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Paludiculture Crops And Nitrogen Kick-Start Ecosystem Service Provisioning In Rewetted Peat Soils

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Abstract

Purpose

Paludiculture (crop cultivation in wet peatlands) can prevent carbon and nutrient losses while enabling biomass production. As vegetation in rewetted peatlands is often nitrogen (N) limited, input of N rich water may promote biomass production and nutrient removal. However, it is unclear how N loading and soil characteristics affect biomass yield, nutrient dynamics, and ecosystem service provisioning in paludicultures.

Methods

We studied the influence of N loading (0, 50, 150, and 450 kg N ha^{-1} yr^{-1}) on biomass production and nutrient sequestration of *Typha latifolia* (broadleaf cattail) and *Phragmites australis* (common reed) on a limed agricultural peat soil after rewetting. To assess the interaction with soil characteristics *T. latifolia* was also grown on a non-limed former agricultural soil.

Results

N loading stimulated biomass production and nutrient uptake of both *T. latifolia* and *P. australis*, with *T. latifolia* showing the most pronounced response. Biomass yield of *T. latifolia* was higher in the limed soil than in the non-limed soil due to a higher pH, despite lower nutrient availability. N was largely taken up by the vegetation, whereas bare soils showed N accumulation in pore and surface water, and 80% loss through denitrification. Phosphorus in the soil was efficiently taken up by *T. latifolia*, especially at high N loads.

Conclusion

N loading in paludicultures with *T. latifolia* and *P. australis* boosts biomass production while kick-starting peatland ecosystem services including nutrient removal. Nutrient availability and pH appear to be decisive soil characteristics when it comes to crop selection.

Introduction

Pristine peatlands worldwide accommodate a unique set of ecosystem services, including carbon sequestration, water quality improvement, biodiversity preservation, water retention and flood control (Zedler and Kercher 2005; Keddy et al. 2009). Accumulation of organic material makes peatlands important sinks and stores for carbon (C) and nutrients. Furthermore, peat has the capacity to store large amounts of water and thus plays an important role in the hydrology and water retention of the landscape (Holden 2005).

Currently, 15 percent of peatlands around the world are drained to enable peat extraction and agriculture (Barthelmes 2016; Joosten 2016). Drainage leads to oxic conditions and accelerated organic matter

decomposition, resulting in a loss of peat. Peat oxidation brings about a myriad of issues including land subsidence, loss of biodiversity, and the transition from C sink to source through enhanced carbon dioxide (CO_2) emissions (Verhoeven and Setter 2009; Miettinen et al. 2017). Although drained peatlands cover only a small fraction of the earth's surface (0.3%), they contribute to 6% of total anthropogenic CO_2 emissions (Tanneberger and Wichtmann 2011). In order to restore peatland ecosystems and associated services such as carbon sequestration and water storage, many rewetting projects have been carried out in the last decades (Zak et al. 2011; Lamers et al. 2015).

Rewetting of former agricultural land often brings challenges, such as eutrophication and loss of productive land. Former agricultural soil often contains many nutrients, which can be mobilized by inundation, leading to eutrophication of water bodies (Van de Riet et al. 2013; Cabezas et al. 2014). Especially in formerly fertilized soils, phosphorus (P) mobilization can lead to poor water quality (Zak et al. 2017). Additionally, rewetting agricultural soils results in loss of productive land, which has economic drawbacks.

A proposed solution to these challenges is paludiculture: the use of wet or rewetted peatlands for biomass production (Wichtmann et al. 2016). Paludiculture offers a means of rewetting without losing the land's productivity, and thus combines agriculture with ecosystem services and functioning (Wichtmann and Wichmann 2011). By cultivating fast-growing perennial crops, excess nutrients from soil and surface water can be extracted, similar to constructed wetlands (Vymazal et al. 2006). By harvesting aboveground biomass, nutrients can be removed in order to prevent leaching and downstream eutrophication (Toet et al. 2005; Hille et al. 2018). Next to that, rewetting of peatlands can reduce CO_2 emissions by carbon sequestration (Günther et al. 2015; 2017), and counteract or even reverse soil subsidence by organic matter accumulation and peat formation (Miller et al. 2008).

As biomass is harvested and nutrients are removed, a paludiculture system will become more nutrient-poor over time. Nitrogen (N) is generally the first nutrient to become limiting for plant growth in peat soils that turn anaerobic after inundation. Under anaerobic conditions, denitrification is stimulated, as facultative anaerobic bacteria use nitrate (NO_3^-) instead of oxygen (O_2) as terminal electron acceptor, resulting in the formation of dinitrogen (N_2) or nitrous oxide (N_2O) (Cameron and Moir 2013). With decreasing O_2 availability, more N_2 and less N_2O is produced. Anammox bacteria can also directly convert ammonium (NH_4^+) into N_2 or N_2O (Kartal et al. 2006). On top of these processes, some plant species create aerobic zones in wet soils by radial oxygen loss (ROL) from their root system. This creates a mosaic of aerobic and anaerobic zones, leading to a coupled nitrification-denitrification (Reddy et al. 1989) that speeds up N depletion.

Next to N limitation, pH will be a determining factor for plant growth. Most commonly grown crops cannot grow well at very acidic soils (< 5). On highly organic soils, such as peat soils, liming is a frequently used strategy on agricultural soils to increase pH. Although wetland species can stand more acidic soils than most commercial crops, earlier studies indicate that Typha grows best at pH of > 4.5.

Although Typha can grow at pH 3.5–4.5 for a short period, cation deficiencies and ammonium toxicity may occur which will hamper growth (Brix 2002; Dyhr-Jensen and Brix 1996). As biomass yield is an important aim in paludiculture, soil pH may be an important influencing factor.

To ensure long-term biomass production, in particular of fast-growing paludiculture crops (“paludicrops"; e.g. *Typha* spec., *Phragmites australis*, *Arundo* spec.; Giannini et al. 2017), a certain nutrient availability and stoichiometry, and pH needs to be provided (Olde Venterink et al. 2003). Productive paludicrops need inlet of N-rich surface water or groundwater to warrant sustained biomass production and removal of P and other nutrients. However, it is unclear 1) how much N needs to be supplied to get optimal biomass yields, 2) how this is influenced by soil pH, and 3) how N supply will affect the nutrient allocation in a paludiculture system. In this mesocosm study, we therefore investigate 1) the effect of N loading on biomass yield and nutrient dynamics in paludicultures with *Typha latifolia* and *Phragmites australis*, 2) the effect of land use history and soil pH in paludicultures with *T. latifolia* and 3) how these factors affect nutrient allocation.

We expect that N supply via the surface water will increase biomass production of both paludicrops, but that *T. latifolia* is more responsive to increased N levels and will remove more phosphorus (P) from the soil, as it normally has lower tissue N:P ratios than *P. australis* (Koerselman and Meuleman 1996; Vroom and Xie et al. 2018). Increasing N loads will lead to excess N and higher N:P ratios, which may induce P or K limitation (Ulrich and Burton 1988). Furthermore, we hypothesize that *P. australis* will suffer from NH_4^+ toxicity at high N loads (Tylova et al. 2008). We also expect that the non-limed peat soil will hamper *T. latifolia* growth and nutrient removal capacity in general (Brix et al. 2002). Results will be discussed with regard to the N and P balance and allocation in rewetted peat soils used for paludiculture, potential nutrient removal ability of paludicrops, suitability of peat soils for paludiculture, and water management strategies in relation to N supply.

Materials And Methods

2.1 Site characteristics and soil sampling

For the experiment that compares the response of *T. latifolia* and *P. australis* to different N loads (hereafter called “vegetation experiment”), 46 soil cores were collected from a drained agricultural peat meadow in Zegveld (ZV), the Netherlands (52°08'N, 4°50'E), at four sub-sites. This peat meadow is an actively fertilized and limed grassland (soil pH 5.6) grazed by cattle with an average peat depth of 6 m.

For the experiment that addresses the effect of soil pH on *T. latifolia* (hereafter called “pH experiment”), 16 additional soil cores were collected in Bûtefjild (BF), the Netherlands (53°15'N, 5°57'E), at four sub-sites. Bûtefjild (BF) is a former agricultural peat meadow where artificial fertilization and liming ceased 20 years ago (soil pH 4.4). Since then it has been extensively managed (sheep grazing and occasional mowing). The remaining peat has an average thickness of 1.5 m.

