

Vegetation growth and sediment dynamics in a created freshwater wetland

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ABSTRACT

Understanding how the hydrological regime in relation to sediment type interferes with ecosystem development is important when wetlands are created with soft muddy material. Especially when plants are used as ecological engineers to promote crest stability and soil formation. We carried out a two-year mesocosm experiment with sediments derived from the Dutch lake Markermeer to identify the effects of the hydrological regime and sediment type on ecosystem functioning in terms of nutrient availability. We measured plant productivity, plant nutrient stoichiometry, and concentrations of N, P, and K in shoots and roots of *Phragmites australis* and *Rumex maritimus* and monitored how the clay-rich sediment from lake Markermeer changed into a wetland soil. Plants grown on Markermeer sediments tend to be N limited when periodically inundated and P limited when not inundated at all. The P availability was determined by the hydrological regime, while the N availability was determined by both the hydrological regime and the sediment type. Ecosystem development on created wetlands can be manipulated by adequate management of the hydrological regime, as plant species respond differently to changes in nutrient availability. This should be considered in eco-engineering projects where plants are used as ecological engineers to fasten ecosystem development on wetlands that are to be created from clay-rich material.

1. Introduction

Wetlands are among the most valuable biomes on our planet providing important ecosystem services such as nutrient cycling, soil formation and wastewater treatment (Costanza et al., 1997; Zedler and Kercher, 2005). In the past 100 years, vast areas of wetlands have disappeared, but programs have been initiated to restore and create wetlands to compensate for this loss (e.g. Mitsch et al., 1998; Verhoeven, 2014). Although most created wetlands have been designed for wastewater treatment (Vymazal, 2011), they can also be designed to increase the ecological value of the ecosystem itself (e.g. Weller et al., 2007; Whigham et al., 2007; Stefanik and Mitsch, 2012). When designing such ecosystems, natural processes are oftentimes used to promote self-design, fasten ecosystem development and to replace conventional engineering structures (Mitsch, 1998). This concept is called ecological engineering and is implemented globally nowadays (Temmerman et al., 2013). However, to make ecological engineering projects successful, it is essential to understand how ecological, geo-mechanical and hydrological processes interact before making any decision on the design of such a project.

An important factor when creating wetlands is the hydrological regime as it determines the plant community and the speed of

ecosystem development (Ernst, 1990; Seabloom et al., 1998; Bernhardt and Koch, 2002; Casanova and Brock, 2002). Periodical inundation often speeds up ecosystem development although the effectivity is unclear. For example, Peterson and Baldwin (2004) showed that flooding significantly decreased plant biodiversity in a freshwater wetland, but Brock et al. (1999) argued that when flooding regimes are managed correctly in terms of depth and duration of the flood, the number of habitat types increases, in turn positively affecting species richness. How wetland ecosystems respond to changes in the hydrological regime also depends on the geochemical composition, as it determines the biogeochemical processes that are induced when the water saturation gets altered (Speelman et al., 2007). For example, oxidation of pyrite can lead to severe acidification of soils, negatively impacting the environment by potential heavy metal release (Golez and Kyuma, 1997). On the other hand, if the sediment contains high amounts of iron-bound phosphorus, alternating water regimes can affect ecosystem development by inducing P mobilization (Satawathanont et al., 1991; Portnoy, 1999; Lamers et al., 2012).

Understanding how the hydrological regime influences ecosystem development in relation to sediment type is important when the concept of ecological engineering is used. Oftentimes, fast initial plant growth is a prerequisite for vegetation to act as ecological engineers,

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especially when wetlands are created with soft muddy material. Wetland creation in lake Markermeer, a lake in the Netherlands located northeast of Amsterdam, is an example. In this lake, a part of the soft clay-rich lake-bed sediment is currently being dredged and used as a building material in creating approximately 10,000 ha of wetland.

Two distinct layers from the lake bed can be used as substrate for the wetlands: the relatively undisturbed consolidated near-shore Holocene marine deposits and the disturbed soft mud layer on top of these deposits. Saaltink et al. (2016, 2017a) showed that these layers have a very distinct geochemical composition, also in terms of pyrite, iron-bound phosphorus and nutrients. The soft clay-rich layer is produced by bioturbation and physical weathering of the near-shore marine deposits and continuously resuspends because of wave action (Van Kessel et al., 2008; De Lucas Pardo et al., 2013).

To improve crest stability and promote soil formation on these artificial wetlands, it is important to understand how the hydrological regime could interfere with ecosystem development and what type of sediment functions best as building substrate. Because conducting small scale experiments can be an effective method to anticipate ecological engineering designs that might follow if implemented on a larger scale (Odum and Odum, 2003), we carried out a mesocosm experiment to identify the effects of the hydrological regime – i.e. periodical inundation vs no inundation – and the sediment type on ecosystem functioning in terms of nutrient availability. To reach this aim, we measure plant productivity, plant nutrient stoichiometry, and concentrations of N, P, and K in shoots and roots of *Phragmites australis* and *Rumex maritimus*. Subsequently, we monitor how the clay-rich sediment from lake Markermeer is changing into a wetland soil by regularly measuring geochemical variables of the sediment. We hypothesize that the hydrological regime especially influences the P availability as Markermeer sediments are rich in pyrite and Fe-P (Saaltink et al., 2016), and alternating water regimes may result in P mobilization as reduction of sulfate decouples iron from phosphorus. We, therefore, expect that in sediments that are periodically inundated more P is available for plants than in sediments that receive no inundation. Since N is available in reduced (i.e. NH_4) as well as oxidized (i.e. NO_x) conditions, N availability is expected to be determined by the sediment type. This study will enhance knowledge on how the interplay between the hydrological regime and the sediment type influences ecosystem functioning by determining nutrient availability. Consequently, applications for management practices in ecological engineering projects can be extracted.

2. Materials and methods

2.1. Experimental mesocosms

A greenhouse experiment was conducted for 2 growing seasons at the greenhouse test facility of Utrecht University in the period April 2015–November 2016. Mesocosms (diameter 30 cm, height 80 cm) were filled up to 50 cm with one sediment type from lake Markermeer. The sediment types were collected in March 2015 by mechanical dredging at a location (coordinates 52.5462N; 5.3878E) within the dredging area assigned for the collection of building material for the wetlands (Flach, 2014). The sediment types used are composed of the sediment from the soft, clay-rich layer (0–10 cm depth) and the underlying, consolidated, near-shore marine deposit of Holocene origin (10–50 cm depth); these sediments are hereafter referred to as mud and clay, respectively. Sediments were stored in air-tight containers at 4 °C prior to the start of the experiment.

Two species were selected to be transplanted in the mesocosms: 1. *Rumex maritimus* (golden dock) – an annual or biennial, dicotyledonous plant species – was chosen because this plant was frequently found on the pilot wetland in lake Markermeer during monitoring studies (Dankers et al., 2015), and 2. *Phragmites australis* (common reed) – a perennial, monocotyledonous plant species – was selected because it is

foreseen that this plant is used as eco-engineering species on the wetlands. Plants were grown from seeds for c. 40 days on nutrient-poor turf soil before transplantation into the mesocosms. Each mesocosm started with three seedlings of *R. maritimus* and three seedlings of *P. australis* (i.e. six seedlings in total). Tinfoil was attached to the inner walls of the mesocosms to improve the light conditions for the seedlings.

