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Nutrient removal potential and biomass production by *Phragmites australis* and *Typha latifolia* on European rewetted peat and mineral soils

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HIGHLIGHTS

- *T. latifolia* and *P. australis* have great potential for nutrient removal in wetlands.
- Both species produce high biomass in a wide range of abiotic soil conditions.
- Substantial carbon sequestration in biomass despite nutrient limitation
- Tissue nutrient ratios are species-specific and *T. latifolia* removes more P and K.
- Winter harvesting produces useful biomass and is more sustainable in the long term.

GRAPHICAL ABSTRACT

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ABSTRACT

Paludiculture, sustainable and climate-smart land use of formerly drained, rewetted organic soils, can produce significant biomass in peatlands whilst potentially restoring several additional wetland services. However, the site conditions that allow maximum biomass production and nutrient removal by paludiculture crops have rarely been studied.

We studied the relationship between soil characteristics, including plant-available nutrients, peak biomass, stand age, harvest period, and nutrient removal potential for two important paludiculture species, *Typha latifolia* and *Phragmites australis*, on rewetted peat and mineral soils in a large-scale European survey.

T. latifolia and *P. australis* were able to produce an aboveground peak biomass of 10–30 t dry matter ha⁻¹ y⁻¹ and absorbed significant amounts of carbon, nitrogen, phosphorus, and potassium in stands older than 3 years. They were able to grow in a wide range of abiotic soil conditions. Low N:P ratios (5–9) and low N content (< 2%) in *T. latifolia* tissue suggest N limitation, but P uptake was still surprisingly high. *P. australis* had higher N:P ratios

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Stand age
Soil characteristics
Biomass use

(8–25) and was less responsive to nutrients, suggesting a higher nutrient use efficiency. However, both species could still produce significant biomass at lower nutrient loads and in winter, when water content was low and nutrient removal still reasonable.

Based on this European wetland survey, paludiculture holds a great potential to combine peat preservation, water purification, nutrient removal, and a high biomass production. Paludicrops take up substantial amounts of nutrients, and both summer and winter harvests provide an effective way to sequester carbon in a range of high-valued biomass products and to control nutrient effluxes from rewetted sites at the landscape scale.

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1. Introduction

Peatlands have long been drained for agriculture, forestry, and peat excavation industries (Joosten, 2016). However, drained peatlands are prone to degradation and greenhouse gas emissions. Currently, 2 Gt CO₂-eq per year are emitted from degraded peatlands worldwide (Joosten et al., 2016). In Europe, peatlands are responsible for 80% of greenhouse gas (GHG) emissions from agricultural areas despite covering only 10% of the land surface (Tanneberger et al., 2017). Additional problems caused by peatland drainage are soil subsidence, increased frequency of salt water intrusion, decreased stability of dikes, increased flood risk (Erkens et al., 2016; Wijedasa et al., 2017) and decreased water quality (Holden et al., 2004; Lamers et al., 2015). Rewetting drained peatlands is therefore urgently needed and recommended (Günther et al., 2020). Moreover, this can also provide other beneficial wetland services, such as water purification, biodiversity support and the creation of water retention areas for drought prevention and temporary storage of storm water runoff, which can counteract the effects of climate change and sea level rise (Thomas et al., 2011; Wenger et al., 2013; Lamers et al., 2015).

Although the rewetting of formerly drained agricultural peat soils can be a mitigation strategy for climate change and soil subsidence (Knox et al., 2015), it can temporarily lead to high nutrient mobilization rates, which may decrease surface water quality (Van de Riet et al., 2013; Grygoruk et al., 2015; Land et al., 2016; Smolders et al., 2019). Particularly phosphate but also ammonium will be exported from the soil matrix into the surface water when the soil becomes anaerobic due to waterlogging (Zak and Gelbrecht, 2007). Although topsoil removal can be an effective solution to prevent this eutrophication (Zak et al., 2017; Harpenslager et al., 2015), this is often expensive and may even be undesirable (Klimkowska et al., 2010).

An alternative solution to ameliorate the initial nutrient release after rewetting is removal of nutrients from surface water and rewetted soil through biomass harvesting of wetland plants, as applied in some constructed wetlands for wastewater treatment (Breen, 1990; Toet et al., 2005; Vymazal, 2007). For example, Giannini et al. (2017) demonstrated significant nutrient removal by biomass harvesting in a rewetted Mediterranean peatland. However, harvesting can also have a negative effect on the nutrient removal capacity of wetland plants, as it interrupts oxygen transport to the roots, impacting the oxidation activity mediated by the aerobic microbial community in the rhizosphere (Wang et al., 2015).

Fast-growing, naturally occurring emergent wetlands plants, such as *Typha latifolia* L. (Martin and Fernandez, 1992), *Phragmites australis* (Cav.) Trin. ex Steud. (Romero et al., 1999), *Arundo donax* L. (Giannini et al., 2017), *Alnus glutinosa* (L.) Gaertn., *Phalaris arundinacea* L. (Karki et al., 2014), and *Carex* spp. (Schulz et al., 2011), can be harvested as crops from rewetted fen peatlands and used in several commercial applications. On rewetted peat soils, this type of agriculture is called paludiculture, which can provide a significant biomass production whilst potentially also restoring other ecosystem functions, such as water retention, reduction of nutrient leaching and greenhouse gas emissions, peat preservation, and biodiversity conservation (Wichtmann et al., 2016; Geurts et al., 2019). Payments for these important wetland ecosystem services should stimulate rewetting and a sustainable use of

peatlands (Redford and Adams, 2009; Tanneberger and Wichtmann, 2011).