Soil cores (total n = 62) were collected from the field using PVC tubes (called “mesocosms”; 15 cm diameter) that were carefully drilled into the soil down to a depth of 30 cm. From each mesocosm, 5 cm of topsoil (including grass and roots) was removed to mimic the most common soil preparation in paludiculture and to remove the soil layer with high labile carbon content. Soil samples were taken from the four sub-sites at each location in order to characterize chemical composition of the soil prior to the experiments. Both experiments were run alongside each other in the greenhouse of the Radboud University and partially overlapped, as the *T. latifolia* treatments on ZV soil were the same for both experiments.

2.2 Experimental set-up

T. latifolia was grown from seeds collected in BF alongside nutrient-rich ditches. For the vegetation experiment, five *T. latifolia* seedlings of 20 ± 5 cm were planted in 16 mesocosms with ZV soil. In 16 other mesocosms with ZV soil, five *P. australis* rhizomes with viable new shoots were planted. Control mesocosms with ZV soil and without vegetation (n = 14) were covered by a black canvas to prevent growth of plants and algae. For the pH experiment, five *T. latifolia* seedlings were planted in 16 additional mesocosms with BF soil. Plants were cut down to a length of 5 cm to ensure comparable starting conditions. During the first two weeks of the experiments, non-viable plants were replaced by new individuals

Rewetting of soils was simulated by adding demineralized water up to a level of 5 cm above the soil surface following the growth of the plants to prevent total submersion of the shoots. Each mesocosm was placed in a plastic bag (open at the top) to prevent water exchange of the cooling water bath. Mesocosms of both experiments were positioned in a water bath, kept at 14°C by a cryostat. Light conditions (irradiance) were maintained at 186 W m^{-2} or higher for 16 h per day, using grow lights if sunlight was not sufficient. Average daytime air temperature in the greenhouse was 21.7°C in March, 22.4°C in April, and 23.8°C in May. The average relative humidity (RH) at daytime was 42.3%. Water levels were kept constant by replacing evaporated water with demineralized water trice a week. Mesocosms were kept at these conditions for five days prior to the initiation of nitrogen treatments in order to stabilize. Twice during the experiment, 5 mL 1M KCl solution (11.1 g K m^{-2}/111 kg K ha^{-1}) was added to each mesocosm to prevent K limitation.

2.3 Nutrient addition

In both experiments, four different N treatments were applied to the mesocosms. N was added as a combination of ammonium nitrate (NH_4NO_3) and ammonium chloride (NH_4Cl) in a molar ratio of 1:1.5, resulting in four different total N loads: 0 kg N ha^{-1} (control), 50 kg N ha^{-1}, 150 kg N ha^{-1} and 450 kg N ha^{-1}. The N load of 50 kg ha^{-1} is based on realistic N concentrations of 5 mg l^{-1} as found in surface waters in the surroundings of Bûtefjild (Kros et al. 2011). The N load of 150 kg ha^{-1} simulates a situation in which this surface water has a one-month retention time in the system. A load of 450 kg N ha^{-1} was chosen as an extreme scenario in the range of constructed wetland loading and removal rates (Land et al.

2016). Four replicate mesocosms were used for each combination of soil, vegetation and N load, with exception of the unvegetated control (ZV) that received 150 and 450 kg N ha^{-1} (n = 3). Total N loads were divided into twelve weekly additions of fertilizer solution, starting one week after planting and lasting until one week before harvest.

2.4 Water sampling and analysis

Surface water and pore water samples were taken five times throughout the experiment. Pore water was sampled from the upper 10 cm of the soil using Rhizon samplers (Rhizosphere Research Products, Wageningen, The Netherlands) attached to a syringe under vacuum. After pH and alkalinity were determined with a Ag/AgCl electrode (Orion Research, Beverly, MA, USA) and TIM 840 Titration Manager (Radiometer Analytical SAS, Villeurbanne, France), surface water and pore water samples were stored at 4°C (after adding 0.1 mL of 65% HNO3 to a 10 mL subsample) and − 20°C until further analyses.

2.5 Soil analysis

Soil samples were taken prior to the experiment (t_0) as well as after plants were harvested (t_1). Samples were collected along the entire depth of the mesocosm and homogenized. To determine bio-available NH_4^+ and NO_3^- concentrations, salt extractions were carried out using 17.5 g of fresh soil, incubated with 50 mL of 0.2 M sodium chloride (NaCl). After 120 min of incubation on a shaker at 105 RPM, pH was determined and fluid was extracted using Rhizon samplers (Rhizosphere Research Products B.V.) under vacuum conditions. In addition, subsamples of fresh soil were dried at 70°C for 48 hours to determine dry weight and bulk density. Bio-available P (Olsen-P) was measured by a 30 min incubation of 3 g dried soil in 60 mL 0.5 M sodium carbonate ($NaHCO_3$) on a shaker at 105 RPM (Henriksen 1965) and extraction using the above method. After the extractions, samples were stored at -20°C until further analysis. Total phosphorous (TP) and total potassium (TK) contents were determined by digesting 200 mg soil in 4 mL HNO_3 (65%) and 1 mL H_2O_2 (35%) in Teflon vessels, heated in an Ethos D microwave (Milestone, Sorisole Lombardy, Italy). After destruction, samples were stored at 4°C until further analysis.

2.6 Biomass growth and analysis

Plant length was recorded weekly. Maximum length of *T. latifolia* was measured for each individual shoot. For *P. australis*, maximum and average length were determined per mesocosm. All aboveground plant biomass was harvested after 91 days, dried at 70°C for four days, weighed, and ground up. TP and TK were determined after digestion, whereas TN and TC was measured using a CNS analyser (methods described below). Belowground biomass yield was estimated along the mesocosm depth using a gouge.

2.7 Chemical analysis

Concentrations of NH_4^+, NO_3^- and phosphate (PO_4^{3-}) were determined by colorimetric methods (Auto Analyser III, Bran and Luebbe GmbH, Norderstedt, Germany) in the water samples that were stored at − 20°C (Geurts et al. 2008). Subsequently, inductively coupled plasma emission spectrometry (ICP-OES)

was used to measure concentrations of Fe, K, and P (IRIS Intrepid II, Thermo Electron corporation, Franklin, MA, USA) in the samples that were stored at 4°C (water and destruction samples) and in the extraction samples (only P). Total carbon (TC) and total nitrogen (TN) were determined in dry soil and plant material by an elemental CNS analyser (NA 1500, Carlo Erba; Thermo Fisher Scientific, Franklin, USA).

2.7 Nutrient budget calculations

N and P budgets were created by determining absolute amounts of N and P in the soil, water and plant fractions of each mesocosm (mg mesocosm^{-1}). Aboveground biomass was multiplied by its respective nutrient concentration. For *T. latifolia*, belowground biomass was multiplied by nutrient contents from a previous study following a similar design that focussed on different N sources (0.56% N, 0.19% P; Vroom et al. 2018). Nutrient concentrations in belowground biomass of *P. australis* were taken from a field study (1.2% N, 0.15%P; Behrends et al. 1996). The amounts of N and P in surface water were calculated by multiplying their concentration with the surface water volume. The amounts of N and P in pore water were calculated similarly, using soil volume and water content. NaCl extractable N was determined by using soil bulk density and moisture content, and subsequent subtraction of pore water N values. Net N and P loss was calculated by subtracting end values (above and belowground biomass, pore water, surface water and soil extractable for N, above and belowground biomass, pore water and surface water for P) from the start values (N load, soil extractable and pore water for N, pore water for P). N and P loss (in %) was calculated by dividing N or P loss by the sum of N or P in all start fractions. Positive loss values indicate removal from the system (e.g. through denitrification or binding to the soil adsorption complex), whereas negative loss values indicate mobilisation from the soil matrix.