Mesocosms were either periodically inundated or received weekly irrigation water. Following Güsewell et al. (2003) and Banach et al. (2009), the periodically inundated mesocosms were flooded for 7 weeks to a height of 10 cm above the sediment, after which the water was removed and the sediment could dry for two weeks. Drying is important for consolidating the soft building material so alternating dry and wet periods should be preferred over long-term inundation. The mesocosms that were not inundated received 17.3 mm water every week, which corresponds to a total water supply of 900 mm yr^{-1} . However, to prevent water stress in the plants grown in the non-inundated mesocosms an extra dose of water was added when temperatures in the greenhouse increased to 30 °C or more (some weeks in July and August). For both hydrological conditions Markermeer water was used, thereby avoiding any impact on sediment geochemistry and plant function caused by chemical differences. Because lake Markermeer is nutrient limited with low values of nitrate, ammonium and phosphate (Noordhuis et al., 2014), nutrient concentrations in the water added to the mesocosms were low, averaged at $0.1 \text{ mg NO}_3^- \text{ L}^{-1}$, $0.01 \text{ mg NH}_4^+ \text{ L}^{-1}$, and $< 0.003 \text{ mg PO}_4^{3-} \text{ L}^{-1}$ (Ministry of Infrastructure and the Environment, 2016).

Six mesocosms were used for each sediment – hydrology combination (24 in total). Seedlings from other plants that spontaneously emerged in the mesocosms were removed immediately.

2.2. Data collection

Aboveground biomass was clipped after each growing season (i.e. November 2015 and November 2016). At the end of the experiment, belowground biomass was measured for three mesocosms per condition (12 in total) by thoroughly washing and sieving the sediment. Plant material was separated per plant species, air-dried for 48 h at 70 °C, weighed, clipped and mixed prior to chemical analysis. Tissue was randomly selected and ground to determine contents of K and P using total reflection X-ray fluorescence (S2 Picofox, Bruker) and N using a CN analyzer (NA1500, Fisons Instruments). Total uptake was calculated by multiplying biomass with tissue concentration.

The sediment samples were collected at the start of the experiment and were freeze-dried prior to geochemical analysis. Elemental contents of Al, Ca, Fe, K, Mg, Mn, Na, P, Sr, Ti, and Zn were determined using ICP-OES following aqua regia destruction. Sulfur contents were measured on an elemental CS analyzer (CS-300, LECO) and the N contents were determined on a CN analyzer (NA1500, Fisons Instruments). Quantitative bulk mineralogical compositions of the crystalline fraction of the sediments were determined by Rietveld refinement from the X-ray diffraction patterns (Scarlett and Madsen, 2006). Organic matter was determined by slowly heating to 550 °C and then calculating the weight loss between 105 and 550 °C (Howard, 1965). A sequential extraction method based on Ruttenberg (1992) was applied to characterize solid P speciation and to determine the content of iron oxides (Table 1). The extractable content of iron oxides was measured from the citrate-dithionite-bicarbonate (CDB) filtrate from the second step using ICP-OES. All geochemical analyses were carried out for 5 replicates per sediment type, except for the XRD analysis (1 replicate per sediment type).

In addition, sediment samples from the topsoil (0–2 cm) were collected in each mesocosm at $t = 6, 11,$ and 18 months as in the topsoil highest geochemical effects caused by the vegetation are expected (Saaltink et al., 2016). These samples were freeze-dried and analyzed immediately in terms of solid P speciation, extractable iron oxides, N and organic matter contents.

Table 1

List of steps used in the extraction procedure of phosphorus (based on Ruttenberg, 1992).

Step	Extractant	Separated P fraction
I	1 M MgCl ₂ , 30 min	Exchangeable or loosely sorbed P
II	A Citrate-dithionite-bicarbonate (CDB), 8 h	Easily reducible or reactive ferric Fe- P
	B 1 M MgCl ₂ , 30 min	
III	A Na acetate buffer (pH 4), 6 h	Amorphous apatite and carbonate P
	B 1 M MgCl ₂ , 30 min	
IV	1 M HCl, 24 h	Crystalline apatite and other inorganic P
V	Ash at 550 °C, 2 h; 1 M HCl, 24 h	Organic P

At the end of the experiment, three replicate samples per mesocosm at 10, 20, and 30 cm depth were retrieved with a gouge (diameter 3 cm), and repeated for three mesocosms per experimental condition. The sediment samples at the same depth were pooled per mesocosm and chemically analyzed in terms of solid P speciation, extractable iron oxides, N and organic matter contents.

2.3. Statistical analyses

Statistical analysis was carried out using SPSS 22.0.0.1. Differences in biomass production, plant tissue concentrations and total uptake of N, P, and K as well as the N:P and N:K ratios between treatments were determined using univariate, general models with a least square difference (LSD) post hoc test ($p < 0.05$) following Webster (2007). From these GLMs, significant interaction effects between the sediment type and the hydrological regime were also identified. To correct for seasonal effects (season 1 vs. season 2), we included time as a fixed factor in our models when assessing significant differences between the treatments. These GLMs were carried out for *R. maritimus* and *P. australis* separately. Significant differences between *R. maritimus* and *P. australis* within treatments were determined using one-way ANOVA with LSD post hoc testing ($p < 0.05$). Differences in geochemical composition of mud and clay were assessed with a *t*-test ($p < 0.05$). No statistics could be applied to the mineralogical sediment composition (XRD analysis) due to absence of replicates, however.

3. Results

3.1. Geochemical and mineralogical composition of lake markermeer sediments

Table 2 presents the geochemical and mineralogical composition of mud and clay. All analyzed major elements (Al, Ca, Fe, K, Mg, Mn, Na, P, S, Sr, and Zn) except for Ti, were significantly higher in mud than in clay ($p < 0.05$ as indicated with an asterisk in Table 2). Sequential P extraction revealed that the significantly higher values in total P in mud (361 mg kg^{-1}) than in clay (213 mg kg^{-1}) ($p < 0.001$) is attributed to significantly higher values for mud in Fe-P ($p < 0.01$), amorphous apatite and carbonate P (Ca-P) ($p < 0.01$) and organic P ($p < 0.001$); exchangeable P and crystalline apatite and other inorganic P (detrital P) did not differ significantly ($p = 0.10$ for exchangeable P; $p = 0.32$ for detrital P).

Relatedly, the two sediment types also differ with respect to their mineralogical composition. The quartz content was higher in clay, whereas the amounts of calcite and pyrite were higher in mud. In total, the amount of non-phyllsilicates (sum of quartz, plagioclase, alkali feldspar, calcite, dolomite, oxides/hydroxides and pyrite) was higher in clay (83.2%) than in mud (73.7%). As a consequence, the amount of phyllsilicates (sum of illite, smectite, kaolinite, and chlorite) was higher in mud than in clay: 26.3% vs 16.8%, i.e. the mud contains more swelling clay minerals.

Table 2Geochemical and mineralogical composition of clay and mud at the start of the experiment ($t = 0$). Average concentrations in dry wt with standard deviations ($n = 5$). Significant differences between clay and mud are indicated by an asterisk ($p < 0.05$).