Paludiculture can also be implemented in buffer strips, situated between areas of intense agriculture and receiving water bodies (sea, lakes, or rivers) or nature conservation areas with low nutrient conditions. In addition, it can act as a hydrological buffer between heavily drained intensive agriculture and natural wetlands.

For restoration and management of protected peatlands, the removal of above-ground biomass is a common practice to establish low nutrient conditions (Olde Venterink et al., 2009). Optimum nutrient removal can be achieved by harvesting at the onset of flowering, when biomass production and nutrient concentrations are highest (Meuleman et al., 2002). However, care needs to be taken with species such as *P. australis* that can be sensitive to summer harvest, resulting in reduced biomass production rates in subsequent years (Asaeda et al., 2006; Hansson and Fredriksson, 2004). In contrast, at least for nutrient uptake in wetlands used for wastewater treatment, *P. australis* suffers no long-term effects after harvesting in September–October when nutrients have already been re-allocated to the rhizomes for vigorous regrowth in spring (Meuleman et al., 2002). This means that proper management (e.g. harvesting period and technique, water level, nutrient loading) and wetland configuration (e.g. shape, size, vegetation type) are crucial to optimize nutrient removal and biomass production in paludiculture (Wichtmann et al., 2016; Ren et al., 2019).

To reach optimal productivity and nutrient removal of paludiculture crops, rewetted peat soils should ideally provide balanced nutrient supply. The availability of N, P, and K is the most important factor determining composition, structure and productivity of wetland vegetation (Willby et al., 2001). In most former agricultural peat soils, P availability will exceed plant requirements and will therefore not be a limiting factor, as P will be mobilized after rewetting (Olde Venterink et al., 2002; Smolders et al., 2006; Zak and Gelbrecht, 2007). Only when P mobilization is higher than P uptake by paludiculture crops will P be released to surrounding areas with undesirable effects (Fisher and Acreman, 2004). Unlike P, N availability generally decreases rapidly after rewetting due to denitrification or anaerobic ammonium oxidation (Gumbrecht, 1993; Jetten et al., 2001), which means that N is likely to become growth-limiting during the initial rewetting stage. K availability is, in contrast, not directly affected by rewetting, meaning that any existing K limitation will persist (Van Duren et al., 1997; Olde Venterink et al., 2002). In addition, regular summer harvesting could also result in K deficiency in the long term.

Most studies of the nutrient uptake potential of *P. australis* and *T. latifolia* have addressed constructed wetlands rather than rewetted peat soils (Vymazal and Kröpfelová, 2010). A comparison between constructed wetlands and natural wetlands showed almost doubled N and P nutrient use efficiency rates in natural wetlands (Meuleman et al., 2002). For paludiculture conditions, however, nutrient uptake dynamics of wetland plants in relation to soil characteristics are poorly known (Schulz et al., 2011; Zak et al., 2014) and mostly based on studies in mesocosm experiments that may not fully resemble field conditions (Vroom et al., 2018; Ren et al., 2019). It is therefore essential to know if paludiculture crops will take up enough nutrients under field conditions to prevent large-scale downstream eutrophication at the landscape scale.

We therefore carried out a European survey including more than 200 rewetted peat and mineral soil sites in the Netherlands, Denmark, and Germany. The main questions addressed by this large-scale study concern nutrient dynamics in rewetted fen peat soils. In particular, how effectively *T. latifolia* (broadleaf cattail) and *P. australis* (common reed) accumulate nutrients and carbon (C), how much nutrients can potentially be removed by harvesting at either peak biomass or in other periods (Dragoni et al., 2017), and how this is related to stand age, nutrient availability in the soil, and other abiotic soil characteristics. More specifically, we wanted to know: 1) whether *T. latifolia* and *P. australis* can absorb as much N, P, and K in rewetted peatlands as in other eutrophic wetlands, 2) whether both species are equally suitable to prevent nutrient mobilization and downstream eutrophication, and 3) how harvesting date influences nutrient stoichiometry and biomass production in the long term.

2. Material and methods

2.1. Sampling

Between 2014 and 2017 more than 200 sites in rewetted (former) peatlands and newly created wetlands were sampled on 25 geographically separated locations in the Netherlands, Germany, and Denmark (Table 1). We included a large range of semi-natural field sites, primarily self-colonized stands of *T. latifolia* and *P. australis* on rewetted mineral and peat soils. These sites mostly consisted of former agricultural soils that had recently been rewetted for climate mitigation, water storage, water purification, nature restoration, or inadvertently. Both organic and mineral soils were included to get a larger gradient in soil conditions. At each site, the upper 20 cm of the soil was sampled with a gouge auger ($\varnothing$ 4 cm) and stored in airtight plastic bags.

Aboveground biomass samples of *P. australis* and *T. latifolia* were harvested from 50×50 cm or 100×100 cm plots, including stems, leaves, and inflorescences when present. This was repeated on 2–9 sites per location. Dead biomass from previous years was excluded. The stems were cut at 30 cm above the soil to prevent flooding of the remaining culm stubble in future, similar to commercial harvesting. Both species were harvested in August or September at peak biomass. In addition, *Typha latifolia* was also harvested in January, February, March, May, June, July, and/or October and *P. australis* was also harvested in January, February, June, and/or October (Table 1). All biomass sampling was from different stands that had not previously been harvested or sampled. Biomass samples were weighed for fresh weight (FW), dried for 72 h at 70 °C, re-weighed for dry weight (DW), and ground for nutrient analysis using a Retsch SM 200 cutting mill.