2.8 Statistical analysis

Statistical analyses were performed using R v. 3.3.2 (R core team 2016). Student's t tests were used to determine differences in soil characteristics between the two soils (Table S1). Biomass yield and nutrient removal were extrapolated from mesocosm size (g mesocosm^{-1}) to values per hectare by multiplying with a factor 0.5659 (ton ha^{-1}) or 565.9 (kg ha^{-1}). Although this may lead to overestimation, the values per hectare seem realistic as they are in the same range as Geurts et al. (2020) found in young stands under field conditions. Nitrogen use efficiency (NUE) was calculated by dividing the dry biomass yield by the plant N content, both per mesocosm. Effects of N load and soil type on biomass yield, nutrient removal and plant nutrient content were tested using two-way ANOVA (with N load, soil type and their interaction) and one-way ANOVA (with N load) for *T. latifolia* and *P. australis*, respectively (Tables S2 and S3). Differences in surface water and pore water chemistry as well as nutrient budgets were tested using two-way ANOVA, using either plant type and N load (vegetation experiment) or soil type and N load (pH experiment) and their interactions as explanatory factors (Tables S4 and S5). We used Q-Q plots, Shapiro-Wilk tests and residual plots to verify model assumptions.

Results

3.1 Site specific peat soil characteristics

ZV peat soil (limed) had a higher pH than BF soil (non-limed), as was expected from its liming history (5.57 and 4.36 respectively, $p = 0.002$). Organic matter content and bulk density indicated that both soils were degraded peat soils (Liu and Lennartz 2019). BF soil also contained higher extractable NH_4^+ ($p = 0.026$), Fe ($p < 0.001$) and P ($p = 0.033$), and had a lower C:N ratio ($p < 0.001$) than ZV peat soil, although BF soil had a lower total-K content ($p < 0.001$) (Table 1).

Table 1 Site characteristics of the two different locations. Values indicate means ± standard errors (n=4). Asterisks indicate significant differences between soils (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

	Limed (ZV)	Non-limed (BF)
H_2O-pH	5.57 ± 0.05	4.36 ± 0.24**
C:N	11.16 ± 0.14	18.15 ± 0.88***
C (%)	20.2 ± 0.8	19.9 ± 2.9
organic matter (%)	44.5 ± 1.8	48.6 ± 5.7
wet bulk density (g FW l^{-1} FW)	790 ± 16.5	948 ± 22.5**
dry bulk density (g DW l^{-1} FW)	314 ± 12.4	448 ± 29.3**
NaCl-extractable $NO3^-$ (µmol l^{-1} FW)	130 ± 34.4	104 ± 67.7
NaCl-extractable $NH4^+$ (µmol l^{-1} FW)	201 ± 46.3	1017 ± 273*
H_2O-extractable K (µmol l^{-1} FW)	204 ± 36.3	113 ± 42.5
H_2O-extractable P (µmol l^{-1} FW)	6.29 ± 3.67	13.17 ± 3.41*
H_2O-extractable Fe (µmol l^{-1} FW)	26.2 ± 3.9	83.2 ± 12.2***
Olsen-P (µmol l^{-1} FW)	616 ± 22.4	1201 ± 109**
Total-N (mmol l^{-1} FW)	405 ± 10.9	348 ± 38.7
Total-K (mmol l^{-1} FW)	20.3 ± 1.64	5.04 ± 0.52*
Total-P (mmol l^{-1} FW)	20.4 ± 1.3	15.4 ± 1.3

3.2 Biomass yield and nutrient removal

T. latifolia produced more biomass than *P. australis* in all treatments of the vegetation experiment: on average 12.7 g DW mesocosm^{-1} and 6.9 g DW mesocosm^{-1}, respectively ($p < 0.001$; Fig. 1). A positive

relationship between N load and biomass production of *T. latifolia* was found on limed ZV soil ($p = 0.001$) increasing from 5.3 to 10 ton ha^{-1}. Biomass production of *P. australis* on ZV soil increased from 2.6 ton ha^{-1} to an optimum of 5.5 ton ha^{-1} at 150 kg N ha^{-1}. However, biomass production did not increase any further at 450 kg N ha^{-1} ($p < 0.05$; Table 2), and algae were observed in the surface water.

In the pH experiment, average biomass production of *T. latifolia* was 40% higher on limed ZV soil compared to non-limed BF soil (12.7 and 7.6 g DW $mesocosm^{-1}$, respectively; $p < 0.001$). The positive relationship between N load and biomass production of *T. latifolia* was also found on BF soil ($p < 0.001$; Table 2), increasing from 2.5 to 5.9 ton ha^{-1}. On both soils NUE of *T. latifolia* was lowest in the treatments receiving 450 kg N ha^{-1} ($p < 0.05$).

Nutrient removal largely followed the same trends as the biomass results (Table 2). Plants stored 31 up to 205 kg N ha^{-1} in aboveground biomass, depending on N load, soil type and plant species. N removal was positively related to N load for both *T. latifolia* (on both soils; $p < 0.001$) and *P. australis* ($p = 0.008$). P removal (5 to 21 kg P ha^{-1}) and K removal (27 to 141 kg K ha^{-1}) by aboveground biomass did not significantly increase with N load. N, P, and K removal by *P. australis* was highest at an N load of 150 kg ha^{-1} compared to lower N loadings ($p < 0.05$). At all N loads of the vegetation experiment, P and K removal rates of *T. latifolia* were higher than *P. australis* on ZV soil ($p < 0.001$ for both). In the pH experiment, P and K removal rates were also higher for *T. latifolia* on ZV soil than on BF soil ($p = 0.003$ and $p < 0.001$, respectively).

Table 2 Extrapolated aboveground biomass yield, nitrogen use efficiency (NUE) and nutrient sequestration by *T. latifolia* on different soils and *P. australis* on ZV soil at different N loads (removable by harvesting). Values shown are mean ± SE (N=4). Letters indicate significant differences between N treatments where applicable (P<0.05).

		T. latifolia		*P. australis*
	N load (kg ha^{-1})	ZV soil	BF soil	ZV soil
Yield (g DW $mesocosm^{-1}$)	0	9.3 ± 1.7	4.5 ± 0.4	4.6 ± 0.4
	50	9.7 ± 1.3	7.1 ± 0.8	5.2 ± 0.8
	150	14.1 ± 1.3	8.5 ± 0.8	9.6 ± 0.8
	450	17.7 ± 3.3	10.3 ± 1.3	8 ± 1.3
NUE (g DW g N^{-1})	0	86.1 ± 6.2	82.2 ± 8.2	63.5 ± 13.7
	50	76.1 ± 7.1	83.3 ± 11.1	69.3 ± 9.5
	150	86.6 ± 3.3	70.6 ± 5.9	45.9 ± 4.2
	450	50 ± 2.9	47.8 ± 7.3	51 ± 14.2
N removal (mg N $mesocosm^{-1}$)	0	107 ± 13	55 ± 3	80 ± 14
	50	132 ± 23	91 ± 17	76 ± 14
	150	164 ± 18	122 ± 13	217 ± 30
	450	362 ± 75	221 ± 15	192 ± 47
P removal (mg P $mesocosm^{-1}$)	0	25.3 ± 10.5	9.5 ± 1.2	8.6 ± 1.8
	50	24.9 ± 2.8	18.6 ± 3.1	12 ± 2.5
	150	32.9 ± 4.3	16.6 ± 2.4	19.8 ± 3.7
	450	37.5 ± 9.5	22.8 ± 3	17 ± 2.1
K removal (mg K $mesocosm^{-1}$)	0	204 ± 77	48 ± 3	68 ± 6
	50	198 ± 18	113 ± 17	70 ± 16
	150	251 ± 37	121 ± 26	178 ± 22
	450	222 ± 35	116 ± 27	119 ± 20

Table 3 Nutrient content and nutrient ratios of *T. latifolia* and *P. australis* at different N loads. Values are shown as mean ± SE (n=4). Letters indicate significant differences between N treatments where applicable (p<0.05).

