The grey block depicts the summer period, when the variable water level treatment (grey lines) was set at 60 cm below surface. In the other months the water level of this treatment was set at 20 cm below surface. Error bars are standard errors

the months of March, August and October (day 27, 193 and 249) with mean values of 50–117 mg/l compared to mean values of 7–14 mg/l in the other water level treatments in those months (Fig. 2c, Table S7). In the other months, no significant effects were found and NO_x concentrations remained relatively low. In June and July (day 124 and 158), data is missing in the WL60 treatments and the variable water level treatments because the cores were too dry for pore water sampling. At 40 cm depth, NO_x concentrations were overall significantly higher in the WL60 treatment than in the other WL conditions (Table S8). Similar to NH_4^+ , no significant effects of water origin and nutrient application were found on NO_x concentrations (Table 3; Figs. S1c, d, S2c, d).

Phosphorus

Overall, the PO_4^{3-} concentration in the pore water taken from the top soil layer significantly increased after May (day 95). This increase was most visible in the saturated water level treatment, where PO_4^{3-} concentrations were significantly higher than in all other water levels from May (day 95) onwards (Fig. 2e; Table S9). Similar patterns were found in the pore water samples taken at 40 cm depth, where PO_4^{3-} concentrations were significantly higher in the WL0 and the WL20 treatment than in the other water level treatments from June (day 124) onwards (Fig. 2f; Table S10). However, concentrations at this depth remained relatively low compared to the concentrations found in the top soil layer. No main effects of nutrient application and water origin were found on the PO_4^{3-} concentration at either depth (Table 3).

P is known to mostly bind to Fe fractions (Richardson 1985; Bridgman et al. 2001) and to a lesser extent to Al fractions (Richardson 1985) and Ca fractions (Boyer and Wheeler 1989) in the soil. In the WL0 treatment, total Fe (Fe_{tot}) concentrations in the pore water of the top soil layer indeed followed a similar trend as the PO_4^{3-} concentrations. For the other water levels, this trend was less clear. Fe_{tot} responded stronger and faster to changes in the water level than PO_4^{3-} . This became evident from the variable water level treatment, which showed that Fe_{tot} concentrations in the pore water at 40 cm depth almost dropped to zero when the water level in this treatment was lowered from 20 to 60 cm. Moreover, Fe concentrations

increased again when the water level was raised back to 20 cm on day 222 of the experiment (Fig. 2j).

SO_4^{2-} is also known to enhance P mobilization via the reduction of SO_4^{2-} to sulphide, which binds better to Fe than PO_4^{3-} (Smolders et al. 2010). In the top soil layer, SO_4^{2-} concentrations were higher in the WL40 and WL60 treatments than in WL0 from the summer onwards (Fig. 2k; Table S11). At 40 cm depth, SO_4^{2-} concentrations were higher in the WL60 and the variable water level treatments compared to the other WL treatments from June (day 124) onwards (Fig. 2l; Table S12). This indicates that SO_4^{2-} reduction may indeed have taken place in wetter treatments. In contrast to most other nutrients, a significant main effect of nutrient application was found in the top soil layer ($p=0.0023$) with SO_4^{2-} concentrations being higher in the treatments receiving a high nutrient application (Fig. S1k). No significant effect of water source on SO_4^{2-} concentrations were found at both depths (Table 3).

Potassium

In the top soil layer, no significant differences were found between the water level treatments during the first three months of measuring (Fig. 2g; Table S13). After that, K_{tot} concentrations were higher in the fully saturated water level treatment (WL0) than in the WL40, WL60 and variable water level treatments (Table S13). Furthermore, in the top soil layer K_{tot} concentrations were overall higher in the high nutrient treatments of the WL0 and the variable water level treatments although this was not strongly significant ($p=0.0275$ and $p=0.0372$, respectively) and mainly visible in the summer months (Fig. S1g). At a depth of 40 cm, K_{tot} concentrations in the pore water were highest in the two wettest water level treatments (WL0 and WL20) from July (day 158) onwards (Fig. 2h; Table S14). Also at this depth K_{tot} concentrations were higher in the high nutrient application treatment in the WL0 treatment compared to the low nutrient application treatment. No main effects of nutrient application and water origin were found at both depths (Table 3).