2.2. Soil and plant analyses

Soil samples were stored at 4 °C until further analyses. Salt extractions were carried out on 17.5 g of fresh soil with 50 mL of a 0.2 M NaCl solution, and water extractions on 17.5 g of fresh soil with 50 mL of demineralized water. After extraction for 2 h on a shaking table at 100 rpm, pH was determined with an Ag/AgCl electrode (Orion Research, Beverly, MA, USA) and TIM 840 Titration Manager (Radiometer Analytical SAS, Villeurbanne, France). Liquid samples were then extracted using Rhizon soil moisture samplers (Rhizosphere Research Products, Wageningen, The Netherlands) and vacuum glass bottles. The liquid extraction samples were stored at 4 °C for elemental analysis (adding 0.1 mL of 65% HNO₃ to a 10 mL subsample) and – 20 °C for nutrient analysis (described below).

Subsamples of fresh soil were dried at 70 °C for 72 h to determine moisture content and bulk density. Subsamples of dry soil were incinerated at 550 °C to determine OM content by loss on ignition. Bio-available P in the soil (Olsen-P) was determined by incubating 3 g dried soil in 60 mL 0.5 M NaHCO₃ for 30 min at 100 rpm (Henriksen 1965), followed by extraction with Rhizon samplers as described above. Dry soils and

plant material were ground and homogenized using a ball mill (Fritsch Pulverisette Ball Mill, Fritsch GmbH, Idar-Oberstein, Germany) at 400 rpm for 4 min. Total N and total C were measured using a CNS analyser (NA 1500, Carlo Erba; Thermo Fisher Scientific, Franklin, USA). Total elemental concentrations were determined after microwave digestion, adding 4 mL HNO₃ (65%) and 1 mL H₂O₂ (35%) to 200 mg homogenized soil or plant material in Teflon vessels, followed by heating in an Ethos D microwave (Milestone, Sorisole Lombardy, Italy).

Inductively coupled plasma emission spectrometry (ICP-OES) was used to measure total concentrations of Al, Ca, Fe, K, Mn, Mg, Na, P, S, Si, and Zn (iCAP 6000, Thermo Fischer Scientific, Bremen, Germany) in the digested plant and soil samples and in the extraction samples that had been stored at 4 °C. NO₃, NH₄, PO₄, and Cl were determined colorimetrically (Auto Analyser III, Bran+Luebbe GmbH, Norderstedt, Germany) in the extraction samples that had been stored at – 20 °C (Geurts et al., 2008).

2.3. Data analyses

Correlations between peak biomass, carbon and potential nutrient removal (i.e. nutrients that accumulated in the biomass, which would potentially be removed by aboveground biomass harvesting – hereafter called ‘nutrient removal’), nutrient ratios (N:P and N:K) and concentrations (N, P, and K) in plant tissue, soil nutrient availability (NO₃, NH₄, P, and K in soil extractions), OM content and other soil characteristics were analyzed by using Pearson correlation coefficients (IBM SPSS Statistics version 25). A multivariate GLM was used to test between-subject effects of species, location, and species $\times$ location. To be able to compare plant-available nutrient concentrations across different soil types, all concentrations were expressed per volume fresh soil.

For these analyses we used the data of the ≥ 3 year old, healthy stands of *T. latifolia* and *P. australis* on mineral and organic soils that were sampled in August or September at peak biomass (72 sites in total, 50 for *T. latifolia* and 22 for *P. australis*; Table 1). To address the role of time since rewetting on biomass production and potential nutrient removal, we selected 65 healthy *T. latifolia* stands. Stands younger than 3 years since rewetting ($n = 15$) were compared against 3–5 year old stands ($n = 24$) and ≥ 5 year old stands ($n = 26$; Table 1). The sites in Volgermeer (3 different soil types) and Zegveld were described before by Harpenslager et al. (2018) and Pijlman et al. (2019) respectively. We did not consider hydraulic load, land use history, nutrient load, and water level fluctuations at the different sites.

The effect of harvest period on biomass production, potential nutrient removal, and water content was studied using data from the specified sampling locations in Table 1. Variables were expressed as a percentage of the peak biomass at each specific site.

3. Results

3.1. Nutrient removal potential and biomass production

T. latifolia and *P. australis* both produced an aboveground peak biomass of up to 30 t dry matter (dm) ha^{–1} y^{–1} in stands older than 3 years (Figs. 1–3). *T. latifolia* produced 12.4 ± 6.6 t dm ha^{–1} y^{–1} on average, and *P. australis* produced 13.8 ± 7.1 t dm ha^{–1} y^{–1} on average (Table A.1). When *T. latifolia* biomass production was higher than 10 t dm ha^{–1} y^{–1}, 4–14 t C, 100–500 kg N, 20–80 kg P, and 100–450 kg potassium (K) per hectare could be removed by harvesting aboveground biomass (Figs. 1–3). For *P. australis* 4–14 t C, 150–600 kg N, 10–60 kg P, and 50–350 kg K per hectare could be removed. Biomass production and N removal did not differ between species, but P and K removal were significantly higher for *T. latifolia* than for *P. australis* ($P < 0.05$; Table A.1). On the other hand, biomass production and removal of N, P, and K all differed significantly between locations ($P < 0.001$), although an interaction effect between species and location was only found for biomass production and N removal ($P < 0.01$).

Table 1

Overview of *T. latifolia* (TL) and *P. australis* (PA) sampling locations. Multiple sites were sampled per location. Year = growing season including the subsequent winter. * = sampling location also used for the harvest period dataset.

