UvA-DARE (Digital Academic Repository)

The ecological effects of water level fluctuation and phosphate enrichment in mesotrophic peatlands are strongly mediated by soil chemistry

Mettrop, I.S.; Rutte, M.D.; Kooijman, A.M.; Lamers, L.P.M.

DOI

[10.1016/j.ecoleng.2015.09.077](https://doi.org/10.1016/j.ecoleng.2015.09.077)

Publication date

2015

Document Version

Final published version

Published in

Ecological Engineering

License

Article 25fa Dutch Copyright Act

[Link to publication](#)

Citation for published version (APA):

Mettrop, I. S., Rutte, M. D., Kooijman, A. M., & Lamers, L. P. M. (2015). The ecological effects of water level fluctuation and phosphate enrichment in mesotrophic peatlands are strongly mediated by soil chemistry. *Ecological Engineering*, 85, 226-236.
<https://doi.org/10.1016/j.ecoleng.2015.09.077>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

UvA-DARE is a service provided by the library of the University of Amsterdam (<https://dare.uva.nl>)

The ecological effects of water level fluctuation and phosphate enrichment in mesotrophic peatlands are strongly mediated by soil chemistry

Ivan S. Mettrop^{a,b,*}, Melchior D. Rutte^b, Annemieke M. Kooijman^a, Leon P.M. Lamers^b

^a Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, NL-1090 GE Amsterdam, The Netherlands

^b Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, NL-6525 AJ Nijmegen, The Netherlands

ARTICLE INFO

Article history:

Received 28 April 2015

Received in revised form

27 September 2015

Accepted 28 September 2015

Keywords:

Drought

Inundation

ANC

Phosphorus

Nitrogen

Rich fen

ABSTRACT

Since the re-establishment of a more natural water regime is considered by water management in wetlands with artificially stable water levels, the biogeochemical and ecological effects of water level fluctuation with different nutrient loads should be investigated. This is particularly important for bio-diverse mesotrophic fens, sensitive to acidification and eutrophication. Mesocosm experiments were conducted to study the interactive effects of water level fluctuation and P-enrichment under controlled summer conditions, using peat cores including vegetation from three fens differing in biogeochemical characteristics.

The effects of fluctuating water levels on biogeochemistry and vegetation appeared to be highly dependent on peat chemistry, and more important than the effects of P-enrichment. Only when plant growth was stimulated by a favorable water level regime, P-enrichment led to increased P-consumption by plants. In rich fens with a high soil Ca-content, 7 weeks of lowered water table (−15 cm) did not lead to a drop in pH. However, soil subsidence, increased N-availability and decline of the rich fen bryophyte *Scorpidium scorpioides* give cause to concern. 7 weeks of inundation (+15 cm) offered possibilities for restoration in these fens, since alkalinity and Ca-concentrations increased, while soil P-mobilization did not occur. Even P-enrichment did not result in increased P-availability, presumably due to Ca-related precipitation of P. In rich fens with a high soil Fe-content, water table lowering should be avoided as well, because of soil subsidence, increased N-availability, decline of the rich fen bryophyte *Calliergon giganteum*, plus acidification due to Fe-oxidation. Shallow inundation, however, is also harmful, especially after mowing and with P-rich water, because plant growth was hampered, presumably by toxicity of NH_4^+ and/or Fe(II). In mineral-poor fens with a high soil P- and S-content, shallow inundation should be avoided, because of tremendous internal P-mobilization. Vitality of the dominant bryophyte *Sphagnum palustre*, however, was not affected. Low water tables affected neither vegetation, nor biogeochemistry, showing resistance to short-term drought in these fens.

Given the strong mediating effect of soil chemistry, risks and benefits of re-establishment of fluctuating water levels with clean or P-rich water need to be considered for different fen types separately in water and nature management.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Mesotrophic fens, which are protected under the European Habitats Directive (H7140 – *Transition mires and quaking bogs*),

are subject to serious deterioration in agricultural areas. Water shortage, acidification, eutrophication, and accumulation of toxins are considered to be major constraints on effective management and restoration of these fens (Lamers et al., 2015). Especially in rich fens, the combined effect of acidification and eutrophication is considered problematic, since characteristic species-rich vegetation communities may rapidly be transformed into relatively species-poor *Sphagnum*-dominated communities (Kooijman, 1992). As a result of differences in their hydrogeological setting and climatological conditions, rich fens show range of different

* Corresponding author at: Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, NL-1090 GE Amsterdam, The Netherlands.