Above-ground biomass

Cumulative above-ground biomass production of the five harvests was highest in the lowest water level treatment and only in the two wettest treatments (WL0 and WL20) showed a significant response to

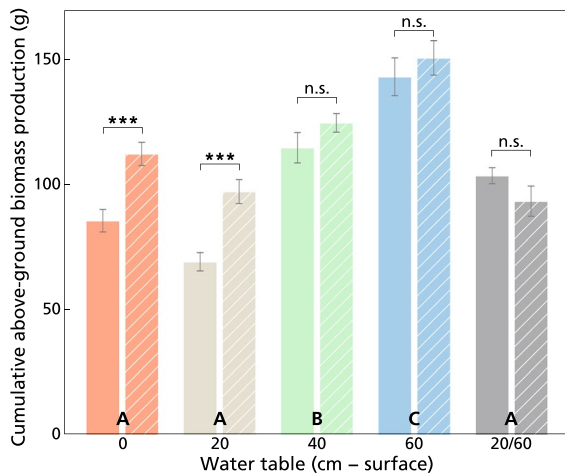


Fig. 3 Cumulative above-ground biomass production over all five harvests. Filled bars: low nutrient application, dashed bars: high nutrient application. The various colours correspond to the different water level treatments as indicated in Fig. 2. Error bars represent 1 SE. In this figure the water origin treatments are combined, $n = 10$. Letters denote the significant differences between the water table treatments; treatments sharing a letter do not significantly differ. Significant differences of nutrient application level are shown for every water table treatment, *** $p < 0.001$, n.s. not significant

nutrient application (Fig. 3). However, the above-ground biomass of the vegetation was significantly higher in the high nutrient treatments in all harvests after harvest 1 ($p < 0.001$) (Figs. 4a–c, S3). Harvest 1 was harvested only a few weeks after the first fertilizer application (Fig. 4a) and consisted of the original vegetation present during peat core collection. At harvest 1, the above-ground biomass was highest in the lowest water level treatment (Fig. 4a, $p < 0.001$). In the following harvests the above-ground biomass in WL60 was not as different (Figs. 4b, c, S3) but in harvest 2 and 4 the above-ground biomass in the WL40 and WL60 treatments were significantly higher than the above-ground biomass in the WL0 and WL20 treatments (Fig. S3). The above-ground biomass showed no significant effect of the water origin treatments (Table 3). Throughout the growing season, the above-ground biomass production overall decreased in all WL treatments (Fig. S3; Table S15).

Nutrient concentrations in the plant tissue

N concentrations in the plant tissue were overall highest in the low water level treatments (Fig. 4d–f),

resulting in more N uptake by the plants in these treatments (Fig. S4a–c). N concentrations in the variable water level treatment showed no significant difference from WL20 during harvest 1, and did not significantly differ from the WL60 treatment during harvest 3 (Fig. 4d, e) which is consistent with the water level in the variable WL treatment during those harvests. P concentrations were overall similar between the water levels but were higher in the wettest treatments (WL0 and WL20) than in the WL60 and variable WL treatments in harvest 5 (Fig. 4g–i). Further, P concentrations were higher in harvest 5 compared to harvest 1 and 3 in all water level treatments (Fig. 4g–l; Table S16). K concentrations were overall lower in harvest 3 and 5 than in harvest 1 (Fig. 4j–l). There were no significant differences in K concentration between water level treatments, water origin treatments and nutrient application treatments (Table 3).

Nutrient limitation

It can be concluded from the N:P ratios that in most water level treatments N was the limiting nutrient (Fig. 5a–c). In the two wettest treatments (WL0, WL20), N:P values remained below 10 and were therefore most clearly N limited. During harvest 3, the variable water level treatment and the WL60 treatments moved towards P limitation with N:P values of 16–18, whereas the other treatments remained N limited (Fig. 5b). Here, the variable water level treatment was set at 20 cm below peat surface. In harvest 5, N:P values in the variable water level treatment dropped again; at this stage the water table in this treatment was increased again from 60 cm below the surface to 20 cm below the surface.