		T. latifolia		*P. australis*
	N load (kg ha^{-1})	ZV soil	BF soil	ZV soil
% N	0	1.18 ± 0.09^{a}	1.26 ± 0.15^{a}	1.77 ± 0.3
	50	1.35 ± 0.12^{a}	1.26 ± 0.16^{a}	1.54 ± 0.23
	150	1.16 ± 0.04^{a}	1.44 ± 0.11^{a}	2.25 ± 0.25
	450	2.02 ± 0.11^{b}	2.26 ± 0.38^{b}	2.32 ± 0.43
% P	0	0.24 ± 0.05	0.21 ± 0.02	0.18 ± 0.02
	50	0.26 ± 0.02	0.26 ± 0.02	0.23 ± 0.02
	150	0.23 ± 0.01	0.19 ± 0.01	0.2 ± 0.03
	450	0.2 ± 0.02	0.22 ± 0.01	0.21 ± 0.01
% K	0	2.02 ± 0.44^{ab}	1.12 ± 0.14^{ab}	1.51 ± 0.12^{ab}
	50	2.12 ± 0.22^{a}	1.57 ± 0.09^{a}	1.33 ± 0.11^{a}
	150	1.75 ± 0.11^{ab}	1.4 ± 0.22^{ab}	1.84 ± 0.15^{b}
	450	1.32 ± 0.21^{b}	1.1 ± 0.15^{b}	1.47 ± 0.06^{ab}
N:P	0	5.59 ± 1.24^{a}	6.08 ± 0.91^{a}	10.01 ± 2.15
	50	5.3 ± 0.78^{a}	4.94 ± 0.47^{a}	6.62 ± 0.71
	150	5.04 ± 0.14^{a}	7.58 ± 0.72^{a}	11.77 ± 2.03
	450	9.98 ± 0.64^{b}	10.13 ± 1.39^{b}	10.73 ± 1.91
N:K	0	0.7 ± 0.18^{a}	1.14 ± 0.09^{a}	1.19 ± 0.2
	50	0.66 ± 0.11^{a}	0.81 ± 0.09^{a}	1.17 ± 0.17
	150	0.67 ± 0.03^{a}	1.09 ± 0.14^{a}	1.27 ± 0.23
	450	1.7 ± 0.39^{b}	2.18 ± 0.48^{b}	1.58 ± 0.29
C:N	0	39.1 ± 2.7^{a}	37.9 ± 2.9^{a}	26.9 ± 4.3
	50	35.1 ± 1.9^{a}	37.1 ± 4.8^{a}	31.3 ± 4
	150	38.2 ± 1.2^{a}	31.6 ± 2.1^{a}	20.5 ± 1.8
	450	24 ± 2.5^{b}	20.4 ± 2.6^{b}	20.5 ± 3.5

3.3 Nutrient stoichiometry

N loading increased the N content of *T. latifolia* ($p < 0.001$) (Table 3), which increased to more than 2% in aboveground biomass on both soils. The N content of *P. australis* also increased to more than 2%, although this effect was not significant ($p = 0.273$). For *T. latifolia*, P content was not affected by N loading, but K content decreased in the 450 kg N ha^{-1} treatment. N:P and N:K ratios also increased significantly in *T. latifolia* receiving 450 kg N ha^{-1} ($p = < 0.001$), reaching average N:P ratios of 10 and N:K ratios of 1.7 to 2.2. *P. australis* showed a higher K content at 150 kg N ha^{-1} compared to 50 kg N ha^{-1} ($p = 0.033$), but N loading had no significant effect on P content ($p = 0.392$) and N:P ($p = 0.255$) or N:K ($p = 0.567$) ratios. C:N ratios strongly decreased in *T. latifolia* treatments receiving 450 kg N ha^{-1} ($p < 0.001$), with no differences between soil types ($p = 0.242$), from 38 to 22 on average. C:N ratios in *P. australis* did not differ significantly between different N loads ($p = 0.134$).

3.3 Pore and surface water nutrients

In the vegetation experiment, N (mainly NH_4^+) accumulated in the pore water in all unvegetated controls as opposed to vegetated treatments ($p < 0.001$; Fig. 2), with concentrations that became 5–40 times higher than at the start of the experiment. This led to surface water N concentrations of 142, 347, 1909, and 7933 µmol/l, respectively, for the increasing N loads, at the end of the experiment (Fig. 3). Pore water NO_3^- in control mesocosms increased after N application, but was depleted in all treatments towards the end of the experiment.

In vegetated mesocosms, NH_4^+ was depleted or strongly decreased in surface water and pore water towards the end of the experiment as the plants increased in biomass, leading to a 97–100% reduction in the *T. latifolia* mesocosms on ZV soil, a 90–98% reduction in the *T. latifolia* mesocosms on BF soil, and a 52–100% reduction in the *P. australis* mesocosms on ZV soil. Surface water NO_3^- was also depleted in all vegetated mesocosms at the end of the experiment, leading to a 97–100% reduction in all treatments.

Pore water P concentrations decreased in *T. latifolia* treatments (81% on ZV soil; 26% on BF soil; $p < 0.001$), but not in *P. australis* or controls ($p < 0.001$; Fig. 4). P concentrations in pore water were highest in BF soil, between 100 and 300 µmol/l at the start of the experiment, but no PO_4^{3-} mobilization to the water column occurred (Figure S1). In ZV soil, PO_4^{3-} mobilization correlated negatively with N load, meaning that mobilization to the water layer occurred mostly in the low N treatments. Added K accumulated to concentrations of around 1500 µmol/l in surface water of unvegetated mesocosms, but was depleted in vegetated mesocosms in all treatments (Figure S2). K did not accumulate in the pore water.

3.4 N budget

N budgets show the division of N over different compartments at the end of the experiment (Table 4). Net N loss, defined as the amount of N not covered in any compartment, correlated positively with N load. Net N losses were up to 62% for treatments receiving 450 kg N ha^{-1}. Net N mineralization occurred at the lowest two N loads. Plants (aboveground and belowground) took up 73–389 mg N $mesocosm^{-1}$ on average, positively related to N load. In unvegetated mesocosms, up to 98 mg N $mesocosm^{-1}$ accumulated in surface water, and up to 135 mg N $mesocosm^{-1}$ in pore water. Soil available N also increased in unvegetated mesocosms (up to 229 mg N $mesocosm^{-1}$), and, less so, in *P. australis* mesocosms receiving 0 and 450 kg N ha^{-1} (up to 96 mg N $mesocosm^{-1}$). In all other vegetated mesocosms, soil N stocks decreased slightly.

3.5 P budget

P budgets show the division of P over different compartments at the end of the experiment (Table 5). Net P mineralisation occurred in all vegetated mesocosms, and was higher at the highest N loads. In most control treatments net P loss occurred, which is defined as the amount of P not covered in any compartment. This net P loss was lower at higher N loads and negative at the highest N load, meaning

that P mineralisation occurred in the latter case. Plants (aboveground and belowground) took up 15–52 mg P mesocosm^{-1}, with higher uptake rates at the highest N loads. In unvegetated mesocosms, up to 0.25 mg P mesocosm^{-1} accumulated in surface water, and up to 2.67 mg P mesocosm^{-1} in pore water.

Table 4 N budget for different paludicrops, N loads and soils. Values are shown as mean ± SE (n=4) and are expressed in mg N mesocosm^{-1}. N loss was calculated by subtracting start values from end values in soil (NH_4^+ and NO_3^- determined by salt extraction), surface water, pore water, and plant fractions. Positive values represent a net N loss and indicate the proportion of N available at the start that is lost from the system, i.e. not found in any other fraction in the end (e.g. gaseous losses of N_2 and N_2O). Negative values represent net N mineralisation (e.g. mobilization and organic matter decomposition). Letters represent significant differences between N load treatments.