Sampling locations	Country	Latitude	Longitude	Year	Selection	Species
Drentsche Aa	NL	53°01'40.2"N	6°39'44.5"E	2015	≥5 y old	TL, PA
Hunze	NL	53°06'02.5"N	6°43'38.3"E	2015	≥5 y old	TL, PA
Volgermeer	NL	52°25'14.8"N	4°59'48.3"E	2014	3–5 y old	TL, PA
Aalbude I	DE	53°51'21.7"N	12°51'44.2"E	2015/16	≥5 y old	TL*, PA
Aalbude II	DE	53°51'24.1"N	12°51'40.3"E	2015	≥5 y old	TL*
Bad Sülze I	DE	54°06'05.4"N	12°40'07.0"E	2015	≥5 y old	TL*, PA
Bad Sülze II	DE	54°06'49.2"N	12°41'37.0"E	2015	≥5 y old	TL*
Bugewitz I	DE	53°47'36.4"N	13°49'50.5"E	2015	≥5 y old	TL*, PA
Kamp I	DE	53°50'27.9"N	13°48'39.6"E	2015/16	≥5 y old	TL*
Kamp II	DE	53°50'32.7"N	13°49'49.6"E	2015	≥5 y old	TL*, PA
Brabrand Lake	DK	56°08'48.4"N	10°05'17.7"E	2015	≥5 y old	PA
Egå Lake	DK	56°13'02.6"N	10°14'04.0"E	2015	≥5 y old	TL
Lingezege	NL	51°55'34.5"N	5°53'22.7"E	2015	<3 y old	TL
Zegveld I	NL	52°08'05.0"N	4°50'10.2"E	2016	<3 y old	TL*, PA*
Zegveld II	NL	52°08'19.3"N	4°50'20.4"E	2017	<3 y old	TL*
Voorschoten	NL	52°07'51.8"N	4°25'23.6"E	2016	<3 y old	TL
Lille Vildmose	DK	56°53'31.8"N	10°11'21.8"E	2016	<3 y old	TL
Tribsees I	DE	54°06'05.8"N	12°44'09.4"E	2011	Harvest period	PA
Tribsees II	DE	54°05'37.8"N	12°44'21.3"E	2011	Harvest period	PA
Ziethen	DE	53°52'20.2"N	13°39'38.7"E	2011	Harvest period	PA
Jargelin	DE	53°52'16.6"N	13°39'32.7"E	2011	Harvest period	PA
Bargischow	DE	53°51'21.7"N	13°47'44.5"E	2011	Harvest period	PA
Bugewitz II	DE	53°47'35.3"N	13°49'48.5"E	2011	Harvest period	PA
Waschow	DE	53°57'59.1"N	13°50'49.5"E	2011	Harvest period	PA
Ferne Wiesen	DE	53°51'13.6"N	13°46'50.4"E	2011	Harvest period	PA

The N:P ratio of *T. latifolia* biomass ranged from 5 to 9 (mean = 6.5), and the N:K ratio ranged from 0.5 to 3 (mean = 1.2; Fig. 4). *P. australis* had significantly higher ratios than *T. latifolia* ($P < 0.001$; Table A.1), with N:P ranging from 8 to 25 (mean = 12), and N:K ranging from 1 to 4.5 (mean = 2.6). There was little overlap in N:P ratios between species. N:P and N:K ratios also differed between locations and there was a significant interaction effect between species and location ($P < 0.001$).

P concentrations in *T. latifolia* biomass ranged from 0.11% to 0.32% (mean = 0.21%), and were always higher than in *P. australis* biomass ($P < 0.001$; ranging from 0.08% to 0.21%; mean = 0.15%) at a given N concentration (Fig. 4). Tissue N concentrations in both species largely overlapped (0.8% to 2%), although they were on average significantly higher in *P. australis* biomass ($P < 0.01$). N, P, and K concentrations also differed between locations ($P < 0.01$), but an interaction effect between species and location was only found for N concentrations ($P < 0.001$; Table A.1).

3.2. Stand age

Maximum aboveground biomass production and nutrient removal in young *T. latifolia* stands (<3 years old) was two to three times lower than in older *T. latifolia* stands (≥3 years old; Fig. 1–3). Stands younger than 3 years since rewetting produced 6.1 t dm ha⁻¹ y⁻¹ on average, whereas stands of 3–5 years old produced 10.6 t dm ha⁻¹ y⁻¹ on average, and stands of ≥5 years old produced 14.1 t dm ha⁻¹ y⁻¹ on average. Average P removal was 7.6, 22.4, and 30.9 kg ha⁻¹ y⁻¹ respectively, average N removal was 62, 131, and 204 kg ha⁻¹ y⁻¹ respectively, and average K removal was 54, 132, and 163 kg ha⁻¹ y⁻¹ respectively.

3.3. Interaction between soil conditions and biomass characteristics

To investigate how soil conditions were related to nutrient removal through biomass harvest, we analyzed the availability and total content of nutrients (Table A.2) and other important elements in the soil.

Fig. 1. P removal rates in relation to biomass production (in aboveground biomass harvested in August or September) on rewetted peat and mineral soil sites. Left: *T. latifolia* and *P. australis* stands of ≥3 years old ($n = 72$). The R^2 is calculated from the Pearson correlation coefficient ($P < 0.001$). Right: *T. latifolia* stands younger than 3 years, 3 to 5 years old, and ≥ 5 years old ($n = 65$). dm = dry matter.

Fig. 2. N removal rates in relation to biomass production (in aboveground biomass harvested in August or September) on rewetted peat and mineral soil sites. Left: *T. latifolia* and *P. australis* stands of ≥ 3 years old ($n = 72$). The R^2 is calculated from the Pearson correlation coefficient ($P < 0.001$). Right: *T. latifolia* stands younger than 3 years, 3 to 5 years old, and ≥ 5 years old ($n = 65$). dm = dry matter.

For *T. latifolia*, water extractable P was negatively correlated with biomass production and removal of N, P, and K ($R^2 = 0.2-0.3$; Table A.3). Water-extractable Al, K, Na, NH_4 , and Zn, and salt-extractable K, Mg, Mn, and P were also negatively correlated with biomass production ($R^2 = 0.2-0.3$). Both indicate higher uptake at higher production.