	Unit	n	Clay	S.D.	Mud	S.D.
<i>Aqua regia/CS/CN</i>						
Al*	mg kg ⁻¹	5	4670	365	10398	219
Ca*	mg kg ⁻¹	5	25872	1661	48058	1288
Fe*	mg kg ⁻¹	5	6538	391	14766	234
K*	mg kg ⁻¹	5	1251	106	2619	72
Mg*	mg kg ⁻¹	5	2674	128	5106	135
Mn*	mg kg ⁻¹	5	161	9	360	10
N*	mg kg ⁻¹	5	617	62	1611	32
Na*	mg kg ⁻¹	5	49	13	97	34
P*	mg kg ⁻¹	5	213	7	361	10
S*	mg kg ⁻¹	5	1191	111	4513	187
Sr*	mg kg ⁻¹	5	70	5	113	3
Ti	mg kg ⁻¹	5	380	23	396	17
Zn*	mg kg ⁻¹	5	88	5	130	3
<i>Seq. P extraction</i>						
Exchangeable P	mg kg ⁻¹	5	3	1	5	2
Fe-bound P*	mg kg ⁻¹	5	14	2	40	10
Ca-bound P*	mg kg ⁻¹	5	42	8	89	18
Detrital P	mg kg ⁻¹	5	148	14	158	14
Organic P*	mg kg ⁻¹	5	16	1	47	11
Fe as oxides*	mg kg ⁻¹	5	508	40	851	39
<i>XRD</i>						
Quartz	%	1	59.8		45.8	
Plagioclase	%	1	8.7		8.2	
Alkali feldspar	%	1	4.6		3.7	
Calcite	%	1	7.3		11.9	
Dolomite	%	1	2.8		2.8	
TiO ₂	%	1	0.3		0.4	
Pyrite	%	1	0.4		1.0	
Phyllsilicates	%	1	16.8		26.3	
<i>Other</i>						
Organic matter*	%	5	2.6	0.2	4.0	0.1

3.2. Geochemical changes in the topsoil

Fig. 1 presents the dynamics of the sediment concentrations of the topsoil (0–2 cm) of the iron oxides, phosphorus pools, N and organic C during the experimental period for the four different treatments. Significant differences between time steps are presented in a supplement (Online Resource 1). Throughout the experiment, the concentrations of these solid compounds were higher in mud (dotted and solid grey lines) than in clay (dotted and solid black lines) ($p < 0.05$), except for detrital P ($p < 0.25$, Fig. 1d). Interestingly, no significant changes were observed due to the different hydrological conditions, except for Ca-P, which was significantly higher in the non-inundated condition in mud ($p < 0.05$, dotted grey line).

Oxidation of the topsoil resulted in a linear increase of iron oxides regardless of the hydrological condition and sediment type (Fig. 1a). A similar increase was observed for the Fe-P concentration in the first 10 months, after which it stabilized during the second growing season ($t = 10$ and 18 months) for the periodic inundated conditions (Fig. 1b). The Fe-P content in the non-inundated conditions decreased significantly between month 10 and 18 ($p < 0.001$). In contrast to the Fe-P concentrations, Ca-P decreased in the first 10 months in mud, after which it increased significantly for both hydrological conditions ($p < 0.01$) (Fig. 1c). These opposed temporal changes in Ca-P and Fe-P are true for mud but not for clay.

Detrital P and organic P varied throughout the experiment, but the concentrations at $t = 18$ months did not differ significantly from the concentrations measured at the start of the experiment (Fig. 1d,e), except for clay that was periodically inundated: the concentration of organic P was significantly higher at $t = 18$ months ($p < 0.05$). Despite the changes described above, the total P concentrations stayed more or less stable with only periodically inundated clay being significantly

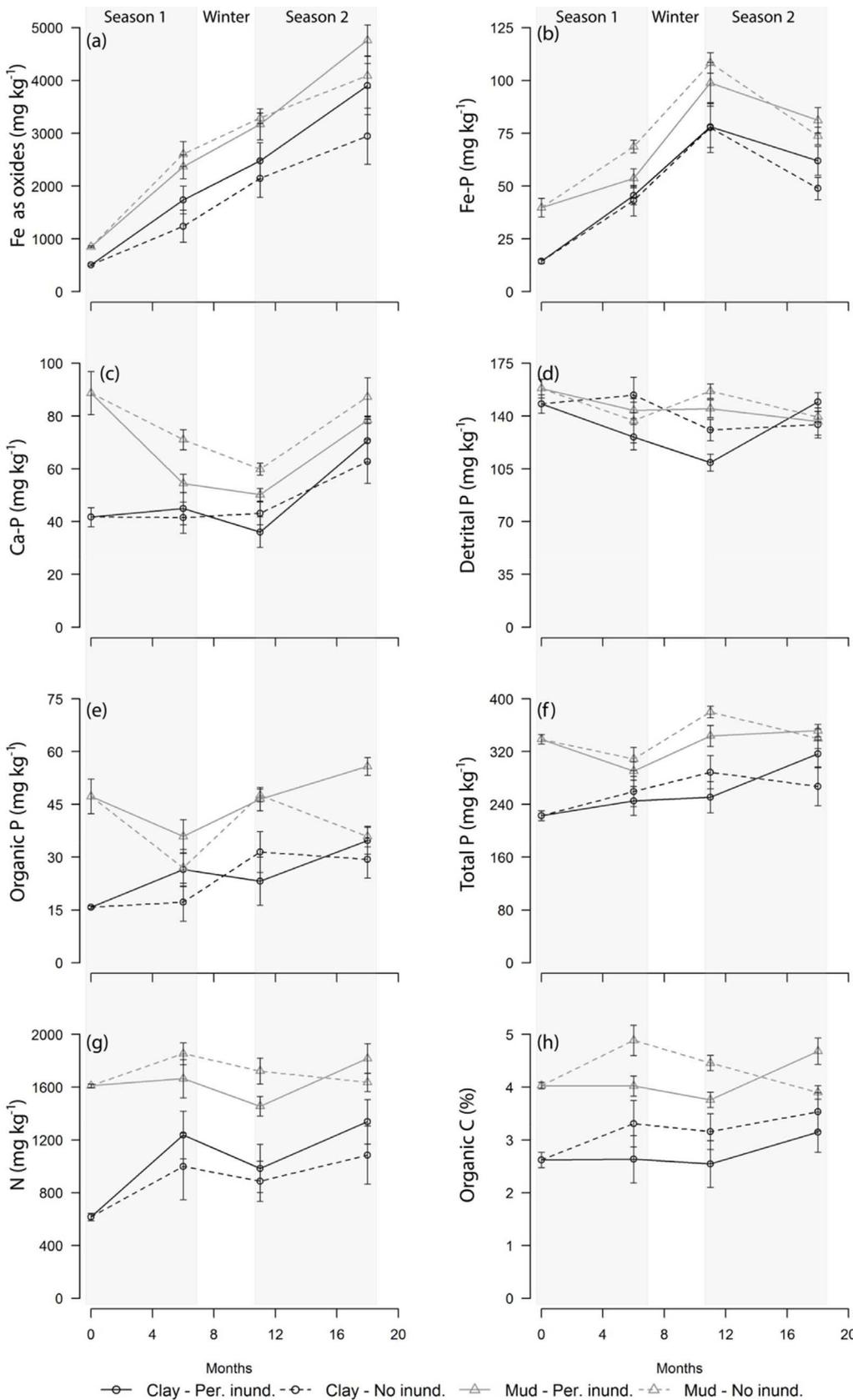


Fig. 1. Time series of geochemical variables in the topsoil (0–2 cm) (n = 6): Fe as oxides (a), iron-bound P (Fe-P) (b), amorphous apatite and carbonate P (Ca-P) (c), crystalline apatite and other inorganic P (Detrital P) (d), Organic P (e), Total P (f) and N (g) in mg kg^{-1} and organic C (h) in%. Error bars indicate S.E.