The low N:K ratios in the WL0 and WL20 treatments further confirm N limitation in these treatments (Fig. 5d–f). In harvest 3 and 5, N:K ratios were higher in the lowest water level treatment (WL60); here, the N:K ratios were around the critical value, which implies that these cores were probably not strongly limited by either N or K, or that they experienced co-limitation.

Most treatments had a K:P well above the critical value of 3.4 (Fig. 5g–i), suggesting that after N limitation, P limitation seems more likely to occur than K limitation. In harvest 5, K:P ratios were significantly lower than in harvest 1 and 3 in all WL treatments, thus moving away from P limitation (Table S17). This effect was mainly caused by an

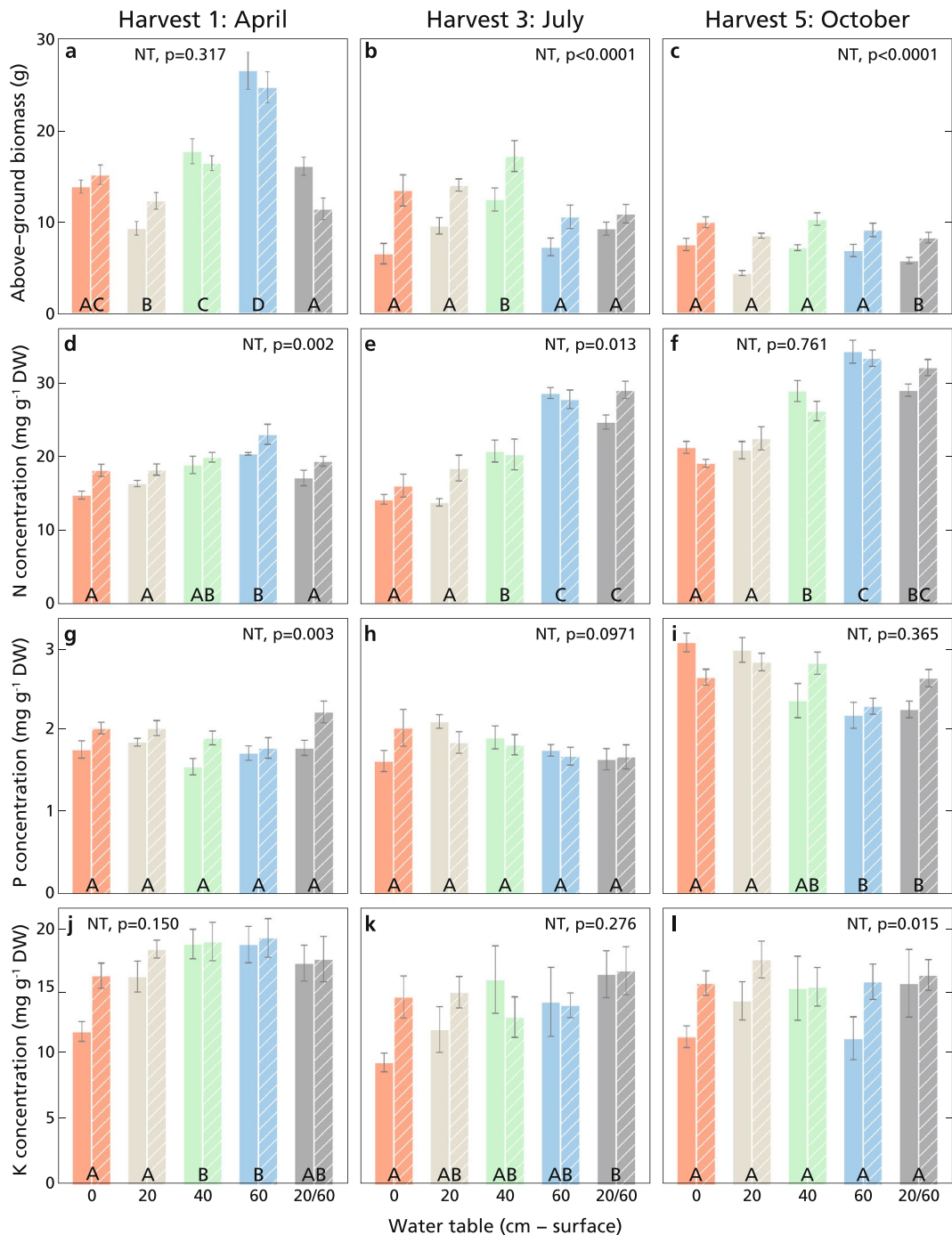


Fig. 4 Above-ground biomass production (a–c) and nutrient concentrations in the plant tissue (d–l) in harvests 1, 3 and 5. DW: dry weight. Filled bars: low nutrient application, dashed bars: high nutrient application. The various colours correspond to the different water level treatments as indicated in Fig. 2. Error bars represent 1 SE. In this figure the water origin treat-