Total N and C content of the soil (both in % and in g l^{-1}) only showed a weakly positive correlation with *T. latifolia* biomass production ($R^2 = 0.2$). Plant Zn concentrations negatively correlated with biomass production and N removal ($R^2 = 0.2-0.3$). Salt-extractable and water-extractable K were negatively correlated with N and P removal ($R^2 = 0.2-0.3$), salt-extractable Mg was negatively correlated with N, P, and K removal ($R^2 = 0.2$), and water-extractable Na and Zn were negatively correlated with P and K removal ($R^2 = 0.2$).

P. australis biomass production was only negatively correlated with soil total Fe ($R^2 = 0.3$) and salt extractable Zn ($R^2 = 0.2$; Table A.4), but not with other nutrients. Plant Mn concentrations were positively correlated with biomass production ($R^2 = 0.5$) and nutrient removal ($R^2 = 0.5-0.6$). Salt-extractable Al was negatively correlated with N, P, and K removal ($R^2 = 0.2-0.4$).

Biomass production of both species had no significant correlation (*Phragmites*), or only a very weak significant correlation (*T. latifolia*; $R^2 = 0.1$), with OM content of the soil (Fig. 5).

We also analyzed which soil conditions determined plant N:P ratios and concentrations of N, P, and K. For *T. latifolia*, soil total Mn, Na, S, Si, Zn, and Fe:P ratio, and salt-extractable NH_4 were positively correlated with plant N concentrations ($R^2 = 0.2-0.4$), whereas soil bulk density negatively influenced plant N concentrations ($R^2 = 0.2$). Soil total Fe was positively correlated with plant P concentrations ($R^2 = 0.2$).

Water extractable K and P, and salt extractable K were all positively correlated with %N, %K, and N:P in plant tissue ($R^2 = 0.2-0.4$). Water-extractable NH_4 , Na, and Cl, and salt-extractable Mg and P were positively correlated with %N and N:P in plant tissue ($R^2 = 0.2-0.4$). A higher pH stimulated K concentrations in plant tissue ($R^2 = 0.5$), whereas salt-extractable Al negatively affected K concentrations in plant tissue ($R^2 = 0.2$).

T. latifolia N concentrations, N:P ratio, and N:K ratio were negatively correlated with soil C:N ratio, but positively with water-extractable Mg and Si ($R^2 = 0.2-0.4$). Plant N:P and N:K ratios were higher when

Fig. 3. K removal rates in relation to biomass production (in aboveground biomass harvested in August or September) on rewetted peat and mineral soil sites. Left: *T. latifolia* and *P. australis* stands of ≥ 3 years old ($n = 72$). The R^2 is calculated from the Pearson correlation coefficient ($P < 0.001$). Right: *T. latifolia* stands younger than 3 years, 3 to 5 years old, and ≥ 5 years old ($n = 65$). dm = dry matter.

Fig. 4. Nutrient stoichiometry in aboveground biomass of *P. australis* and *T. latifolia* at peak biomass (harvested in August or September) on rewetted peat and mineral soil sites in ≥ 3 years old stands ($n = 72$). Left: N:P and N:K ratios in plant tissue. Right: %N and %P in plant tissue. The R^2 is calculated from the Pearson correlation coefficient ($P < 0.01$).

water-extractable S, and salt-extractable S and Si were higher ($R^2 = 0.2$ – 0.3). The N:P ratio in plant tissue was negatively correlated with soil total Ca and Mg, and with salt-extractable Fe, but positively with soil total S, Si, and Zn ($R^2 = 0.2$ – 0.3). The N:K ratio in plant tissue was positively correlated with extractable Zn ($R^2 = 0.2$ – 0.3), but negatively with soil total P ($R^2 = 0.2$).

For *P. australis*, soil total Mg, P, and C:N were negatively correlated with N and P concentrations in plant tissue ($R^2 = 0.2$ – 0.6), whereas soil total N content (in g l^{-1} soil) was positively correlated with these tissue nutrient concentrations ($R^2 = 0.2$). Salt-extractable NH_4 correlated positively with plant N and P concentrations ($R^2 = 0.2$ – 0.3). Salt-extractable and water-extractable Mg and S negatively correlated with N concentrations in plant tissue ($R^2 = 0.2$ – 0.4). High soil Fe:P ratios coincided with high concentrations of N, P, and K in plant tissue ($R^2 = 0.2$ – 0.3), whereas the water-extractable Fe:P ratio was negatively

correlated with these concentrations ($R^2 = 0.2$ – 0.4). Water-extractable Si was positively correlated with plant N:P and N:K ratios, and with plant C content ($R^2 = 0.3$ – 0.5). Plant K content was positively influenced by water-extractable P, salt-extractable Fe, and soil OM content ($R^2 = 0.3$ – 0.4).

3.4. Harvest period

The results of harvesting in different periods are shown in Figs. 6 and 7. For *T. latifolia* at the Dutch locations (Fig. 6a), N removal, and biomass production increased with harvests between May and September (peak biomass), whereas K removal decreased after July, and P removal decreased after August. For the German locations, biomass production and nutrient removal of *T. latifolia* peaked in August and decreased afterwards (Fig. 6b). *P. australis* at the German locations also had the highest biomass, P removal, and N removal in August, but K removal was highest in September (Fig. 7). After September, nutrient removal rapidly decreased for both species, as did *T. latifolia* biomass production, whereas *P. australis* biomass production remained quite stable until October.

Water content in harvested biomass decreased between spring and winter, and was lowest in February (Fig. 8). In *T. latifolia*, water content was higher throughout the year and it decreased from 88% to 49%, whereas in *P. australis* it decreased from 66% to 17%.