higher at the end of the experiment ($p < 0.01$) (Fig. 1f). The concentration of N in clay was significantly higher at the end of both growing seasons ($t = 6$ and $t = 18$) compared to the start for periodically inundated clay ($p < 0.01$) (Fig. 1g). No differences were

observed for organic C (Fig. 1h). In general, the sediment type mainly affected changes in the geochemical composition of the topsoil, while the hydrological regime had only a marginal effect.

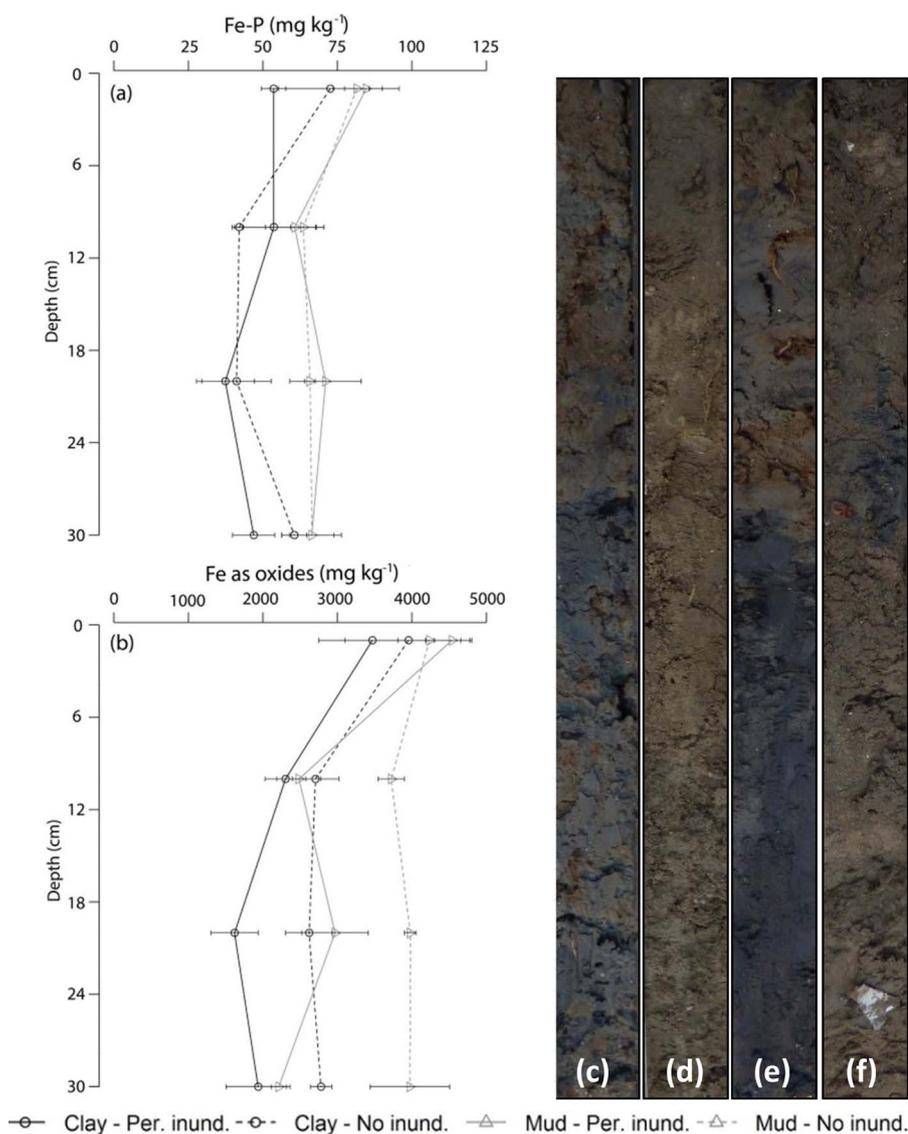


Fig. 2. Sediment depth profile for iron-bound P (Fe-P) (a) and Fe as oxides (b) in mg kg^{-1} (\pm S.E.) at $t = 18$ months ($n = 9$). Random photographs of a sediment core in periodically inundated clay (c), non-inundated clay (d), periodically inundated mud (e) and non-inundated mud (f) of 30 cm depth.

3.3. Sediment depth profile

Fig. 2 presents a depth profile for the concentrations of Fe-P and iron after 18 months. Interesting is that no significant difference was observed between the hydrological conditions for the Fe-P concentration (Fig. 2a). Mud had significantly higher concentrations throughout depth than clay ($p < 0.01$). In contrast, iron oxides were significantly higher in the sediments that were not inundated ($p < 0.05$ for both clay and mud) (Fig. 2b), meaning that periodical inundation did not inhibit oxidation processes at the top soil, but clearly had an effect on oxidation processes at larger depth. In the periodically inundated sediments, concentrations of iron oxides decreased in mud from 3500 mg kg^{-1} at the topsoil to 1900 mg kg^{-1} at 30 cm depth and for clay from 4500 mg kg^{-1} to 2200 mg kg^{-1} . Remarkably, the concentrations at 30 cm depth were higher than the initial concentrations as presented in Table 2 (508 mg kg^{-1} in clay and 851 mg kg^{-1} in mud).

3.4. Plant tissue composition

Table 3 shows how sediment type and the hydrological condition affected the average concentrations of N, P, and K and the N:P and N:K ratios in leaves and roots for *P. australis* and *R. maritimus*. Significant differences between the sediment types are indicated by orange rectangles and significant differences between the hydrological conditions

are indicated by blue rectangles.

The uptake of N was significantly higher in non-inundated mud and clay for roots of *P. australis* ($p < 0.05$ for clay; $p < 0.01$ for mud) and for roots and shoots of *R. maritimus* grown in mud ($p < 0.001$). More generally, periodical inundation had a negative effect on N uptake although not always statistically significant. This effect was more pronounced in *R. maritimus* than in *P. australis*. The N concentrations were furthermore higher in plants grown in mud than in clay, which was significant for roots in *P. australis* ($p < 0.05$) and for roots and shoots in *R. maritimus* ($p < 0.001$ for roots and shoots) grown in the non-inundated sediment. This is in line with the finding that the N concentration in mud was significantly higher than in clay (Table 2, Fig. 1c). So, both the hydrological regime and the sediment type affected the N tissue concentration for both species. Moreover, a significant ordinal interaction effect between the sediment type and the hydrological regime was found for shoots in *R. maritimus* ($F(1, 44) = 13.205$, $p = 0.001$), further indicating that the effect of the hydrological regime depends on the sediment type (and vice versa).