		Start (t=0)			End (t=91)						
Soil	Species	N load	Soil extractable	Pore water	Aboveground biomass	Belowground biomass	Surface water	Pore water	NaCl-N	Net N loss	% N loss
Bûtefjild	*T. latifolia*	0	41.6 ± 14.9	5.5 ± 0.7	54.7 ± 2.9^{a}	18.9 ± 14.1	0.16 ± 0.12	0.3 ± 0.1^{a}	39.2 ± 11.1	-70.6 ± 0.7^{a}	-150
		50	38.5 ± 15.3	8.7 ± 1.3	90.6 ± 16.6^{ab}	14.8 ± 5.5	0.11 ± 0.06	0.4 ± 0.1^{a}	22.8 ± 5.7	24.9 ± 25.7^{a}	18
		150	38.8 ± 15.8	8.3 ± 1.5	122.2 ± 12.9^{ab}	27.3 ± 9.2	0.3 ± 0.14	0.6 ± 0.1^{a}	19.6 ± 7.1	142.4 ± 19.1^{b}	46
		450	41.6 ± 14.7	5.6 ± 0.6	220.6 ± 15^{b}	32.1 ± 11.4	4.18 ± 3.08	9.5 ± 4.6^{b}	49.6 ± 25	526.4 ± 29.2^{c}	62
Zegveld	*T. latifolia*	0	15.9 ± 1.9	3.6 ± 0.9	107.2 ± 13.3^{a}	21.9 ± 5.3	0.02 ± 0.02	0.3 ± 0.1	21 ± 6.2	-137.5 ± 14.1^{a}	-707
		50	16.7 ± 1.7	2.7 ± 0.7	132 ± 23.1^{a}	43.1 ± 9.9	0 ± 0	0.4 ± 0.1	22.1 ± 2.4	-112.3 ± 17.7^{a}	-104
		150	16.7 ± 1.5	2.7 ± 0.5	164.3 ± 18.1^{a}	56.6 ± 21.2	0.09 ± 0.03	0.3 ± 0.1	12.4 ± 2.4	50.8 ± 30.2^{b}	18
		450	13.2 ± 4.5	6.2 ± 4.9	362.2 ± 74.8^{b}	27.1 ± 10.8	1.2 ± 0.79	1.1 ± 0.5	21.7 ± 6.9	401.3 ± 75.6^{c}	49
	P. australis	0	15.2 ± 0.9	4.3 ± 1.5	80.4 ± 14.5^{a}	47.9 ± 3.7	0.03 ± 0.02	2.6 ± 1.4	95.9 ± 36.7	-207.4 ± 43.3^{a}	-1065
		50	17.3 ± 1.3	2.1 ± 0.6	75.6 ± 14^{a}	29.4 ± 4.9	0.99 ± 0.83	2.8 ± 1.6	41.8 ± 16.2	-33.8 ± 17.1^{b}	-31
		150	16.7 ± 1.7	2.8 ± 1	217.4 ± 30.2^{b}	61.1 ± 4.6	0.05 ± 0.02	0.9 ± 0.4	19.9 ± 4.3	-14.8 ± 24.9^{c}	-5
		450	15 ± 2.6	4.5 ± 2.4	192.2 ± 47.1^{ab}	61.1 ± 8.1	12.55 ± 5.43	23.2 ± 11.6	91.9 ± 14	412.9 ± 16.6d	51
	Control	0	16.8 ± 1.1	2.7 ± 0.9	NA	NA	1.76 ± 0.53^{a}	16.1 ± 3^{a}	103.4 ± 24.4^{a}	-101.8 ± 26.7^{a}	-523
		50	17.4 ± 1.8	2.1 ± 0.6	NA	NA	4.29 ± 0.85^{a}	17.7 ± 2.2^{a}	93.5 ± 6.5^{a}	-7.7 ± 7.4^{b}	-7
		150	15.9 ± 1.6	2.7 ± 0.4	NA	NA	23.63 ± 3.64^{b}	36.4 ± 9.1^{a}	121.5 ± 16.4^{ab}	102.2 ± 9.5^{c}	36
		450	18.2 ± 0.4	2.5 ± 0.3	NA	NA	98.18 ± 11.36^{c}	135.4 ± 10.6^{b}	228.5 ± 57.1^{b}	345.7 ± 81.5^{d}	42

Table 5 P budget for different paludicrops, N loads and soils. Values are shown as mean ± SE (n=4) and are expressed in mg N mesocosm^{-1}. P loss was calculated by subtracting start values from end values in surface water, pore water, and plant fractions. Positive values represent a net P loss and indicate the proportion of P available at the start that is lost from the system, i.e. not found in any other fraction in the end (e.g. binding to the soil adsorption complex). Negative values represent net P mineralisation (e.g. mobilization and organic matter decomposition). Letters represent significant differences between N load treatments.

			Start (t=0)	End (t=91)					
Soil	Species	N load	Pore water	Aboveground biomass	Belowground biomass	Surface water	Pore water	Net P loss	% P loss
Bûtefjild	*T. latifolia*	0	6.6 ± 2.7	9.5 ± 2.5	6.4 ± 7.7	0.17 ± 0.08	10.4 ± 7.5	-8.4 ± 9.2	-128
		50	15.4 ± 18	18.6 ± 6.2	5 ± 3	0.17 ± 0.12	8.9 ± 8.1	-30 ± 17.7	-195
		150	8.4 ± 1.5	16.6 ± 4.7	9.2 ± 5	0.23 ± 0.04	8.6 ± 6.8	-25.4 ± 14.6	-302
		450	5.6 ± 4.4	22.8 ± 6	10.9 ± 6.2	0.15 ± 0.06	4.7 ± 7.6	-34.5 ± 13.7	-614
Zegveld	*T. latifolia*	0	2.6 ± 2.2	25.3 ± 20.9	7.4 ± 2.9	0.11 ± 0.1	1 ± 0.6	-36.7 ± 22.1^{a}	-1422
		50	2.4 ± 1.4	24.9 ± 5.6	14.6 ± 5.4	0.2 ± 0.09	0.4 ± 0.2	-41.3 ± 10.4^{ab}	-1732
		150	1.6 ± 0.5	32.9 ± 8.6	19.2 ± 11.5	0.13 ± 0.09	0.3 ± 0.2	-53.3 ± 15.1^{c}	-3260
		450	2.2 ± 3.3	37.5 ± 19	9.2 ± 5.9	0.19 ± 0.16	0.6 ± 0.7	-48.1 ± 24.2^{bc}	-2231
	P. australis	0	1.9 ± 0.6	8.6 ± 3.7	6 ± 2	0.21 ± 0.15	2.7 ± 1.1	-13.6 ± 4^{a}	-713
		50	1.1 ± 0.5	12 ± 5	3.7 ± 2.7	0.25 ± 0.17	1.5 ± 0.3	-13.7 ± 2.5^{ab}	-1280
		150	2 ± 1.5	19.8 ± 7.4	7.6 ± 2.5	0.14 ± 0.11	2 ± 1.7	-27.3 ± 8.1^{c}	-1350
		450	2.4 ± 0.4	17 ± 4.1	7.6 ± 4.4	0.19 ± 0.11	1.8 ± 0.6	-25.1 ± 2.2^{bc}	-1048
	Control	0	1.8 ± 1.1	NA	NA	0.48 ± 0.34	2.9 ± 1.1	1.6 ± 0.3^{a}	91
		50	1.6 ± 1.2	NA	NA	0.28 ± 0.2	2.6 ± 1	1.4 ± 1.2^{ab}	88
		150	2 ± 1	NA	NA	0.13 ± 0.07	2.1 ± 1.2	0.4 ± 0^{c}	22
		450	3 ± 0.7	NA	NA	0.07 ± 0.04	2.7 ± 2.1	-0.2 ± 1.6^{bc}	-7

Discussion

This study shows that crop choice, nitrogen loading and soil characteristics (e.g. lime legacy) are important controls on ecosystem service provisioning in paludicultures by driving carbon sequestration (growth), nutrient dynamics and potential nutrient removal by biomass harvesting. Growing paludicrops can prevent excessive nutrient export to the surface water following rewetting. We found that intermediate N loads (50 to 150 kg ha^{-1}) stimulate P removal without accumulation of N in the surface water. In contrast, high N loads (450 kg ha^{-1}) or the absence of paludicrops result in nutrient accumulation in the surface water in the long term. Furthermore, biomass production of *T. latifolia* may become hampered in low pH soil, following the absence of liming, which requires additional management such as different crop choice or water table regulation. In the long run, K availability needs to stay in balance with N loads and K removal to optimize nutrient removal rates.

N loading stimulates biomass production and nutrient removal

As expected, N load had a positive effect on biomass production of both *T. latifolia* and *P. australis* (Geurts et al. 2020), although the highest N load did not increase *P. australis* biomass anymore, whereas more algae growth was observed. This is probably caused by NH_4^+ accumulation and toxicity (Tylová et al. 2008). Of the two paludicrops we expected that *T. latifolia* would be more responsive to increased N input, because of its lower N:P ratios in plant tissue (Mason and Bryant 1975) and higher NUE (Hirtreiter and Potts 2012, Ren et al. 2019) compared to *P. australis*. This was also shown in our experiment: N:P ratios of 6 in *T. latifolia* and 10 in *P. australis* in the 0 N treatment. Vroom and Xie et al. (2018) found even lower N:P ratios of 3.4 in a *T. latifolia* experiment without N addition. At the highest N load, N:P ratios increased to 10 in *T. latifolia* and 11 in *P. australis*. All these N:P ratios, however, still suggest N limitation according to the threshold of 14 found by Koerselman and Meuleman (1996) for fen vegetation dominated by meadow species (e.g. grasses, sedges). Higher N:P ratios were measured in a nutrient addition experiment by Ren et al. (2019), who found ratios of around 30 in *T. latifolia* and 12–20 in

different *P. australis* genotypes. Differences in nutrient ratios between these studies may be due to life stage, as the plants in our experiment were relatively young when harvested, meaning that less nutrient re-allocation to belowground plant parts occurred. Both species had a lower NUE (< 55 g dry weight per g N) at the highest N treatment (*T. latifolia*) or the two highest N treatments (*P. australis*) compared to the lower N treatments (> 60 g dry weight per g N). This effect of increasing N availability on NUE was also shown for *T. angustifolia* by Steinbachová-Vojtíšková et al. (2006) and can be attributed to a less efficient N uptake at higher N loads.