ments are pooled, $n = 10$. Overall significance of nutrient application level (NT) is indicated for every harvest. Letters denote the significant differences between the water table treatments within every harvest; treatments sharing a letter do not significantly differ

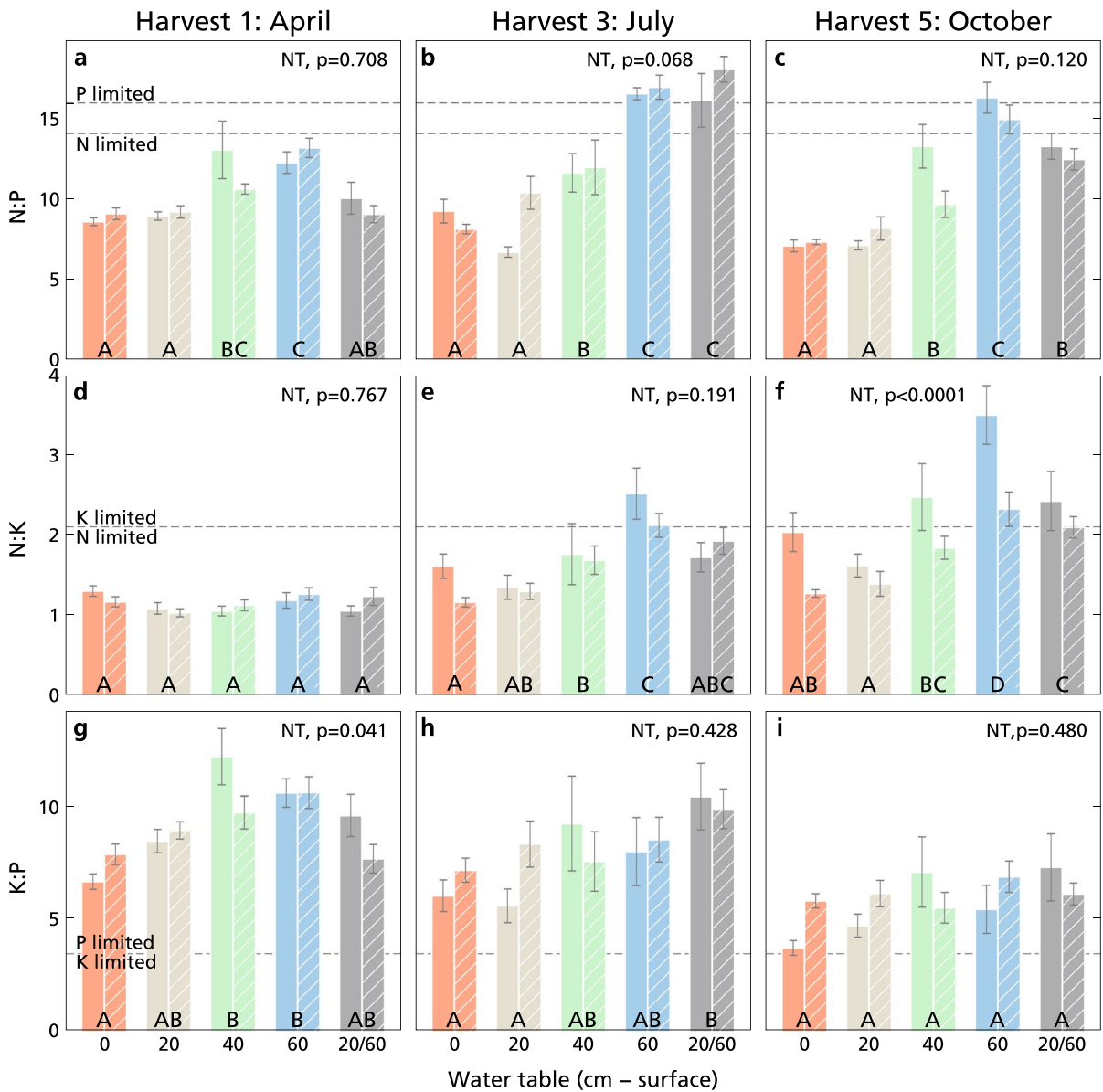


Fig. 5 Nutrient ratios in the above-ground biomass for harvests 1, 3 and 5. N, P or K limitation is indicated by the dotted lines following the critical nutrient ratios: N:P 14.5, N:K=2.1, and K:P=3.4 and co-limitation between a N:P ratio of 14–16 as described in the method section. Filled bars: low nutrient application, dashed bars: high nutrient application. The various colours correspond to the different water level treatments as

indicated in Fig. 2. Error bars represent 1 SE. In these figures the water origin treatments are pooled, $n=10$. Overall significance of nutrient application level (NT) is indicated for every harvest. Letters denote the significant differences between the water table treatments within every harvest; treatments sharing a letter do not significantly differ

increase in P concentrations in the plant tissue in harvest 5, which is especially visible in the wetter treatments (Fig. 4i; Table S16).

Discussion

The mesocosm experiment consisted of a full factorial design in which 100 peat cores were exposed to

five different water levels, two nutrient application levels and two water origins (groundwater and surface water). Over an eight-month period, we sampled pore water at two depths each month and harvested above-ground plant biomass five times. Results showed that water level strongly affects nutrient concentrations in the pore water, with higher NH_4^+ , PO_4^{3-} and K_{tot} concentrations found in the high water level treatments. Nutrient application and water origin had little to no effect on nutrient availability in the pore water, but total above-ground biomass of the vegetation was higher in the high nutrient treatments than in the low nutrient treatments from harvest 2 onwards. Vegetation was primarily N-limited, and N concentrations in the vegetation decreased with increasing water levels, indicating stronger nitrogen limitation upon rewetting. The stronger N limitation in the wetter treatments also explains the stronger biomass response in the wetter treatments when fertilizer is added. Neither P nor K concentrations in the above-ground plant tissue responded to increased PO_4^{3-} and K_{tot} concentrations in the pore water, which can be attributed to the fact that vegetation is N limited, and assuming that no luxury consumption of P and K is taking place.