In contrast to N, the average P concentrations were higher in plants grown in the periodically inundated sediments, meaning that wetter conditions enhance P uptake. This was significant for roots and shoots of *P. australis* ($p < 0.001$ for shoots; $p < 0.01$ for roots), although *R. maritimus* had highest P concentrations in the shoot. No clear differences were found between clay and mud, while total P and other P

Table 3

Average concentration (\pm S.E.) of N, P, and K (% of dry wt) as well as N:P and N:K ratio in shoots ($n = 12$; season 1 and season 2) and roots ($n = 3$; season 2) of *P. australis* and *R. maritimus* for the sediment types (Clay and Mud) and the hydrological regimes (periodical inundation = Per. inund.; no inundation = No inund.). A significant difference ($p < 0.05$) between mud and clay is indicated by orange rectangles (i.e., horizontal configuration) and a significant difference ($p < 0.05$) between periodical inundation and no inundation is indicated by blue rectangles (i.e., vertical configuration).

Element	Plant species	<i>P. australis</i>			<i>R. maritimus</i>			
		Hydrology	Clay	Mud	S.E. sed.	Clay	Mud	S.E. sed.
N	Shoot	Per. inund.	1.44	1.54	± 0.06	1.15	1.12	± 0.08
		No inund.	1.62	1.67	± 0.07	1.40	1.90	± 0.15
		S.E. hydrology	± 0.06	± 0.07		± 0.08	± 0.17	
	Root	Per. inund.	0.53	0.67	± 0.05	0.57	0.64	± 0.02
		No inund.	0.88	1.20	± 0.11	0.91	2.13	± 0.37
		S.E. hydrology	± 0.10	± 0.13		± 0.09	± 0.41	
P	Shoot	Per. inund.	0.13	0.14	± 0.01	0.25	0.25	± 0.02
		No inund.	0.09	0.07	± 0.01	0.21	0.18	± 0.02
		S.E. hydrology	± 0.01	± 0.01		± 0.02	± 0.02	
	Root	Per. inund.	0.12	0.14	± 0.01	0.08	0.13	± 0.02
		No inund.	0.05	0.06	± 0.01	0.14	0.08	± 0.03
		S.E. hydrology	± 0.02	± 0.02		± 0.04	± 0.02	
K	Shoot	Per. inund.	1.66	1.49	± 0.05	2.44	2.51	± 0.16
		No inund.	1.65	1.52	± 0.07	2.60	3.16	± 0.28
		S.E. hydrology	± 0.06	± 0.06		± 0.27	± 0.21	
	Root	Per. inund.	1.42	1.73	± 0.15	1.17	1.62	± 0.14
		No inund.	1.43	1.49	± 0.25	1.04	1.04	± 0.34
		S.E. hydrology	± 0.19	± 0.21		± 0.33	± 0.31	
N:P ratio	Shoot	Per. inund.	11.1	11.8	± 0.52	5.0	5.1	± 0.52
		No inund.	19.9	28.1	± 2.29	8.0	14.0	± 1.72
		S.E. hydrology	± 1.50	± 2.50		± 0.74	± 1.84	
	Root	Per. inund.	4.6	4.7	± 0.27	7.1	5.1	± 0.76
		No inund.	18.1	24.8	± 3.00	13.0	28.2	± 5.76
		S.E. hydrology	± 3.18	± 5.10		± 6.16	± 5.84	
N:K ratio	Shoot	Per. inund.	0.88	1.07	± 0.05	0.51	0.46	± 0.05
		No inund.	1.01	1.12	± 0.05	0.66	0.85	± 0.07
		S.E. hydrology	± 0.05	± 0.05		± 0.06	± 0.07	
	Root	Per. inund.	0.39	0.40	± 0.05	0.48	0.40	± 0.03
		No inund.	0.71	0.90	± 0.13	1.64	2.95	± 0.63
		S.E. hydrology	± 0.11	± 0.15		± 0.75	± 0.66	

fractions were significantly higher in mud (Table 2, Fig. 1b,c,e,f). This suggests that the hydrological condition is driving P availability in these sediments.

As a result of these differences in plant nutrient concentrations between the hydrological conditions, the N:P ratios in roots and shoots of *P. australis* were significantly higher when grown in the non-inundated sediments ($p < 0.001$ for shoots grown in mud; $p < 0.01$ for shoots grown in clay and roots grown in mud; $p < 0.05$ for roots grown in clay). For *R. maritimus*, this was only significant for mud ($p < 0.001$ for shoots; < 0.05 for roots). Furthermore, the N:P ratio was significantly higher in mud than in clay for shoots of *P. australis* ($p < 0.05$) and *R. maritimus* ($p < 0.001$) that were grown in the non-inundated sediment. For shoots in *R. maritimus*, a significant ordinal interaction effect was found between the sediment type and the hydrological regime ($F(1,44) = 8.010, p = 0.008$).

No significant differences were found for the K concentration in

both leaves and roots of *P. australis* and *R. maritimus*. Hence, the differences observed in the N:K ratio in roots and shoots were caused by N. Upon result, the N:K ratio was higher in non-inundated mud and clay, which was only significant for roots of *P. australis* ($p < 0.05$) and for shoots and roots of *R. maritimus* grown in mud ($p < 0.01$ for shoots; $p < 0.05$ for roots). All these results show that periodical inundation had a negative impact on the uptake of N and a positive impact on the uptake of P. Although differences in sediment P concentrations were large, the sediment type had only an effect on the uptake of N.

3.5. Biomass production

Fig. 3 presents biomass production per treatment for both plant species. Overall, shoot production was higher in mud than in clay for both seasons ($p < 0.01$). Interesting is that no significant differences in overall shoot production were found between the hydrological