4. Discussion

4.1. Nutrient removal

The data from our large-scale European wetland survey demonstrate that paludiculture can efficiently remove nutrients from rewetted peat soils and shallow waters. Both *P. australis* and *T. latifolia* had high biomass production and achieved high nutrient uptake rates, and therefore both have a high purification capacity, as regards reducing soil and water eutrophication. The removal of N, P, and K increased almost linearly to values up to 600 kg N ha^{-1} , 80 kg P ha^{-1} , and 450 kg K ha^{-1} with increasing biomass production on rewetted peat soils with spontaneous development of *T. latifolia* and *P. australis* (Figs. 1–3). This shows that these species respond to increased nutrient availability, especially the availability of N as the main limiting nutrient, although they still had not reached their maximal N uptake capacity as no N saturation was observed. Giannini et al. (2019) also found high uptake capacities of 510 kg N ha^{-1} for *T. latifolia* and even $1530 \text{ kg N ha}^{-1}$ for *P. australis*

Fig. 5. OM content of the soil in relation to aboveground biomass production (harvested in August or September) of *T. latifolia* (dashed line) and *P. australis* (dotted line) on rewetted peat and mineral soil sites in stands of ≥ 3 years old ($n = 71$). The dashed line separates mineral soils (left; $< 30\%$ OM) from organic soils (right; $> 30\%$ OM). The R^2 is calculated from the Pearson correlation coefficient. Only for *T. latifolia* there was a very weak significant correlation between OM content of the soil and biomass production ($P < 0.05$). dm = dry matter.

Fig. 6. Relative aboveground biomass production and nutrient removal of *T. latifolia* at different harvest periods throughout the year and subsequent winter ($n = 2-11$ per month). Maximal biomass production and nutrient removal is set to 100%. A: data from Zegveld in 2016 and 2017 (2 locations), Bad Sülze (2 locations), Bugewitz, and Kamp (2 locations) in 2015 and 2016.

in a rewetted Mediterranean peatland with spontaneous vegetation development. Martin and Fernandez (1992) reported an uptake capacity of $1830 \text{ kg N ha}^{-1}$ in a constructed wetland planted with *T. latifolia*.

Generally, *T. latifolia* has a higher maximum nutrient uptake capacity than *P. australis* (Ren et al., 2019; Zak et al., 2014). That *T. latifolia* had higher biomass production and P and K removal capacity than *P. australis* suggests that it may be a more efficient paludiculture crop than *P. australis* for extracting nutrients from surface water and soil, and may therefore be more eligible for ecosystem service payments (Redford and Adams, 2009) and more suitable for nutrient removal schemes (Grosshans, 2014).

The low N:P and N:K ratios and low N content ($<2\%$) of *T. latifolia* biomass (Fig. 4) indicate stronger N limitation than *P. australis*

Fig. 7. Relative aboveground biomass production and nutrient removal of *P. australis* at different harvest periods throughout the year 2011 and subsequent winter 2011/2012. Maximal biomass production and nutrient removal is set to 100%. Data were used from Aalbude, Bad Sülze, Bugewitz (2 locations), Kamp, Triebsees (2 locations), Zithen, Jargelin, Waschow, Bargischow, and Ferne Wiesen ($n = 4-48$).

Fig. 8. Moisture content of *T. latifolia* and *P. australis* aboveground biomass throughout the year. *T. latifolia* data ($n = 2-15$ per month) were used from Zegveld (2 locations), Aalbude (2 locations), Bad Sülze (2 locations), Bugewitz, and Kamp (2 locations). *P. australis* data ($n = 5-75$ per month) were used from Zegveld, Aalbude, Bad Sülze, Bugewitz (2 locations), Kamp, Triebsees (2 locations), Zithen, Jargelin, Waschow, Bargischow, and Ferne Wiesen.

(Koerselman and Meuleman, 1996), resulting in relatively high P and K uptake (on average 27 kg P ha^{-1} and 148 kg K ha^{-1}) compared to *P. australis* (on average 20 kg P ha^{-1} and 103 kg K ha^{-1}). This luxury consumption is also known from other studies (Willby et al., 2001). *P. australis* was less responsive to nutrients, suggesting a higher nutrient use efficiency (Ren et al., 2019). Additionally, our data suggests that *P. australis* may prevail at sites with lower N, K, and P availability in soil or surface water, and will therefore be more sustainable in the long-term if the nutrient supply becomes more depleted.

It is also important to note that N losses are promoted by denitrification (and potentially also anammox) under wet, anaerobic conditions, where denitrification rates of several hundreds of $\text{kg N ha}^{-1} \text{ y}^{-1}$ (up to $1.5 \text{ kg N ha}^{-1} \text{ d}^{-1}$ cf. Veraart et al., 2011) can occur. As soil N mineralization is reduced after rewetting (Bridgman et al., 1998), surface water input of N may become a key factor for the productivity of paludiculture crops. Given a summer biomass production of 10 t dm ha^{-1} , average nutrient removal rates of *T. latifolia* would be 21 kg P ha^{-1} and 120 kg K ha^{-1} . Nutrient removal rates of *P. australis* (14 kg P ha^{-1} , 67 kg K ha^{-1}) would be somewhat lower. These rates largely overlap with P mobilization rates reported for rewetted fertilized peatlands ($10-50 \text{ kg P ha}^{-1} \text{ y}^{-1}$, cf. Van Diggelen et al., 2014; Van de Riet et al., 2013), and it is therefore very likely that paludiculture will prevent substantial downstream eutrophication. However, in some cases natural or constructed wetlands on eutrophic soil can release more nutrients to the surroundings than they receive, but this is most likely during autumn senescence if biomass is not harvested in summer (Fisher and Acreman, 2004). Additional depletion of soil P can be expected at sites with high *T. latifolia* biomass production that tend to have higher rates of P removal depending on additional N supply from surface water and upwelling groundwater. K depletion may become important in productive *T. latifolia* stands and eventually also in *P. australis* stands that are harvested in summer (Van Duren et al., 1997). Winter harvest will allow for nutrient reallocation to belowground organs and may therefore stabilize plant-available K pools in the long-run.