All variables changed significantly over sampling month, which is likely a combination of a time lag for the processes in the peat cores to adjust to the experimental conditions, and a clear seasonal effect in many variables. Many of the processes that drive the variables studied here (e.g. decomposition, mineralization, chemical equilibria, plant growth) are temperature dependent and their rates are therefore likely to respond to changes in temperature over the season. In addition to a significant main effect of sampling month, all variables also showed a significant interaction effect between water level and sampling month, indicating that the changes over time for all variables differed between water level treatments. This interaction effect can be attributed to differences between water level treatments becoming more apparent at the peak of the growing season, i.e. at high process rates due to favorable temperatures. E.g. we observe the highest rate of NH_4^+ accumulation in the wettest treatments during the summer months, when N-mineralization is highest (Koerselman et al. 1993). Although we tried to limit temperature fluctuations and temperature differences between water level treatments as much as possible by installing the tanks

belowground, we cannot fully exclude additional effects from temperature differences between water level treatments because we did not measure soil temperature over time in our peat cores.

Water level

Water level strongly affected nutrient availability in the pore water. We observed higher NH_4^+ concentrations under wet anaerobic circumstances (WL0) during the summer months (Fig. 2a, b), whereas NO_x concentrations (consisting predominantly of NO_3^- ; not shown) were highest in drained soils (WL60) after summer (Fig. 2c, d). This indicates decomposition of organic matter and subsequent nitrogen mineralization, especially during the summer months when high temperatures stimulate these processes. In the high water level treatments, where nitrification levels are low due to the anaerobic conditions, this leads to NH_4^+ accumulation, which is often observed when rewetting heavily degraded fens (Zak et al. 2010). NH_4^+ accumulation in the wettest treatments was even more expressed in the deeper soil layers. Where part of the NH_4^+ may have been lost due to oxidation to NO_3^- and subsequent denitrification in the top layer, the limited possibilities of oxygen diffusion prevents this process from occurring in the deeper soil layers (Smolders et al. 2013). In the drained treatments, the observed high nitrate concentrations are likely the result of higher organic matter decomposition and N mineralization compared to the high water level treatments (Olde Venterink et al. 2002). Here nitrate may have accumulated since denitrification is hampered in oxic conditions (Tiemeyer and Kahle 2014).