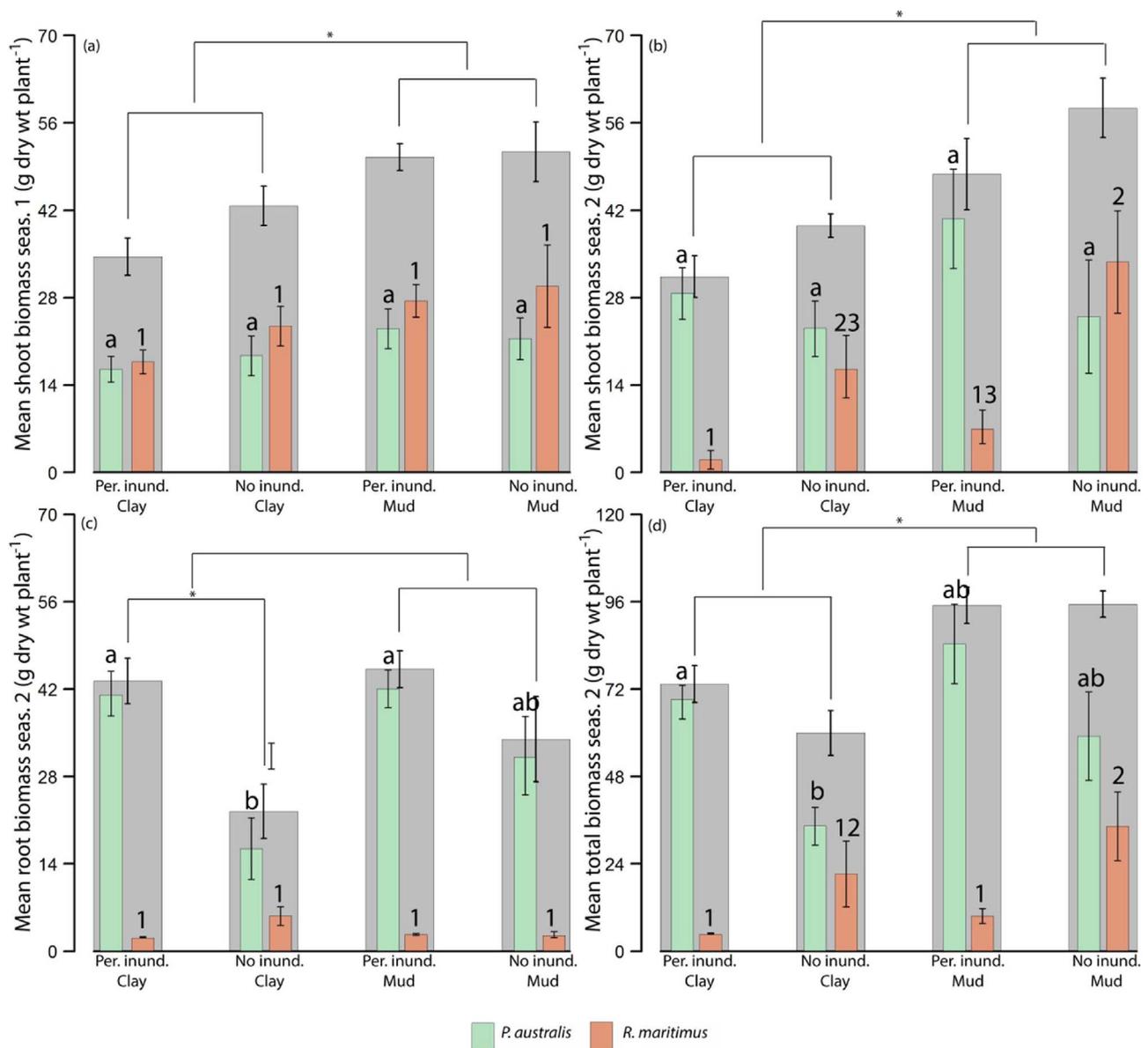


Fig. 3. Shoot biomass production in season 1 ($n = 6$; $t = 6$ months) (a) and season 2 ($n = 6$; $t = 18$ months) (b), as well as root biomass production (c) and total biomass production (d) in season 2 ($n = 3$; $t = 18$ months) (g dry wt plant⁻¹) in all four conditions (Clay vs Mud and periodical inundation vs no inundation) separated for *P. australis* (green bars) and *R. maritimus* (orange bars) as well as the aggregate value of the two species (gray bars). Error bars indicate S.E. Significant differences between aggregates are indicated by an asterisk. Species specific significant differences between treatments are indicated by different letters (*P. australis*) and different numbers (*R. maritimus*) ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

conditions in both seasons (Fig. 3a,b). However, in the periodically inundated treatments, shoot biomass of *R. maritimus* decreased significantly in season 2 ($p < 0.05$ for clay; $p < 0.01$ for mud). Moreover, in the sediments that were periodically inundated, *P. australis* produced significantly more aboveground biomass than *R. maritimus* in season 2 ($p < 0.001$ for clay; $p < 0.01$ for mud).

In contrast to shoot production, no significant difference between the two sediment types was found in root production. However, root production was higher in the sediments that were periodically inundated (Fig. 3c), but this was only significant for clay ($p < 0.05$). *P. australis* produced more belowground biomass than *R. maritimus* in all four conditions. Overall, the sediment type mainly influenced shoot biomass production, while the hydrological regime had an impact on root biomass production. These effects on biomass production were mainly caused by a decrease in shoot biomass of *R. maritimus* and an increase in root biomass of *P. australis* in the periodically inundated treatments in season 2.

3.6. Nutrient uptake

Fig. 4 presents total uptake of N, P, and K per treatment for both plant species. Fig. 4a shows that significantly more N was incorporated in the plants that were grown in mud than in clay ($p < 0.05$), probably due to the higher N concentrations in this sediment type (Table 2, Fig. 1g). Moreover, uptake of N was significantly lower in the periodically inundated sediments ($p < 0.001$ for mud; $p < 0.05$ for clay), which was caused by reduced uptake of *R. maritimus* compared to the control treatment. No significant difference in N uptake was found for *P. australis* between all treatments. In concordance with the plant P concentrations presented in Table 3, no significant difference was found between the two sediment types for the uptake of P in general. However, a significant difference was found in P uptake of *P. australis* in the periodically inundated treatments ($p < 0.05$) (Fig. 4b). Moreover, the amount of P taken up by *P. australis* was higher in the periodically inundated sediments ($p < 0.01$ for clay and $p < 0.001$ for mud). The