4.2. Sustainable biomass production and C sequestration

The average biomass production of *P. australis* and *T. latifolia* in this survey was higher than the mean dry matter yield of drained and fertilized grasslands ($11 \text{ t dm ha}^{-1} \text{ y}^{-1}$) receiving total N loads of $>400 \text{ kg ha}^{-1} \text{ y}^{-1}$ (Oenema et al., 2012). Under the most suitable conditions (i.e. high N availability) summer harvest of both plants exceeded $15 \text{ t dm ha}^{-1} \text{ y}^{-1}$ up to $20-30 \text{ t dm ha}^{-1} \text{ y}^{-1}$ in our field study, which is even similar to maize yields (Giannini et al., 2017). These very high biomass production rates were also found in other studies (Heinz, 2012;

Köbbing et al., 2013; Grosshans, 2014; Gelbrecht et al., 2008; Vymazal and Kröpfelová, 2010). The hydrology on these locations was optimal for the growth of *T. latifolia* and *P. australis*, often leading to monospecific stands with a high biomass quality. This means that besides removing nutrients, the harvested biomass can also be used to effectively sequester C in several long-lasting biomass products (Wichtmann et al., 2016; Svedarsky et al., 2019). However, *P. australis* will sequester more C in the long-term than *T. latifolia*, as it is a peat forming plant species (Van den Berg et al., 2016), which makes it a more interesting species for creating a negative GHG balance (Tanneberger and Wichtmann, 2011).

Surprisingly, some young stands of *T. latifolia* already produced 10 t dm ha⁻¹ y⁻¹ or more without extra nutrient input besides the >100 kg N ha⁻¹ that was available in soil and water. Ren et al. (2019) showed that *T. latifolia* and different clones of *P. australis* could also grow quite well at lower nutrient loads (37.5 kg N ha⁻¹ y⁻¹) with a substantial biomass production (>10 t dm ha⁻¹ y⁻¹). This means that a significant, economically attractive biomass production of these species can even be reached at low N loads (Ren et al., 2019) or at low foliar N:P ratios (Vroom et al., 2018). Differences in biomass production and nutrient removal between 3 to 5 year old stands and ≥5 year old stands of *T. latifolia* were mainly driven by 3 sites, which means that nutrient removal potential largely overlaps and that 3 year old stands can already be considered mature.

4.3. Interaction between soil conditions and biomass characteristics

Surprisingly, we did not find biomass production of *T. latifolia* and *P. australis* to be affected by soil OM content (Fig. 5). Cole et al. (2001) also found no relationship between biomass production and soil OM in constructed wetlands. Most other studies report higher biomass production in organic soils than in mineral soils (Lenssen et al., 1999), but this is often related to the associated difference in nutrient availability between these soil types when external nutrient loading is low. Presence or absence of a peat soil is therefore not a requirement for high biomass production, provided that nutrient availability is sufficiently high. However, extra benefits in terms of ecosystem services compared to traditional drainage-based land use, such as GHG emission reduction, counteraction of soil subsidence, and peat preservation, are provided only when paludiculture crops are grown on wet and rewetted peat soils (Knox et al., 2015; Geurts et al., 2019).

Most other soil characteristics only showed weak correlations with biomass production and plant nutrient uptake. As expected, *T. latifolia* had high plant N concentrations and also high N:P and N:K ratios on sites with a low soil C:N ratio. However, soil extractable nutrients (NH₄ and P) were negatively correlated with biomass production and nutrient uptake by *T. latifolia*. For the total nutrient availability over time, external input by surface water inflow, groundwater supply, and atmospheric deposition have to be included next to the actual stocks in the soil. These patterns therefore merely reflect higher uptake of easily available nutrients at higher biomass production, as soil samples were taken in August or September when biomass production peaked. This leads to a lower nutrient availability in the soil and accumulation of nutrients in the plant (Willby et al., 2001). In addition, only healthy stands were used in our data analyses, because factors other than soil characteristics may have played a predominant role in the development of unhealthy stands.

Therefore, it is difficult to define a range of soil conditions from our dataset that is suitable for paludiculture with *T. latifolia* and *P. australis*. It is, however, well-known that both species grow well in a very broad abiotic range (Brix et al., 2010). With respect to pH, for instance (Brix et al., 2002; Calheiros et al., 2008), both species only suffer from pH values below 4 to 4.5 because of lower cation availability and nutrient uptake (Dyhr-Jensen and Brix, 1996) or ammonium toxicity (only for *P. australis*; Tylová et al., 2008). Such low pH values were not observed in our study, and soil extractable cations like Mg, Mn, and K

were even negatively correlated with biomass production and nutrient removal rates of *T. latifolia*. Hence, concentrations of these cations were not limiting plant growth in our investigated wetlands. Overall, this means that plant characteristics, including nutrient content and biomass production, will give a better indication of the efficiency of paludiculture than soil characteristics.

4.4. Implications for management and biomass use

There are various options for biomass use depending on the harvest period and frequency. The actual harvest date is crucial for each specific application, as it determines biomass quality (fodder value, protein content, water content, fiber content, combustion traits), biomass production, nutrient removal, and potential for regrowth. This is also dependent on differences between locations in terms of soil characteristics and climatic conditions, which deserve further study. Maximal nutrient removal will be reached in summer at peak biomass. Harvesting in winter will lower biomass production by 30–50% compared to summer harvesting, but still with reasonable nutrient removal rates for *T. latifolia* that are about two times higher than for *P. australis* (Figs. 6 and 7).