Higher denitrification rates and hence less N remaining in the system are also a plausible explanation for the stronger N limitation in the water-saturated treatments as shown by the low N:P ratio (Fig. 5a–c) and lower N concentrations in the plant tissue (Fig. 4d–f). N:P ratios in the vegetation seem to strongly respond to variability in water levels, which becomes clear from the N:P ratios in the variable water level treatment. In this treatment, the growth period of vegetation between harvests 4 and 5 consisted of 21 days at a water level of 60 cm below surface level and 22 days at a water level of 20 cm below surface level. Yet, the N:P ratio dropped from ca.

16–18 in harvest 3 to ca. 12.5 in harvest 5. However, the above interpretations of denitrification rates and how these relate to plant N limitation are, although likely, slightly speculative and only could have been tested by measuring denitrification.

Our results show strong phosphorus mobilization in the top soil layer upon rewetting, which confirms earlier findings of PO_4^{3-} mobilization upon the rewetting of drained agricultural fens (Van Dijk et al. 2004; Zak and Gelbrecht 2007; Zak et al. 2010). We also found increased pH values in the pore water in the fully water-saturated treatment (ca 6.2 compared to pH values of ca 5.3 in the lowest WL treatment). An increase in pH may result in a lower redox potential and hence likely has resulted in Fe and SO_4^{2-} reduction, leading to PO_4^{3-} mobilization. Strong PO_4^{3-} mobilization in response to changes in soil pH after rewetting has also been observed in field studies of fen meadow restoration projects (Van Dijk et al. 2004). This illustrates a potential risk for increased availability of P upon rewetting. However, overall P concentrations in the above-ground plant tissue did not strongly respond to the increased PO_4^{3-} concentrations in the pore water. This suggests that plants can also access other forms of P, for example in the form of inorganic P bound to Fe complexes (Emsens et al. 2017) or P absorbed to or complexed with organic matter (Kooijman et al. 2020). However, since vegetation in our experiments was N-limited, P dynamics seem less important and will not be discussed further.

K_{tot} in the pore water increased after rewetting, which was also observed in several other studies (e.g. Koerselman et al. 1993). Since K availability is strongly linked to adsorption to clay particles and adsorption increases under aerobic circumstances (Scheffer and Schachtschnabel 1989), it may indeed be expected that K availability increases after rewetting. Yet, there are multiple studies that did not observe increased K concentrations upon rewetting (e.g. Olde Venterink et al. 2002) or even found higher K concentrations with desiccation (Grootjans et al. 1986). Despite higher K concentrations in the pore water under wet conditions, the K content in the above-ground biomass was not affected, probably again due to the fact that plant growth in our experiment was limited by N.

Nutrient application

Nutrient application resulted in little to no changes in the availability of most nutrients in the pore water (Table 3). The monitoring of the tank water surrounding the peat cores did not indicate more nutrient leaching out of the cores with a high nutrient application than out of the cores with a low nutrient application (data not shown). This does not necessarily mean that nutrients did not leach out, since denitrification (nitrogen) and precipitation (phosphorus) in the tanks cannot be excluded.

Although no significant effect of nutrient application was found on nutrient concentrations in the pore water (Fig. S1a–d), nutrient application resulted in a higher above-ground biomass in all harvests other than harvest 1 (Figs. 4a–c, S3). During most of the growth of harvest 1, nutrients were not yet applied to the peat cores which explains this lack of response. For all other harvests, it is likely that part of the nutrients applied were taken up by the vegetation. This seems to be mainly as a result of increased N uptake as is indicated by the higher N content in the plant tissue under high nutrient application (Fig. S4a–c) and stronger response in the WL treatments that were most N limited (WL0 and WL20), which is in line with what may be expected under N-limited conditions.