E-mail addresses: I.Mettrop@uva.nl, Ivan@samange.net (I.S. Mettrop).

hydrological regimes from no fluctuation to fluctuations between -50 cm and >1 m, affecting vegetation and peat accumulation (Lamers et al., 2015). In agricultural areas, however, water level fluctuations are generally constricted within narrow limits by intensive hydrological management. In pristine wetlands, however, water levels vary with the meteoric and groundwater balances in and around these wetlands (Baker et al., 2009), affecting biogeochemical processes and plant succession. Therefore, water management authorities are considering re-establishment of fluctuating water levels in order to optimize the generic ecological quality in non-pristine fens (Cusell et al., 2013a). However, soil biogeochemical characteristics largely differ among different fen types, as influenced by Ca-rich or Fe-rich surface water and groundwater, or by historical flooding with sulfate-rich seawater. Also, with a higher incidence of water table fluctuation, water quality becomes an important factor, especially when fens are inundated from time to time. To support water management authorities in decision-making, therefore, a better understanding of the different biogeochemical and ecological effects of fluctuating water levels with different water qualities for various fen types is essential.

During periods of drought, aerobic oxidation processes prevail due to oxygen intrusion into the soil, potentially decreasing the acid neutralizing capacity (ANC) and pH (Stumm and Morgan, 1996), and increasing N- and P-mineralization (Olde Venterink et al., 2002; Mettrop et al., 2014). These effects could hamper the development of protected brownmoss vegetation in rich fens, especially during summer (Cusell et al., 2013b). However, temporary drought may be beneficial to some extent, since Fe-oxidation can lead to rapid binding of phosphate in the soil (Richardson, 1985), temporarily reducing P-availability in porewater that can be important to maintain P-limitation. Although the general effects are relatively well known, the actual impact of drought may strongly differ among fens with different biogeochemical characteristics. In Fe- and S-rich fens, the effects of drought-induced oxidation and acidification may be stronger than in Ca-rich fens, because Ca is not redox sensitive and changes in pH can be buffered (Stumm and Morgan, 1996). The response of P-availability to drought may also differ among fen types, since the P-binding capacity of the soil under oxic conditions is expected to strongly depend on the Ca and/or Fe contents.

During wet periods, the water table increases and inundation may occur. In the case of Ca-HCO_3^- rich water, inundation and infiltration can increase soil ANC (Cusell et al., 2013a, 2015). In addition, inundation leads to the sequential reduction of nitrate, iron and sulfate as alternative terminal electron acceptors. Since these microbial processes generate alkalinity, the ANC may further increase (Stumm and Morgan, 1996). At the same time, however, P-availability may increase as a result of net P-mobilization (internal eutrophication) due to Fe reduction (Patrick and Khalid, 1974). Especially in Fe-rich soils with high P-contents, this anaerobic P-mobilization can be severe (Zak et al., 2010; Cusell et al., 2013b). Moreover, high sulfate reduction rates and formation of iron sulfides (FeS_x) may result in additional P-mobilization in S-rich soils (Smolders and Roelofs, 1993; Caraco et al., 1989; Lamers et al., 1998b). In addition, anaerobic conditions may lead to the formation of potential phytotoxins such as NH_4^+ , H_2S , and Fe(II) (Lamers et al., 2015).

Increased surface water influence, as a result of inundation, can also lead to higher nutrient inputs (external eutrophication) (e.g. Wassen et al., 1996). In relatively nutrient-poor (mesotrophic) fens adjacent to agricultural areas, external P-input can be highly detrimental (Lamers et al., 2015), and its effect strongly depends on biogeochemical characteristics of the peat soil.