By harvesting the aboveground biomass, nutrients can be removed from the system, which prevents possible nutrient leaching and downstream eutrophication after rewetting (Toet et al. 2005; Hille et al. 2018). Average P removal by *T. latifolia* on the limed agricultural peat soil was over two times higher than that of *P. australis* (17 and 8 kg P/ha respectively). Differences in P removal between the two species were also shown by Geurts et al. (2020). P removal increased with increasing N load and was comparable with other studies on *Typha* (Mason and Bryant 1975; Vroom and Xie et al. 2018), but lower than in constructed wetlands with a mixed vegetation (Mitsch et al. 2000; Land et al. 2016; Giannini et al. 2019) that may have a lower P-availability in general. On the other hand, N uptake of *P. australis* was relatively high, and at 150 kg N ha^{-1} N removal of *P. australis* was even > 30% higher than that of *T. latifolia* on the limed agricultural soil (122 and 93 kg N/ha respectively). These N removal rates were high compared with other mesocosm studies (Vroom and Xie et al. 2018), but low compared to annual N removal rates in constructed wetlands (Mitsch et al. 2000; Land et al. 2016; Giannini et al. 2019). At the highest N load, *T. latifolia* had an almost two times higher N removal than *P. australis* (202 and 105 kg N/ha respectively). Of the two crops studied, *T. latifolia* is therefore the preferred crop to produce biomass and to remove N (especially NH_4^+) and P at high N loads.

Soil pH determines biomass production and nutrient removal of T. latifolia

Differences in soil pH, as a result of a different liming history, had a large effect on the biomass production of *T. latifolia*. Despite higher nutrient availability (i.e. N and P), *T. latifolia* growth was hampered on the non-limed former agricultural peat soil with a low pH (4.4), resulting in a 27–52% lower biomass, a 25–49% lower N removal, a 28–50% lower P removal, and a 46–74% lower K removal than on the limed agricultural peat soil. Nutrient uptake (i.e. nutrient content in plant tissue) was only affected for K, which was significantly lower on the non-limed soil (17–45%), whereas N and P uptake did not differ on the two investigated soil types. We cannot rule out that the first potassium gift was applied too late, hampering growth in the first 4–5 weeks of the experiment. It is known from other studies that nutrient uptake and cation supply become frustrated at a pH < 4 (Dyhr-Jensen and Brix, 1996; Brix et al. 2002). In our experiment, however, reduced uptake of K at low pH was the main factor limiting plant growth, because uptake of Ca and Mg was even higher on the non-limed soil than on the limed soil. On both investigated soil types *T. latifolia* biomass significantly increased with increasing N input. Biomass yield of *T. latifolia* in the 0 N treatment on the non-limed former agricultural soil (2.5 ton dm/ha) was comparable with the same treatment in the study of Vroom and Xie et al. (2018), whereas yield of the 0 N treatment on the limed agricultural soil (5.3 ton dm/ha) was more comparable with the same treatment in

the study of Ren et al. (2019). The *T. latifolia* biomass yield of the 150 N treatment on both soils (4.8 and 8.0 ton dm/ha for BF and ZV soil respectively) was in the same range as Vroom and Xie et al. (2018) found for this treatment, but lower than Ren et al. (2019) reported. This could be a result of a higher K loading throughout their experiment.

Despite the low N:P ratios and expected N limitation in *T. latifolia*, (co)limitation of other nutrients is also possible, especially when N loads increase (Ulrich and Burton 1988). Because of very low K availability in the former agricultural soil halfway the experiment, and therefore possible K limitation, extra K was added twice. This finally resulted in K percentages of 1.1 to 1.6 in *T. latifolia* on this soil type, which is still low, and therefore dilution of K in plant tissue and a high N:K ratio of 2.1 was observed at the highest N load. This is comparable with the N:K ratios Ren et al. (2019) found, although they harvested during plant senescence, meaning that K allocation to the roots had already started. The N:K ratio is on the high end of the range in K limitation thresholds for wetland plants of 1.2 to 2.1 found in literature (Pegtel et al. 1996; Olde Venterink et al. 2003; Lawniczak et al. 2009), and therefore K limitation cannot be excluded at this high N load. We expect that cation competition between NH_4^+ and K^+ also plays a role at increasing N loadings (Ten Hoopen et al. 2010). N:K ratios in the treatments with lower N loads were significantly lower, and therefore clearly not K limited. However, all K:P ratios were higher than 3.4, which is an indication of P limitation instead (Olde Venterink et al. 2003). This means that the observed decreased K uptake could have been caused by P limitation.

N loading flips N mineralization to N loss in paludiculture systems

Results show that both paludicrops can mitigate the N accumulation observed in the soil, pore water, and surface water of the unvegetated control treatments by taking up the excess of N. Grace (1988) also found a large reduction (90–95%) in sediment NH_4^+ concentrations by *Typha* growth. It seems unlikely that this mitigation effect is caused by enhanced denitrification in the treatments with plants, because increased oxygen concentrations by ROL would normally decrease denitrification rates (Veraart et al. 2011). Microbial processes in rewetted peat are known to remove NO_3^- from NO_3^- enriched surface water and this removal rate increases with N load (Cabezas et al. 2012), although the fraction removed may decrease at higher loadings (Land et al. 2016). In our experiment, net N loss to the atmosphere is also highest at the highest N load, irrespective of plant presence. Therefore, there is net mineralization at the lower N loads and net N loss to the atmosphere at higher N loads. Vroom and Xie et al. (2018) only found a slightly higher N loss at a higher N load.

Microbial activity in the soil, and therefore mineralization, including denitrification, and coupled nitrification-denitrification are enhanced by extra N input (Reddy et al. 1989). Extra N input also leads to more biomass production and therefore to more P uptake by plants, more net P mineralisation by bacteria, and less P mobilization to the water layer. The latter is also valid in the unvegetated treatments. There are also clear differences in P dynamics between the two soil types. Whereas total P concentrations are higher in the limed agricultural peat soil, pore water P and Olsen-P are higher in the former agricultural peat soil. This is probably due to the lower pH in the non-limed soil, as acid soil types

tend to have higher P mineralization rates than more neutral soil types (Bridgham et al. 1998). Higher pore water P concentrations in this soil did not lead to a higher P mobilization to the water layer as plants took up most of the available P. Moreover, dissolved iron concentrations in this soil were higher than in the limed agricultural peat soil, and this iron can effectively bind phosphorus at the water-peat interface (Zak et al. 2004; Geurts et al. 2010)

Management options

The choice for a certain paludicrop and the potential nutrient removal ability depends on the nutrient availability and pH of the soil. We found that a higher nutrient load cannot compensate the negative effects of a low pH and therefore acid soils with bog peat are less suitable for *T. latifolia*, and more suitable for *Sphagnum* farming (Temmink et al. 2016; Gaudig et al. 2017; Vroom et al. 2020). More neutral soils with a higher nutrient availability are suitable for fast-growing species like *Typha* spec., *P. australis*, and *Arundo* spec. (Tho et al. 2017; Ren et al. 2019). Cropping *Carex* species on rewetted soils warrant further investigation given *Carex's* plasiticity to a wide pH range and their high carbon sequestration potential (Hinzke et al. 2021). Rewetting using alkaline ditch water and restoring groundwater flow, often high in bicarbonate, may prevent low pH conditions that hamper plant growth excessively.