Water origin

With some rewetting techniques, such as sub-surface irrigation, surface water is used for the rewetting process. Since surface water has a different chemical composition than groundwater this could affect the nutrient dynamics in the peat. Especially SO_4^{2-} concentrations are typically higher in surface water in peat areas, which could result in more internal eutrophication upon rewetting. For example, surface water which contains high concentrations of SO_4^{2-} and NO_3^- can increase decomposition rates (Smolders et al. 2010) because N mineralization can continue under anaerobic conditions in peat soil, with sufficient degradable organic matter available that functions as an alternative electron acceptor. Further, high SO_4^{2-} concentrations in the water used for rewetting can also trigger P mobilization. This risk is especially high when polluted surface water is used (Lamers et al. 1998; Smolders et al. 2006).

Although both SO_4^{2-} and NO_3^- concentrations were about 10 times higher in the surface water than in the groundwater (Table S1), we did not observe an effect of water origin on SO_4^{2-} concentrations in the pore water, nor did we find higher NH_4^+ or PO_4^{3-} concentrations upon rewetting in the pore water of cores placed in groundwater vs. surface water. We assume the higher SO_4^{2-} concentrations in the surface water did not significantly contribute to the relatively large quantity of SO_4^{2-} and S already present in the peat cores (Table 1; Fig. 1k, l). Hence, in peat soils with high S stocks, (sub-surface) irrigation with surface water will likely not result in more NH_4^+ or PO_4^{3-} release as the soil itself is the main SO_4^{2-} source (Vermaat et al. 2016).

Implications for management and restoration

Over 90% of the peatlands in the Netherlands have been drained, mostly for agricultural purposes. This has resulted in large-scale peat degradation, carbon emissions, soil subsidence and biodiversity loss. Currently, agreements are in place to raise the groundwater table in order to combat the negative side-effects of drainage. Generally, two approaches can be distinguished: (i) nature restoration on former agricultural peat meadows, and (ii) farming with higher water levels. Both come with their own challenges and trade-offs, which are further elaborated upon below.

Nature restoration

Although our research setup did not include a treatment without nutrient application and did therefore not include a treatment combination representing full wetland restoration on former agricultural land, we still made a number of observations on the impact of rewetting with relevance to this type of restoration. Overall, the effects of our nutrient treatments on vegetation productivity underlined the need to limit external input of nutrients for successful restoration. Increases in plant productivity in response to nutrient input has been shown to increase competition for light, resulting in dominance of fast-growing, often more general, species (Hautier et al. 2009). Given the nutrient legacy imposed by the long history of fertilization, restoration is often difficult on peat soils that were previously in agricultural use (Klimkowska et al. 2007). Especially P mobilization is identified

as a major bottleneck. In line with previous studies (e.g. Van Dijk et al. 2004; Zak et al. 2010) our results showed a significant increase in PO_4^{3-} concentrations upon fully rewetting, regardless of the nutrient application level used. Furthermore, we found higher NH_4^+ concentrations in our fully rewetted treatments. The release of these nutrients upon rewetting may also affect the surface water in ditches, canals and lakes via leaching of the released nutrients, thereby also affecting nature areas adjacent to rewetted farmland.

Farming on rewetted peatlands

Given the problems with soil nutrient legacies in wetland restoration projects, continuation of (low-intensity) dairy farming on rewetted peatland with water tables of only several decimeters below the surface is a less researched yet potentially more feasible solution to apply at a large scale, especially in densely populated countries with a high agricultural need such as the Netherlands (Zak and McInnes 2022). The Dutch government is preparing legislation that will force water authorities to raise water levels in the peat meadow area to 20–40 cm below the surface, and it has made the Dutch dairy farming sector on peat soils responsible for slowing down soil subsidence and reducing greenhouse gas emissions from peat meadows (Van Mulken et al. 2023). Our results showed that fewer plant available nutrients became available when the groundwater level was raised to 20 cm below the surface compared to fully rewetting. Both NH_4^+ and PO_4^{3-} concentrations in the top 10 cm were much lower with a water level of 20 cm below the peat surface than with the completely saturated water level (Fig. 1a, c). As partial rewetting results in less internal eutrophication, we think that partial rewetting could also result in less nutrient leaching to surface waters, which will benefit the water quality in the area. However, especially when partial rewetting occurs with the help of submerged drains, it is crucial to look into the water quality and associated nutrient dynamics as the exchange between soil and surface water is likely to increase. Guidelines need to be developed about the soil- and surface water quality conditions under which the use of submerged drains are expected to lead to a poorer or better water quality. Since our mesocosm needed different water volumes in the tanks, and monthly replenishment, this

study was not set up to identify these nutrient leaching effects.