The main objective of this study was to test the effects of water level fluctuation and water quality for fens differing in

biogeochemical characteristics. To be able to study the interacting effects under controlled conditions, we carried out a mesocosm experiment involving two rich fens differing in soil Fe-content and a mineral-poor fen with a high soil P-content, typical for fen types in many parts of the world. Water level effects were not only studied separately, but also subsequently, to assess whether the effects of drought could be restored by inundation, and vice versa. Studying these different water level sequences over time is also important for the field situation because vegetation development varies greatly over the growing season. We measured soil surface height, ANC, nutrient dynamics and vegetation development. It was hypothesized that increased surface water P-loads would particularly promote vegetation growth. Further, we expected that drought would result in acidification, particularly in Ca-poor fens, because these are considered to be more sensitive than Ca-rich fens (Lucassen et al., 2002). Inundation was hypothesized to result in alkalization, but also in internal P-mobilization, particularly in Fe-rich fens.

2. Material and methods

2.1. Three fen types

Peat cores were collected from three different locations with characteristic fen types, differing in chemical composition of peat and porewater.

The Stobbenribben rich fen ('ST'; $\text{N}52^\circ 47'5.5''$, $\text{E}5^\circ 59'1''$; dominated by *Scorpidium scorpioides* (Hedw.) Limpr.) is part of the Ramsar wetland area Weerribben-Wieden, and characterized by supply of lithotrophic base-rich surface water (Van Wirdum, 1991). As a result, relatively high pH and Ca-concentrations were detected in soil porewater (Table 1). The low soil P_{tot} content and high Ca_{tot} content of 247 mmol kg^{-1} d.w. resulted in a relatively high average soil molar Ca:P ratio of 27. Vegetation was dominated by Cyperaceae, predominantly *Carex elata* (All.), and to a lesser extent *Carex lasiocarpa* (Ehrh.), *Carex diandra* (Schrank) and *Carex rostrata* (Stokes).

The Binnenpolder Tienhoven rich fen ('BPT'; $\text{N}52^\circ 10'30.7''$, $\text{E}5^\circ 6'0.4''$; dominated by *Calliergon giganteum* (Schimp.) Kindb.) is part of the Vechtplassen area, and characterized by discharge of base-rich and Fe-rich groundwater in the former floodplain of the river Vecht. Although Ca-concentrations were relatively high, this site was especially rich in Fe, with porewater Fe-concentrations around $500 \mu\text{mol L}^{-1}$. In addition, soil Fe_{tot} content was respectively 6–7 times higher than in the other two locations, resulting in a relatively high molar Fe:P ratio of around 13. Vegetation was dominated by *Menyanthes trifoliata* (L.) and Juncaceae, predominantly *Juncus subnodulosus* (Schrank), and *Juncus articulatus* (L.).

The mineral-poor Ilperveld fen ('ILP'; $\text{N}52^\circ 26'35.7''$, $\text{E}4^\circ 55'56.1''$; dominated by *Sphagnum palustre* (L.)) was characterized by high porewater S_{tot} concentrations and a relatively high soil S_{tot} content, as a relic of flooding by the former Zuiderzee inland sea in the past. This fen type was further characterized by very high porewater o- PO_4 concentrations of around $40 \mu\text{mol L}^{-1}$, respectively 75 and 370 times higher than for the ST and BPT rich fen types, while soil P_{tot} was only 1.3–2 times higher. Vegetation was dominated by *Phragmites australis* (Steud.) and *Carex riparia* (Curtis).

2.2. Experimental setup

In each fen type, 24 peat soil cores of the upper 30 cm, including mosses and vascular plants, were collected in December 2012 using PVC columns with a diameter of 16 cm and a length of 50 cm. Since sampling took place in winter, biomass was still low. The cores were subsequently used in a 14 week mesocosm-experiment.

Table 1
Initial soil characteristics of the three fen types. Means with standard deviations ($n = 24$) are shown, different letters indicate significant differences between fen types, and F -ratios are shown with their level of significance: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. D.w. = dry weight of peat soil.