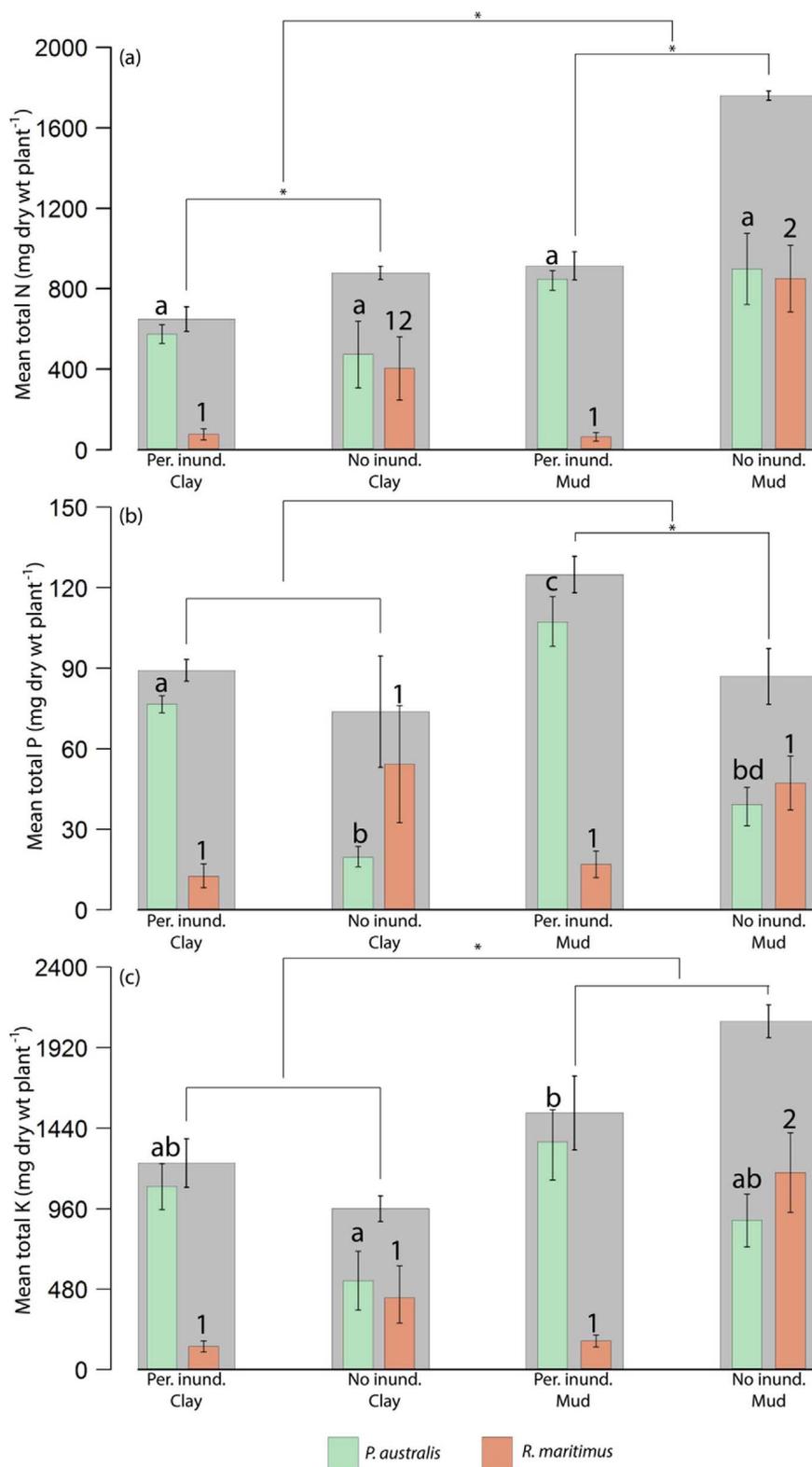


Fig. 4. Total uptake of N (a), P (b), and K (c) in season 2 (mg plant⁻¹) in all four conditions (Clay vs Mud and periodical inundation vs no inundation) separated for *P. australis* (green bars) and *R. maritimus* (orange bars) as well as the aggregate value of the two species (gray bars). Error bars indicate S.E. Significant differences between aggregates are indicated by an asterisk. Species specific significant differences between treatments are indicated by different letters (*P. australis*) and different numbers (*R. maritimus*) ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

uptake of K was significantly higher in mud than in clay ($p < 0.01$) due to increased uptake of K in *R. maritimus* grown in mud ($p < 0.05$). No overall significant differences were found between the hydrological conditions. To summarize, the hydrological regime influenced the uptake of N in *R. maritimus* and P in *P. australis* and the sediment type influenced the uptake of N and K in *R. maritimus*.

4. Discussion

4.1. Plant effects

The results show that plant nutrient-acquisition was influenced by both the hydrological regime and the sediment type. *Rumex maritimus* showed hampered uptake of N when both mud and clay were periodically inundated (Table 3; Fig. 4a). Likely, this is the case because *P.*

australis has high radial oxygen loss (Brix et al., 1996; Dickopp et al., 2011; Tercero et al., 2015), which sustains an oxygenated zone around the roots under waterlogged conditions. This is because such a zone promotes nitrification, and plants tend to perform better when NO_3 is present as an N source (Falkengren-Grerup, 1995). Significantly more N was taken up in mud, as mud contained twice the amount of N compared with clay at the start of the experiment (Table 1). Shoot N values of *R. maritimus* were below the critical threshold for N limitation in the periodically inundated treatment only (c. 1.4%; cf De Wit et al., 1963). Shoot N values of *P. australis* did not indicate N limitation in any treatment and might explain why this species outcompetes *R. maritimus* in the periodically inundated treatment.

In contrast to N-acquisition, root and shoot P concentrations of *P. australis* were significantly higher in the periodically inundated sediments. In roots and shoots of *R. maritimus*, no significant effect of periodical inundation could be discerned, which implies that decreased oxygen concentration in the periodically inundated treatment does not have a negative impact on the uptake of P. *Phragmites australis* clearly outcompetes *R. maritimus* in the second season in the periodically inundated treatments (Fig. 3b). Combined with the finding that *P. australis* is more efficient than *R. maritimus* in P acquisition in the periodically inundated treatments (Fig. 4) this is convincing evidence for concluding that in wet conditions *P. australis* is winning competition because it more effectively acquires essential nutrients.

Two mechanisms might explain this positive effect. First, a decrease in oxygen concentration in the sediment can also be an advantage when grown in iron-rich sediments as it reduces iron plaque formation on roots. Iron plaque induces a form of indirect iron toxicity by acting as a barrier against iron, which in turn has adverse effects on the nutrient uptake and translocation mechanisms in the plant (Snowden and Wheeler, 1995; Xu et al., 2009; Tripathi et al., 2014). Furthermore, Saaltink et al. (2017a) showed that iron plaque formation primarily affected the uptake of P, not N. They also showed that *P. australis* produced substantial amounts of iron plaque in aerated conditions, while little iron plaque formation was discerned on roots of *R. maritimus*. This also explains why we observed a positive effect of inundation on nutrient uptake in *P. australis* only. However, it must be noted that the shoot P concentrations in *R. maritimus* were above that of P limitation (c. 0.07% cf De Wit et al., 1963). Second, as the sediment contains high amounts of pyrite and iron-bound phosphorus, alternating water regimes can induce P mobilization (Satawatanont et al., 1991; Portnoy, 1999). This is because in reducing conditions, reduction of sulfate leads to P mobilization as Fe(II) favors sulfur over phosphorus in mineral precipitation. These two mechanisms might explain why periodical inundation has a negative effect on the uptake of N but not on P. Although mud appeared to be more nutritious in terms of P, no significant difference in P tissue concentration could be discerned between the two sediment types. Overall, P availability in our experiments, apparently is determined by the hydrological regime, while N availability is determined by both the hydrological regime and the sediment type.

As a consequence of the inhibited uptake of N, the shoot N:P ratios of *R. maritimus* were low when grown in the periodically inundated sediments and were indicative of N limitation, while the shoot N:P ratios of *P. australis* indicated only moderate N limitation (c. < 14; cf Koerselman and Meuleman, 1996). However, when *P. australis* was grown in the non-inundated sediments, shoot N:P ratios were high and suggested P limitation (c. > 16; cf Koerselman and Meuleman, 1996). These results show that plants grown on Markermeer sediments tend to be N limited when periodically inundated and P limited when not inundated at all.

The aforementioned differences in the nutrient acquisition by plants between treatments affected biomass production: the sediment type dictated changes in the production of shoots, while the hydrological regime influenced the production of roots.

4.2. Sediment effects

In contrast to plant nutrient-acquisition, the hydrological regime did not determine changes in the geochemical composition that occurred at the top layer of 2 cm. It is likely that raised belowground biomass production of *P. australis* enhanced aeration in the periodically inundated treatments due to increased radial oxygen loss (Reddy et al., 1990), which negated the effect of inundation which normally reduces conditions. It must be noted that the rate at which iron oxides increase is constant throughout the experiment (Fig. 1a), implying that absence of plants between growing seasons did not hamper the rate of oxidation. This might have occurred by Venturi-induced convection of gases through rhizomes of *P. australis* – i.e. clipped and dead culms still function as air tubes. Armstrong et al. (1991) showed that this mechanism raises oxygen concentrations in the soil during winter.