If partly rewetted fields remain in agricultural use, it is important to be aware that grass yields will likely be lower under these wetter conditions and that their quality in terms of nutrient contents may change compared to current conditions. This may strongly affect milk yields, milk quality and thus farm profitability. This is especially the case when partial rewetting is combined with a shift to less intensive agriculture, i.e. lower nutrient inputs. In our case, the cumulative yield in cores receiving a low nutrient application was 45% lower at a water level of 20 cm below the surface than the cumulative yield in the cores with a water level of 60 cm below surface level. The latter is the current practice in dairy farming on peat meadows. With a high nutrient application, this difference was reduced to 30% as the wetter treatments overall showed a stronger response to nutrient application. Although this may mitigate the negative consequences for the farmer, a high nutrient application may lead to an increased risk of nutrient leaching to surface waters and to lower diversity in the grassland sward. However, the observed difference was mainly caused by the first harvest where above-ground biomass was much higher in the lowest water level treatment (Fig. 3a). We think this is because lower water tables allow for early spring vegetation growth. Our study further showed that N concentrations in the vegetation decrease with higher groundwater tables (Fig. 3d–f). N concentrations are a good indication of the crude protein content of the grass, and strong reductions in N-fertilization and concomitant reductions in crude protein concentrations have been shown to reduce milk production (Valk et al. 2000). Hence, with lower yields and lower N concentrations in these yields, fewer cows can be supported under higher water levels unless the external input of roughage and concentrate feed is increased. This requires an adapted business model to compensate for the loss of income, for example with payments for ecosystem services that are delivered with raised groundwater tables (Bonn et al. 2014). Furthermore, partial rewetting might slow down soil subsidence and CO₂ emissions, but with part of the peat still exposed to oxygen it will not fully stop the process. Therefore, it should be carefully considered whether the investment of measures that result in partial rewetting is worthwhile before implementing them on a large scale, especially

since their long-term effects are unknown (Andersen et al. 2017).

Conclusion

In this study, we aimed to better understand the nutrient dynamics upon (partial) rewetting of former agricultural peat soils with different intended land uses. To this end, we performed a mesocosm experiment in which peat cores were exposed to different water levels, water origins and nutrient application levels. Our results revealed that PO₄³⁻ and NH₄⁺ availability increase upon fully rewetting but remain relatively low under partial rewetting with a water table of 20 cm below the surface. Furthermore, we show that biomass production is affected by rewetting, especially in early spring, and that biomass production strongly responds to nutrient application. Overall, the vegetation was N limited. The high nutrient availabilities under fully rewetted circumstances show that nature restoration is unlikely to be successful unless further measures to reduce nutrient availability, such as top soil removal, are taken. If this is not possible or has undesired additional effects, the best option for degraded peatlands like the one in this study, would be partial rewetting, which will probably restrict internal eutrophication, i.e. diminish the unwanted release of nutrients. Partial rewetting could be combined with low-intensity agriculture although lower yields need to be acknowledged; these could be compensated via payment for ecosystem services. However, soil subsidence cannot be fully stopped and climate goals may not be achieved with partial rewetting. Our study highlights that different trade-offs between different goals of rewetting may arise from the specific combination of local peat characteristics, hydrology and management. Rewetting without regret therefore requires careful analysis of the local biogeochemical conditions of the peat in relation to the targets to be met before deciding on the exact rewetting strategy.

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Author contributions All authors formulated the research objectives and designed the methodology. AvdL collected and analysed the data and wrote the first draft of the manuscript. All authors contributed to the data interpretation, edited draft versions of the manuscript and gave final approval for publication.

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Data availability Data used for this study is available via <https://doi.org/https://doi.org/10.24416/UU01-3U9LXM>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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