Variable	ST	BPT	ILP	$F_{2,69}$
<i>Soil porewater</i>				
pH	6.6 (0.2) ^b	6.5 (0.2) ^b	6.0 (0.2) ^a	59.2**
Alkalinity (meq L ⁻¹)	3.1 (0.8) ^b	7.1 (1.4) ^c	1.7 (0.5) ^a	191.8**
Ca ($\mu\text{mol L}^{-1}$)	1503.5 (408.5) ^b	3685.9 (953.1) ^c	528.9 (129.5) ^a	172.3***
Fe ($\mu\text{mol L}^{-1}$)	6.6 (4.0) ^a	477.3 (160.9) ^c	97.5 (59.2) ^b	126.5**
S ($\mu\text{mol L}^{-1}$)	47.3 (17.9) ^b	22.4 (4.6) ^a	176.5 (50.4) ^c	171.1**
o-PO ₄ ($\mu\text{mol L}^{-1}$)	0.5 (0.2) ^a	0.1 (0.0) ^a	37.0 (24.2) ^b	55.1**
<i>Soil</i>				
Fe _{tot} (mmol kg ⁻¹ d.w.)	33.2 (15.3) ^a	184.7 (24.0) ^b	26.3 (6.0) ^a	679.9***
Ca _{tot} (mmol kg ⁻¹ d.w.)	246.6 (18.2) ^c	192.6 (22.9) ^b	126.2 (14.8) ^a	244.9***
S _{tot} (mmol kg ⁻¹ d.w.)	109.8 (29.1) ^b	65.6 (9.2) ^a	117.7 (14.6) ^c	22.7***
P _{tot} (mmol kg ⁻¹ d.w.)	9.3 (1.4) ^a	13.8 (1.3) ^b	18.5 (3.6) ^c	54.6***
Ca _{tot} :P _{tot} (mol mol ⁻¹)	27.0 (4.2) ^c	14.0 (1.8) ^b	8.4 (1.8) ^a	266.9***
Fe _{tot} :P _{tot} (mol mol ⁻¹)	3.6 (1.7) ^b	13.4 (1.7) ^c	1.7 (0.4) ^a	460.9***
Fe _{tot} :S _{tot} (mol mol ⁻¹)	0.3 (0.2) ^a	2.9 (0.5) ^b	0.3 (0.1) ^a	578.0***

The 24 soil cores per fen ($n_{\text{tot}} = 72$) were treated with different water qualities and water level regimes. Within the factor water quality we distinguished between ‘clean’ or ‘P-rich’ supply-water. With regard to water level treatment three different situations were simulated: (1) a control treatment with water levels at the surface (0 cm) throughout the experiment, (2) a situation with initial drought, with water levels at -15 cm, followed by inundation, with water levels at $+15$ cm, and (3) the reverse regime: first inundation, then drought. Four cores were assigned per treatment combination ($n = 4$). The experiment was conducted in a 18°C climate room to simulate summer conditions (relative air humidity of 50–60% and 16 h of light with a PAR intensity of $150 \mu\text{mol m}^{-2} \text{s}^{-1}$). To be able to assess vegetation development during the water level sequences over time, all above-ground vegetation was clipped at soil surface level just before the start of the treatments.

The experiment was conducted under summer conditions, because microbial activity considerably increases with increased temperature. Therefore, increased internal alkalization (Cusell et al., 2013a, 2013b, 2015) and potential toxic concentrations for fen bryophyte spp. (Paulissen et al., 2004) are expected especially in summer. In addition, plant activity also increases with temperature, so the interaction between plant development and biogeochemical responses in the peat soil are best to examine under summer conditions. Finally, infiltration of supply-water was expected to occur mainly under summer conditions (Cusell et al., 2015). We chose for water level treatments of 7 weeks, because these relatively short periods of drought and inundation are shown to occur in isolated rich fens with fluctuating water levels, as indicated by field redox measurements (Appendix A in Mettrop et al., 2014, 2015). Changes in the water level of only $+15$ cm and -15 cm are shown to strongly enhance reduction and oxidation respectively, at least after 3 weeks (Cusell et al., 2013b).