Plants do not only have the capacity to increase oxygen levels in the sediment, we also found indications that they alter the distribution of the phosphate pools in the sediment. During soil development these wetland sediments can either have elevated Fe-P concentrations by transformation from dissolved Ca-P in season 1 or elevated Ca-P concentrations by transformation from Fe-P in season 2. The increase of Ca-P between month 10 and 18 suggest elevated concentrations of dissolved phosphate in the porewater (Wang et al., 2011). In our experiment, the source of dissolved phosphate comes from Fe-P (Fig. 1b). This surprising result may be attributed to the ability of plants to dissolve iron oxides by H^+ and OH^- excretion by roots leading to mobilization of P (Bertrand et al., 1999). Moreover, Moorby et al. (1988) reported that H^+ release by roots is stimulated when P becomes deficient. This might be a reason why Fe-P dissolved only in the second season.

4.3. Implications for eco-engineering

The findings presented in this study can be implemented in eco-engineering projects where wetlands are to be created from clay-rich material. First, alternating the hydrological regime can enhance P availability for plants, especially in sediments with substantial amounts of Fe-P. Therefore, management of the hydrological regime opens possibilities for manipulating ecosystem development on the wetland, as the species assemblage of the future wetland and the succession that occurs is a response to changes in nutrient availability (e.g. Bedford et al., 1999). In our study, periodical inundation led to a relatively fast colonization of the target species *P. australis*. Second, the concentration of nutrients in the sediment influences aboveground biomass production. Fast shoot growth is especially preferred in lake wetlands build with soft mud as leaves and stems dampen shear stress on the substrate by attenuating waves (Nepf, 2012). In our study, muddy bed sediment contained higher concentration of nutrients than the consolidated clay deposit. To optimize the design of the eco-engineering project in lake Markermeer, we therefore suggest using mud for highest shoot production and to manage the hydrological regime to steer the P availability. After initial consolidation and crest stabilization of the sediment on the wetland, controlling the hydrological regime can also be used to promote biodiversity, as P availability is an important determinant for species richness (Olde Venterink et al., 2003). The main findings of this study are schematically summarized in Fig. 5.

5. Conclusions

The results of this study show that the hydrological regime and the sediment type influenced ecosystem functioning by determining nutrient availability. Periodical inundation had a positive effect on the P availability in the sediment, especially for aerenchymatous species such as *P. australis*. However, *R. maritimus* showed hampered uptake of N when periodically inundated. Two mechanisms might explain why periodical inundation had a positive effect on P availability: (1) reduction of iron plaque formation on roots of *P. australis*; and (2) induced

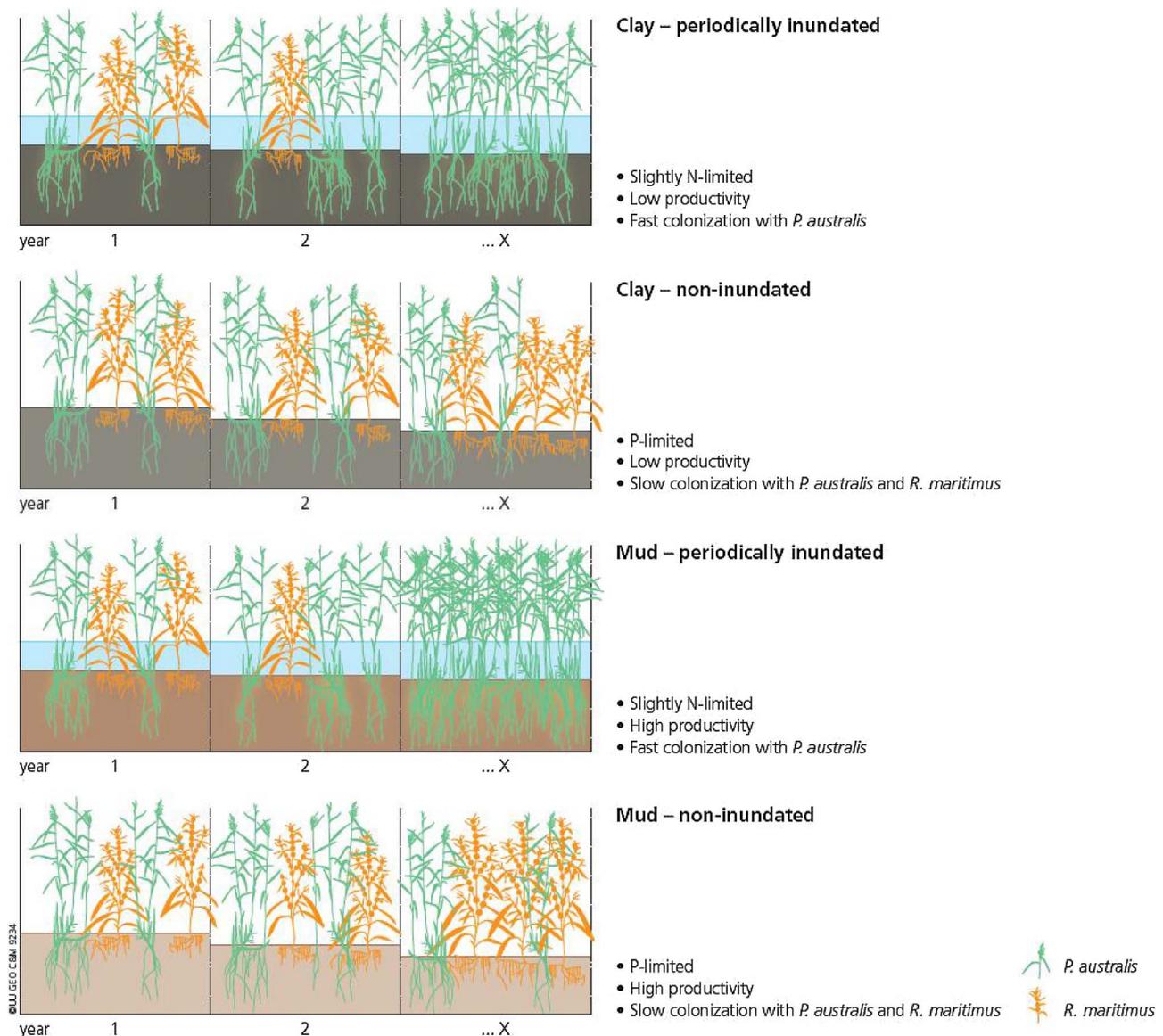


Fig. 5. Schematic summary of main effects on ecosystem functioning based on each treatment used in this study.

P mobilization by reduction of sulfate. In general, the results show that the P availability is determined by the hydrological regime, while the N availability is determined by both the hydrological regime and the sediment type. Despite these effects on nutrient availability no significant changes were discerned in total aboveground biomass production for *P. australis*, although root biomass was significantly higher in periodically inundated sediments. The sediment type in the mesocosms influenced plants to some extent, especially because of differences in sediment N concentrations. Furthermore, we found indications that plants alter the distribution of the phosphate pools in the sediment, probably by solubilizing Fe-P, thereby promoting Ca-P nucleation. These findings can be implemented in eco-engineering projects where plants are used as ecological engineers to fasten ecosystem development on wetlands that are to be created from clay-rich material.

Data accessibility

A dataset containing all relevant data acquired in this study is archived at DANS Data Archiving and Networked Systems) and is accessible to all users (Saaltink et al., 2017b).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2017.11.020>.

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