Water management is very important in a paludiculture. First of all, the water level should stay within the optimal range for a specific paludicrop to avoid loss in biomass production and vitality. Secondly, nutrients should be supplied through the inlet of water (Temmink et al. 2016; Geurts and Fritz 2018; Ren et al. 2019; Vroom et al. 2020). As we showed, N supply is of particular importance, because N partly disappears from the soil after rewetting by denitrification (Cameron and Moir 2013) and anaerobic ammonium oxidation (Kartal et al. 2006). The retention time of the water and the hydraulic load is also crucial in that respective, which is already known for constructed wetlands (Vymazal et al. 2006; Wu et al. 2015), but not studied specifically for a paludiculture situation yet. A high retention time and a low hydraulic load can encourage nutrient limitation, whereas a low retention time and high hydraulic load can lead to nutrient leaching downstream from the paludiculture site. For the same reason the use of artificial fertilizers is not desirable. Care should also be taken when high labile carbon concentrations (i.e. DOC) are present in the inlet water, because these can induce methanogenesis and subsequently increase CH_4 emissions (Vroom and Xie et al. 2018).

We have shown that paludiculture can combine biomass production with effective water purification, and nutrient removal, next to water retention, peat preservation, CO_2 emission reduction, and soil subsidence reversal. Therefore, paludiculture is especially suitable for and useful in buffer zones between agricultural areas and nature areas. The effectiveness increases by intermediate to high (50–150 kg N) N loads. Very high N loads may maximize yields, but are not desirable because of potential crop damage, nutrient leakage after the growing season and higher costs.

Declarations

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Conflicts of interest/Competing interests

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Availability of data and material

The datasets generated during and/or analysed during the current study are available in the Radboud Data Repository.

Code availability (software application or custom code)

Not applicable.

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Figures

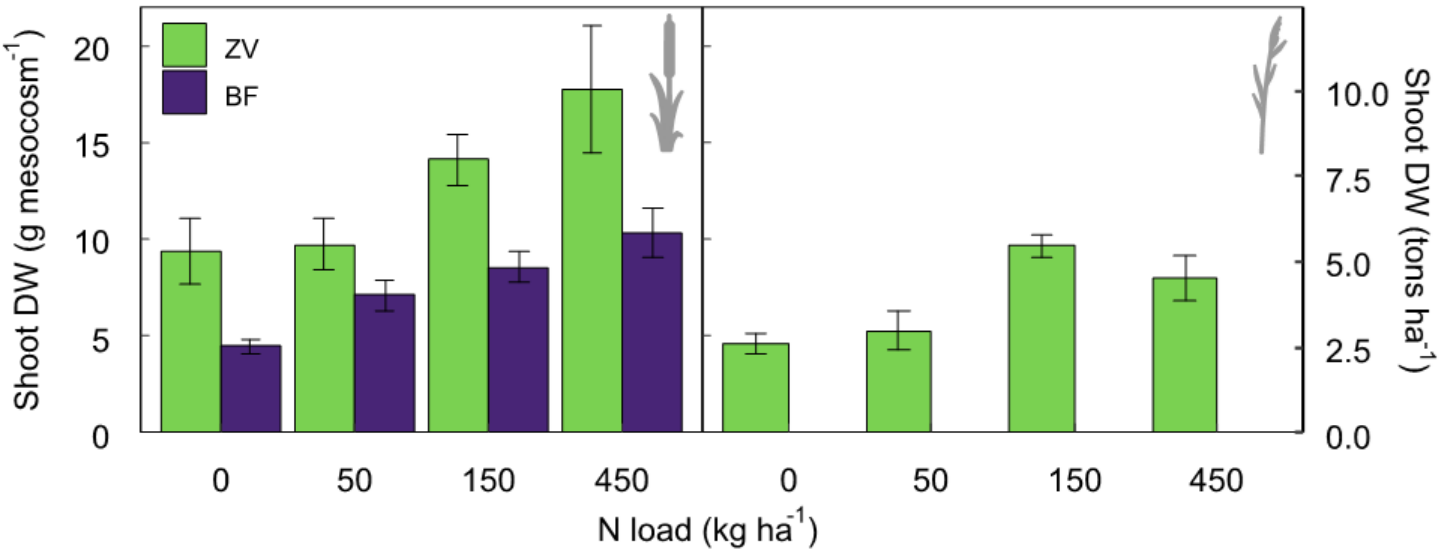


Figure 1

Shoot dry weight of T. latifolia on different soils (left panel) and P. australis on ZV soil (right panel) at different N loads after 95 days (n=4 per treatment). Error bars represent standard errors.

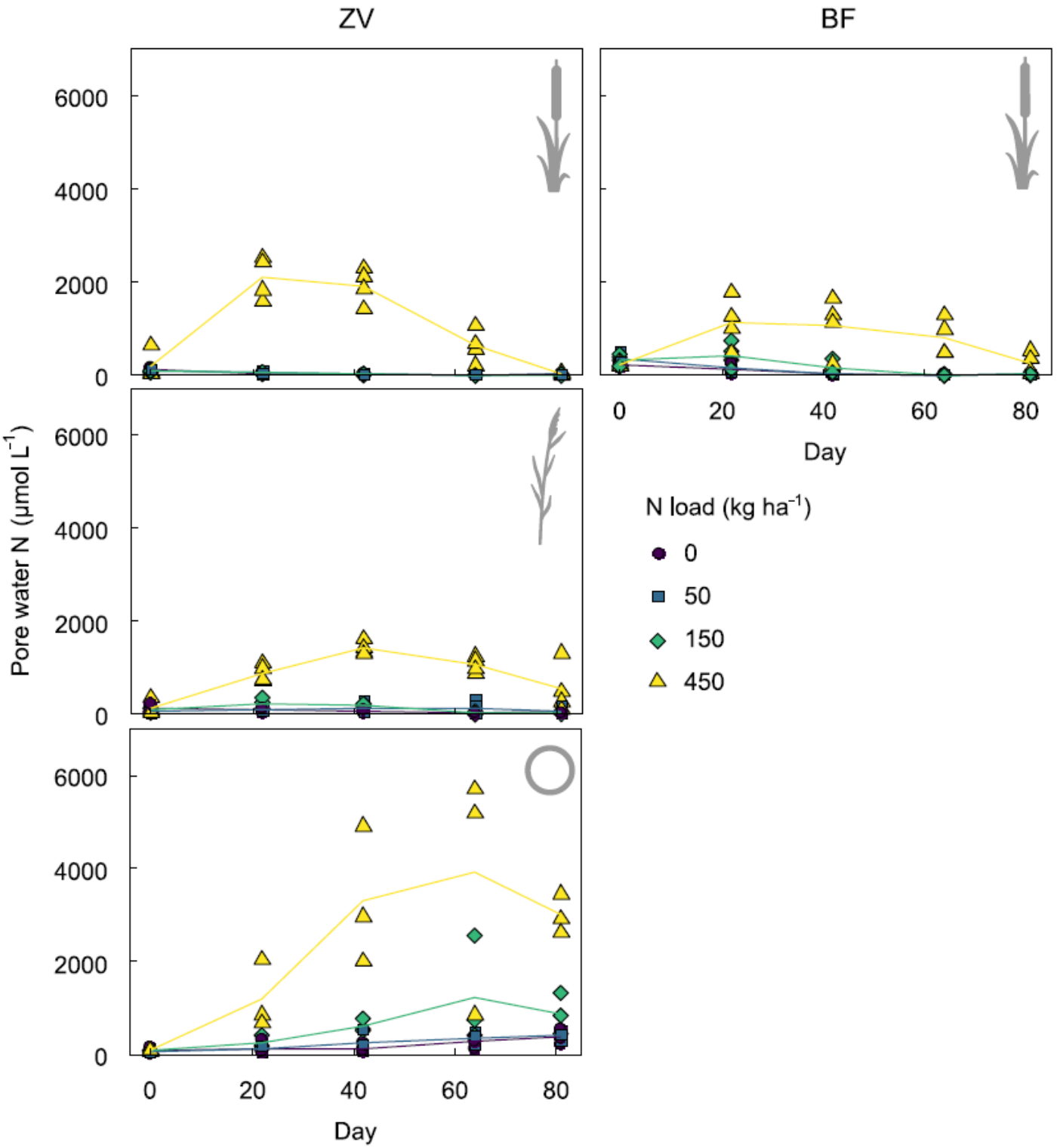


Figure 2

Plant-available N (NH4+ + NO3-) concentrations in pore water over time for different N loads. Left panels: ZV soil, right panel: BF soil. Markers indicate individual mesocosms (n=4 per treatment) and can overlap. Lines indicate average trends.