Uniform water qualities were applied for all fen types (Table 2). The quality of the water supplied was based on the natural surface water in ST. As a result, water quality treatments for BPT and ILP differed from water quality in the field situation. This was, however, necessary in order to be able to statistically compare the effect of ‘water quality’ among the different fen types.

Table 2
Chemical composition of the supplied water.

Chemical compound	Concentration ($\mu\text{mol L}^{-1}$)
CaCl ₂ ·2H ₂ O	1500
MgCl ₂ ·6H ₂ O	300
KCl	100
NaHCO ₃	2000
NaH ₂ PO ₄ ·H ₂ O	15 (only P-rich treatments)

Water quality and level were regulated by placing the peat cores (with 4 pores of 5 mm diameter drilled at 1 cm above the bottom of their PVC columns) inside outer columns filled with either clean or P-rich water (Fig. 1). In case of inundation, flow of water through the peat cores was simulated with a pumping system (Masterflex L/S), by which supply-water was added drop wise on top of the inner core and was discharged from the system via the outer core to simulate field conditions as well as possible. PO₄ concentrations in the P-rich supply-water amounted to $15 \mu\text{mol L}^{-1}$, which is high but representative for surface waters in fens situated in or adjacent to agricultural areas in the Netherlands (e.g. Koerselman et al., 1990). This concentration was much higher than the initial pore-water concentrations of the rich fens ST and BPT, but much lower than in the ILP fen. A flux of 56.6 L water per m² per day was applied via the pumping system, resulting in a P-supply of 9.6 g P per m² per year in the case of P-rich treatment.

The experiment was divided into ‘period 1’ and ‘period 2’ by a water level turning point halfway through the experiment ($T = 7$ weeks), after which the cores with a -15 cm water level were subject to a $+15$ cm water level and vice versa. Period 1 represented the field situation shortly after winter, when plant biomass is still small. Period 2 represented the situation further in the season, when vegetation has already developed. Water level changes were regulated by raising or lowering the inner core 30 cm, while the water level remained unchanged in the outer core. In the cores subject to drought or control treatment, which were not part of the pumping system, water levels were adjusted with demineralized water three times a week to compensate for evapotranspiration.

2.3. Measurements

Peat soil characteristics of the upper 10 cm were determined by microwave destruction of 200 mg aliquots of dry, ground soil with 4.0 mL HNO₃ (65%) and 1.0 mL HCl (37%), and ICP analysis (Bettinelli et al., 1989). Porewater samples from the upper 10 cm of the peat soil were collected every week with permanently installed soil moisture samplers (Rhizon SMS-10 cm; Eijkelkamp Agrisearch Equipment, the Netherlands), connected to vacuumed serum bottles of 50 mL. pH-values were measured with a standard Ag/AgCl electrode and alkalinity was determined by titration down to pH 4.2 by using 0.01 mol L^{-1} HCl. Concentrations of o-PO₄, NO₃, NH₄ and dissolved organic matter (DOC) in porewater were measured using auto-analyzer (Skalar, San++ System, fitted with Skalar, SA1074). Total dissolved concentrations of Ca, Fe, and S were measured by an ICP Spectrometer (IRIS Intrepid II, Thermo Electron Corporation). In addition, water samples from the outflow of inundated cores were analyzed once during both periods. It was easy to distinguish

Fig. 1. Experimental set-up. Via the principle of communicating vessels the water level in the soil cores was regulated. Reference cores with a water level at 0 cm (A) remained unchanged throughout the experiment. Drought (–15 cm) was simulated by raising the inner columns by +30 cm (B), and inundation (+15 cm) was simulated by a pumping system (C).

between the peat substrate and the green and vital living moss layer on top of the peat soil. The height of the peat soil surface, just beneath this living layer, was measured relative to the top of the inner core at a weekly base.