Summer biomass can be used for the production of biogas or fiber-rich fodder (Sahito et al., 2015; Dragoni et al., 2017). To obtain an optimal fodder value, *T. latifolia* biomass should be harvested in spring when protein content is highest (Pijlman et al., 2019). Biomass that is harvested in winter, preferably after a frost period, can best be used for producing insulation or building materials because of the lower water content. As *T. latifolia* has a higher water content than *P. australis* in winter (Fig. 8), pre-drying is needed for most applications, although new techniques are being developed for which wetter biomass can be used (e.g. production of mycelium-based materials; Elsacker et al., 2019). Water content in *P. australis* winter biomass is already often below the threshold of 15–30%, under which biomass can be used for combustion or thatching without pre-drying (Lewandowski et al., 1995; Hartmann, 2009; Köbbing et al., 2013).

Late harvest concepts can be suitable management tools for improving biomass quality, as previously shown for biofuel utilization of *P. australis* (Kask et al., 2013; Giannini et al., 2016). Plant nutrient content is also influenced by different processes including relocation from shoots to rhizomes at the end of the growing season, leaf shading, and nutrient leaching by precipitation (Granéli, 1984). To further improve biomass quality there is also a need for application-related management, e.g. harvesting *T. latifolia* in spring before inflorescences are set. *T. latifolia* inflorescences in the winter harvest reduce the biomass quality for some uses (e.g. pelleting) and can be a problem for mechanical harvesting. Harvesting more than once a year is also possible if nutrient availability is sufficient (Dragoni et al., 2017; Pijlman et al., 2019). However, long-term effects of early or multiple harvests on biomass regrowth and quality are still unclear. The harvest period depends on the aim of paludiculture, which can either be optimal nutrient removal, biomass production for a specific application, or nature conservation.

Nitrogen is an important growth limiting factor for paludiculture crops after rewetting (Vroom et al., 2018) as it limits biomass production and nutrient removal capacity (P and K) of fast-growing species like *T. latifolia* and *P. australis*. The use of N-rich surface water, groundwater, or farm run-off could increase the bioavailability of N and enhance wetland ecosystem services even further, such as water purification, nutrient extraction from the soil, and nutrient removal by biomass harvest. This could stimulate farmers to efficiently use N and P from their farm effluents and comply with environmental legislation concerning nutrient losses (Land et al., 2016). Paludiculture can then serve as a water and nutrient buffer zone between drained agricultural areas and wetland nature reserves, which can also create additional income for landowners beyond biomass revenues, when payments schemes for ecosystem services are established (Redford and Adams, 2009; Tanneberger and Wichtmann, 2011). However, a high N load is

not a prerequisite for paludiculture. Considerable biomass production can be achieved with lower N loads (Ren et al., 2019), because background loads of atmospheric N deposition ($>20 \text{ kg ha}^{-1} \text{ y}^{-1}$ in the Netherlands), N mineralization in the soil ($65 \text{ kg ha}^{-1} \text{ y}^{-1}$; Grootjans et al., 1985), and N fixation by the crop itself ($18 \text{ kg ha}^{-1} \text{ y}^{-1}$; Biesboer, 1984) are often significant.

5. Conclusion

Biomass production on rewetted peat and mineral soils allows a high biomass production ($10\text{--}30 \text{ t dm ha}^{-1} \text{ y}^{-1}$) together with other important wetland ecosystem services: water purification, carbon sequestration ($4\text{--}14 \text{ t C ha}^{-1}$), nutrient removal ($100\text{--}600 \text{ kg N ha}^{-1}$, $10\text{--}80 \text{ kg P ha}^{-1}$, and $50\text{--}450 \text{ kg K ha}^{-1}$), water retention, water storage, and peat preservation. Because *T. latifolia* and *P. australis* absorb substantial amounts of nutrients, their harvest can be an effective measure to control nutrient effluxes from rewetted sites. In our study *T. latifolia* and *P. australis* were able to produce significant biomass on a large range of rewetted soils, even at low nutrient loads, making these species very suitable for broad implementation in paludiculture across Europe. However, tissue nutrient concentrations and nutrient ratios were species-specific and therefore nutrient removal potential also differed between species.

Harvesting turns out to be an important management tool that can optimize biomass production and quality in relation to nutrient removal and carbon storage in plant organs. Requirements for biomass quality differ strongly between applications (solid biofuel, biogas, fodder, or building material) and can be adjusted to specific site conditions. In winter, especially *T. latifolia* can still provide reasonable biomass production and nutrient removal rates. Further research is needed to optimize nutrient dynamics for a long-term perspective of paludiculture.

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CRedit authorship contribution statement

Jeroen J.M. Geurts: Investigation, Data curation, Formal analysis, Writing - original draft. **Claudia Oehmke:** Investigation, Data curation, Writing - original draft, Visualization. **Carla Lambertini:** Investigation, Writing - review & editing. **Franziska Eller:** Investigation, Writing - review & editing. **Brian K. Sorrell:** Investigation, Writing - review & editing. **Samuel R. Mandiola:** Investigation. **Albert P. Grootjans:** Investigation, Writing - review & editing. **Hans Brix:** Supervision. **Wendelin Wichtmann:** Writing - review & editing, Supervision. **Leon P.M. Lamers:** Writing - review & editing, Supervision. **Christian Fritz:** Investigation, Writing - review & editing, Supervision.

Declaration of competing interest

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

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