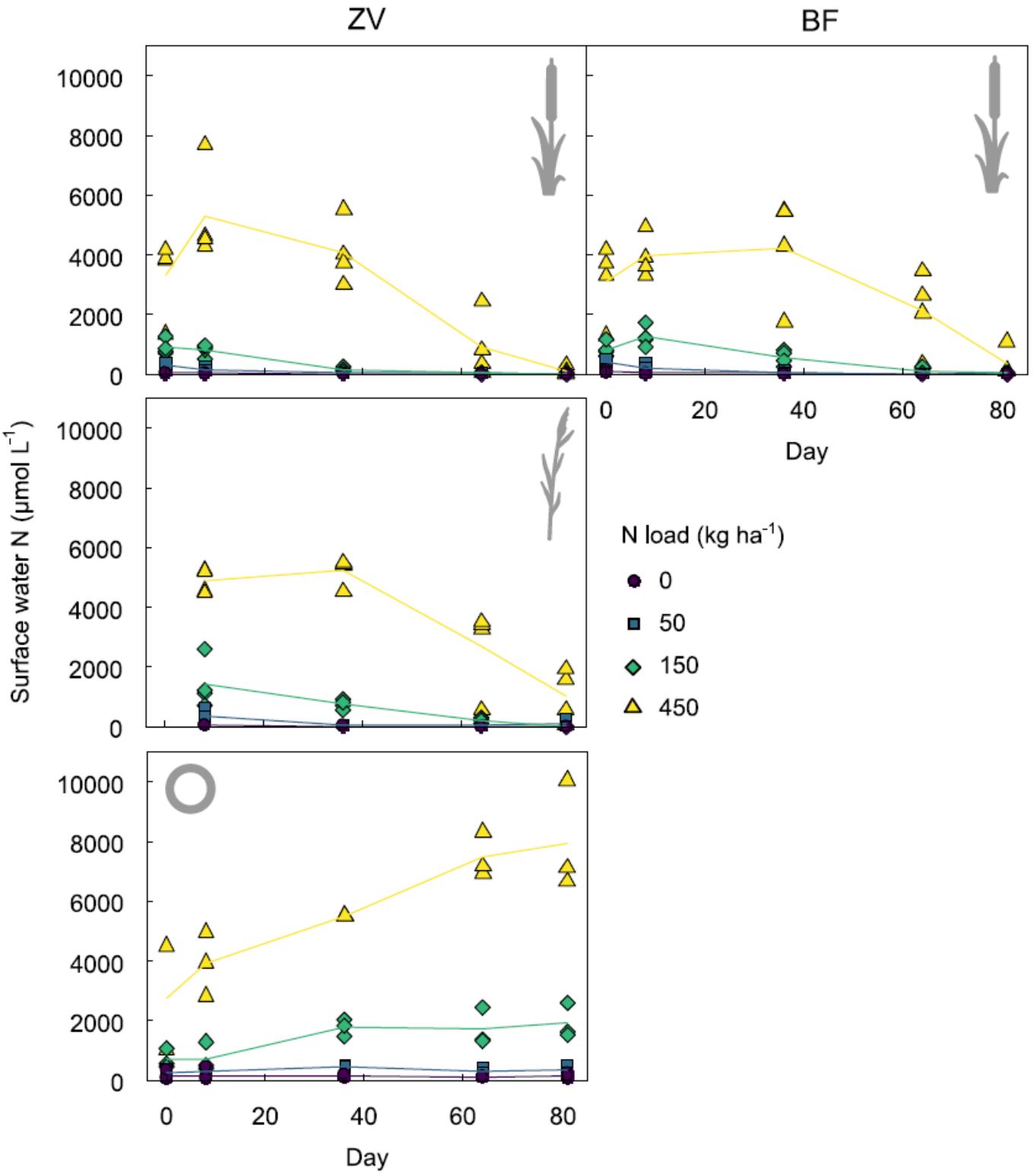


Figure 3

Plant-available N (NH4+ + NO3-) concentrations in surface water over time for different N loads. Left panels: ZV soil, right panel: BF soil. Markers indicate individual mesocosms and can overlap. Lines indicate average trends.

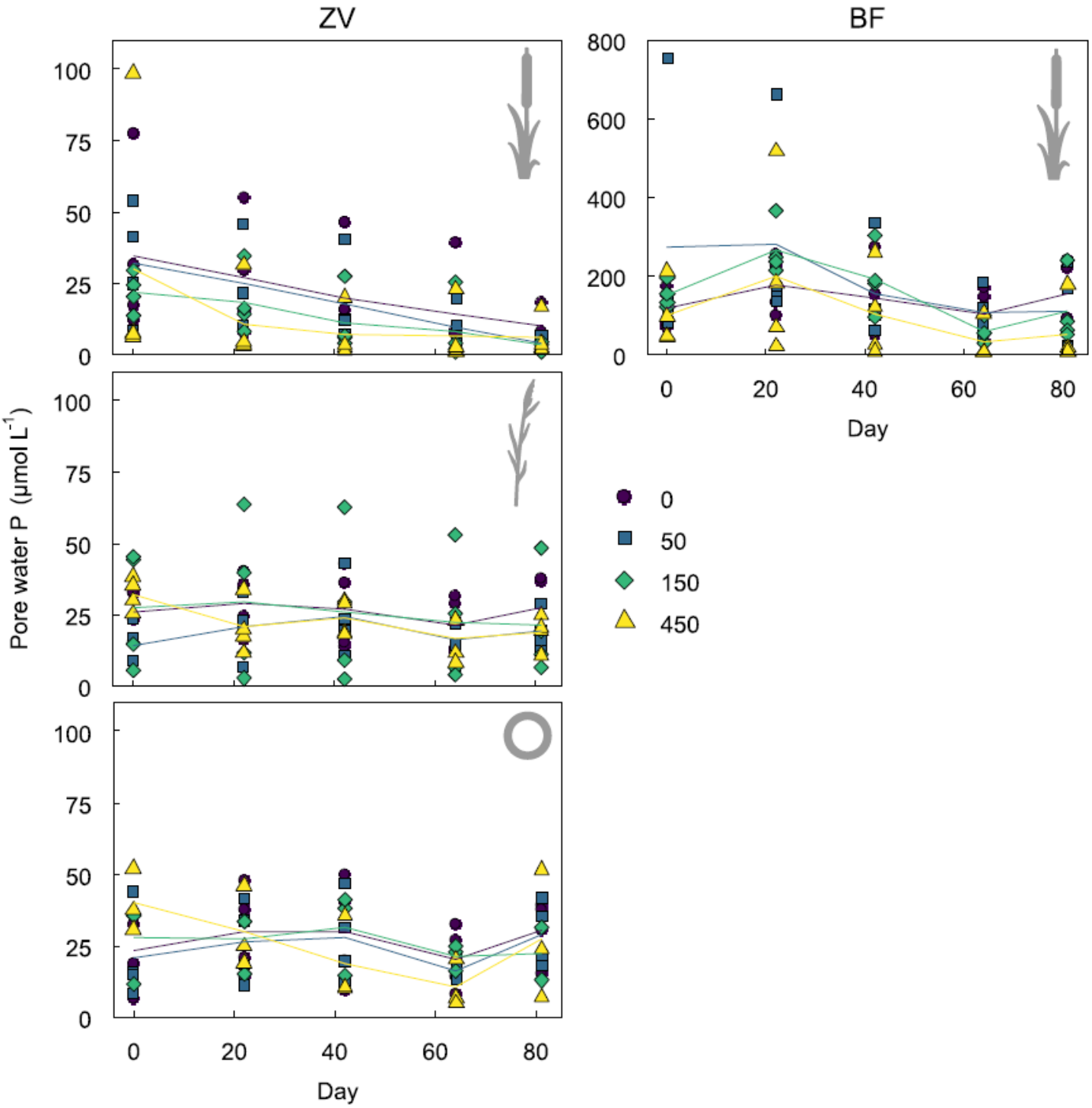


Figure 4

P concentrations in in pore water over time for different N loads. Left panels: ZV soil, right panel: BF soil. Note: different Y axis scale for T. latifolia on BF soil. Markers indicate individual mesocosms (n=4 per treatment) and can overlap. Lines indicate average trends.

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