Plant community composition was recorded just before the turning point of the water level and at the end of the experiment. At these moments moss vitality was also assessed by measuring photosynthetic yields at the apex of five randomly selected individuals from each core after 30 min of dark adaption, using pulse-amplitude modulated (PAM) chlorophyll fluorometry in combination with saturating pulse analysis of fluorescence quenching (Junior-PAM fluorometer, Heinz Walz GmbH, Germany). Vitality was expressed as $(F_m - F_0)/F_m$, in which F_m stands for the maximum fluorescence upon intense light pulse and F_0 for the minimum of chlorophyll fluorescence at reduced light intensity, both measured regarding photosynthetic system II. At the end of the experiment above-ground plant biomass was harvested, dried at 70 °C, separated into five groups of most common species (Cyperaceae, Juncaceae, Poaceae, Menyanthaceae and a 'rest group'), and finally weighted per vegetation group. Total C and N contents in dried, ground plant biomass were measured with a CHNS analyzer (Elementar, Vario EL Cube, Hanau, Germany). Total P in dried plants was measured by total microwave digestion and ICP analysis, as described for soil analysis. Potential nutrient limitation for vegetation was assessed using vascular plant foliar N:P ratios (Koerselman and Meuleman, 1996).

2.4. Statistical analyses

Initial differences between the three fen types were tested by one-way ANOVA with LSD (least significant difference) post hoc analyses, using 'fen type' as fixed factor.

Analysis of the treatment effects was conducted for each fen type separately, because of the large differences in chemical characteristics between the fen types. A linear mixed model was used

to test the response to the two fixed factors 'water quality' and 'water level'. Since samples were taken several times consecutively from the same cores, the model was run with a residual repeated covariance structure ('AR(1): Heterogeneous') and time as repeated effect. In order to assess potential effects of the shift in water level halfway, the factor water level was categorized into six separate treatments: 0 cm in period 1, –15 cm in period 1, +15 cm in period 1, and 0 cm in period 2, –15 cm in period 2, +15 cm in period 2. Differences resulting from these water level treatments were further tested by LSD post hoc analyses, and differences between the reference cores with water levels at 0 cm in period 1 versus period 2 were used as indicator for the effect over time.

Measurements on vegetation characteristics at the end of the experiment were tested for significant differences between fen types by applying a one-way ANOVA with LSD post hoc analyses, using 'fen type' as fixed factor. Differences between treatments were tested separately per fen type by applying a two-way ANOVA with LSD post hoc analyses, using water level and water quality as two main fixed factors.

All statistical analyses were performed using SPSS 20.0 for Windows (IBM Inc., 2011). *P*-values in the text are indicated as follows: **P* ≤ 0.05, ***P* ≤ 0.01, ****P* ≤ 0.001.

3. Results

For reasons of clarity, responses to the treatment combinations are presented in the following order: (1) development of the above-ground vegetation as measured at the end of the experiment, (2) responses of soil and porewater characteristics during the experiment, and (3) moss vitality at the end of the experiment.

3.1. Above-ground vegetation development

Total above-ground biomass at the end of the experiment was clearly lower in ST than in BPT and ILP ($F_{2,69} = 14.2^{***}$) (Fig. 2A).

Fig. 2. Above-ground biomass per m² divided into different vegetation groups (A) and P_{tot} in above-ground biomass per m² (B) at the end of the experiment. Different water level treatments are indicated, and P stands for P-addition. Means with S.E. are shown (n=4).

Remarkably, supply of P-rich water did not lead to an overall increase in above-ground biomass in any fen type (ST: $F_{1,18} = 0.0^{NS}$; BPT: $F_{1,18} = 0.0^{NS}$; ILP: $F_{1,18} = 1.0^{NS}$). Plant species composition was, however, affected by water quality. Cyperaceae declined with P-enrichment in the reference cores with water levels at 0 cm in all fen types.

Water level treatment did not affect total biomass in ST ($F_{2,18} = 1.8^{NS}$), and biomass remained relatively low in all treatments. In BPT and ILP however, biomass was 3–4 times higher than in ST, and affected by water level treatment. Biomass was lower when the soil was first inundated, and then subjected to drought, than in the reference cores or the cores subjected to inundation after drought ($F_{2,18} = 4.1^*$ and $F_{2,18} = 3.5^*$). In BPT, the reduction in biomass when initially inundated was stronger with supply of P-rich water than with clean water, as indicated by an interaction between water level $\times$ water quality ($F_{2,18} = 3.1^*$). In ILP, particularly *P. australis* was stimulated by inundation after drought.

The three fen types clearly differed in plant tissue nutrient contents and type of nutrient limitation (Appendix B.1). ST was characterized by the highest N:P ratio in vegetation of 40 on average ($F_{2,67} = 49.1^{***}$), which was mainly due to the lower plant P content ($F_{2,68} = 15.4^{***}$), suggesting P-limitation. In BPT and ILP, N:P ratios were on average 27 and 16 respectively, which suggest P-limitation for BPT and balanced availability of N and P for ILP. In ST and BPT, water quality did not affect plant N:P ratios in general ($F_{1,16} = 4.3^{NS}$ and $F_{1,18} = 4.2^{NS}$). However, for both fens, water quality showed interactive effects with water level ($F_{2,18} = 4.8^*$ and $F_{2,18} = 5.9^*$). In the inundation after drought treatment, in which

vegetation growth was higher than in other treatments, tissue P-contents were higher with P-rich than with clean water, and N:P ratios 2 times lower. This indicates that the extra P was actually taken up by the vegetation, in contrast to the treatment with inundation first that strongly hampered biomass growth. In BPT, after drought, inundation with P-rich water even led to N:P ratios lower than 16, indicating balanced availability of N and P. In ILP, where P-availability was already relatively high, plant N:P ratios were neither influenced by P-enrichment ($F_{1,18} = 0.5^{NS}$) nor by water level ($F_{2,18} = 2.0^{NS}$).

Total P-uptake by above-ground phanerogams per m² was generally the highest when the soil was inundated with P-rich water after drought (Fig. 2B), as indicated by interactions of water level $\times$ water quality (ST: $F_{2,17} = 3.0^*$; BPT: $F_{2,18} = 12.3^{***}$; ILP: $F_{2,18} = 3.9^*$). This peak coincided with higher tissue P-contents for all three fen types, and with a clear increase in biomass in BPT and ILP. Only when plant growth was stimulated by a favorable water level regime, P-enrichment led to increased P-consumption by vegetation. In contrast, in the control treatment and especially when the soils were inundated from the start of the experiment, total P-uptake per m² by the vegetation was low in all three fen types, even when P-rich water was supplied.

3.2. Soil and porewater characteristics

All statistics of treatment effects during the experiment are shown in Appendix B.2.

3.2.1. Soil surface height

For all fen types, the reference cores with water levels at 0 cm showed no significant changes over time. As expected, soil surface height was influenced by water level treatment in all fen types, although this effect strongly depended on the sequence of the change (Appendices A.1 and B.2). Inundation led to a slight increase of the soil surface of 1–2 cm in all fen types, both with and without prior drought. Drought during the first period did not show any effect. However, drought during period 2 led to significant subsidence of 3–5 cm in all fen types when preceded by inundation, when vegetation development was limited. In ST and ILP, this subsidence was stronger under P-rich conditions.

3.2.2. Porewater pH and ANC

Water quality (P addition) did not significantly influence Ca-concentrations, alkalinity or pH in any fen type (Appendix A.2:a,b,c). Water level, however, did affect these three parameters (Appendix B.2). Reference cores with water levels at 0 cm showed no change over time. Drought, however, decreased alkalinity for all fen types, accompanied by decreased Ca-concentrations especially for BPT. The decrease in alkalinity by drought was stronger when preceded by inundation in ST and ILP, resulting in lowered pH. BPT, however, showed a remarkable increase in pH with drought, leading to pH values of 7.0 on average, despite the strong decrease in alkalinity from 6.5 to 1.5 meq L⁻¹ during period 1.

In ST and BPT, Ca-concentrations only increased upon inundation in period 2, when preceded by drought. Ca-concentrations increased to concentrations around 2000 $\mu\text{mol L}^{-1}$ and 2500 $\mu\text{mol L}^{-1}$ respectively, due to input of extra Ca from the supply-water. In ILP, Ca-concentrations gradually increased during both periods. Although alkalinity was also expected to increase due to supply of base-rich water and/or reduction processes, for ST and ILP this only happened upon inundation in period 2, when preceded by drought. In BPT, inundation led to different alkalinity responses than in ST and ILP. In BPT, which had higher alkalinity in porewater than the supply-water, dilution resulted in a decrease in alkalinity during inundation in period 1.

3.2.3. Porewater Fe, S and DOC

Porewater Fe-, S- and DOC-concentrations were generally not affected by P-addition (Appendices A.3:a,b,c and B.2). Also, the reference cores with water levels at 0 cm showed no significant changes in Fe-, S- and DOC-concentrations over time. However, in all fen types, the decrease of alkalinity upon drought was accompanied by a strong decrease in Fe- and increase in S-concentrations in porewater. Oxidation of Fe²⁺ resulted in decreased concentrations of dissolved iron, while oxidation of S²⁻, partly enclosed in FeS_x, resulted in the formation of dissolved SO₄. Inundation showed the opposite response, with increased dissolved Fe-concentrations in all fen types, indicating reduction of Fe³⁺ to more soluble Fe²⁺. Dissolved S-concentrations simultaneously decreased, indicating SO₄ reduction and subsequent FeS_x formation with part of the Fe²⁺ that became available.

In ST, where S-concentrations were moderately high, and especially in the S-rich ILP, these changes in soluble Fe and S-concentrations with drought were accelerated when preceded by inundation. This may point to increased formation of FeS_x during the preceding inundation period, which is oxidized during subsequent drought. In the Fe-rich BPT, oxidizable S-concentrations were low anyhow, in accordance with the low S_{tot} concentrations and high Fe:S ratio in the soil (Table 1).

Remarkable was the accelerated increase in Fe-concentrations in BPT upon inundation with P-rich water during period 1, accompanied by a considerable increase in DOC. This response was absent when clean water was supplied. In addition, this response was only observed in BPT. The increase in Fe-concentrations

upon inundation with P-rich water in BPT was, however, not observed during period 2, when preceded by drought, and when the above-ground biomass had strongly increased.

3.2.4. Porewater nutrients

Despite differences in P-input via supply-water, porewater o-PO₄ concentrations were generally not affected by water quality in any fen type (Appendix B.2). Upon P-enrichment, o-PO₄ concentrations were generally much lower than the 15 $\mu\text{mol L}^{-1}$ of the supply-water in the rich fens ST and BPT, and values remained at the same low levels measured upon clean water treatment (Appendix A.4:a). Also, o-PO₄ concentrations in the outflow of the outer columns were very low for all fen types (predominantly under the detection limit of 0.05 $\mu\text{mol L}^{-1}$). Because vegetation uptake only played a role in the inundation after drought treatment, when above-ground biomass was high, the absence of an increase in o-PO₄ concentrations upon P-enrichment in ST and BPT presumably points to chemical sorption of P in the soil. In ILP, however, porewater o-PO₄ concentrations were much higher than in the supply-water in both clean and P-rich treatment, and approximately 10 $\mu\text{mol L}^{-1}$ higher with P-enrichment.

Contrary to P-addition, water level fluctuations significantly affected porewater o-PO₄ concentrations (Appendices A.4:a and B.2). The reference cores with water levels at 0 cm showed no significant changes over time, but differences between drought and inundation were highly significant. In all fen types, drought led to a decrease of porewater o-PO₄ concentrations, presumably because oxidized iron precipitated with P as Fe-P complexes. Inundation, on the other hand, increased o-PO₄ concentrations in all fen types as a result of Fe reduction and concomitant P-mobilization.

These water table effects on porewater o-PO₄ concentrations clearly differed among fen types. In the Ca-rich ST, o-PO₄ concentrations were relatively low and only slightly increased upon inundation after drought. In the Fe-rich BPT, however, o-PO₄ concentrations clearly increased upon inundation during both periods. Moreover, a significant water level $\times$ water quality interaction indicated that o-PO₄ concentrations increased especially upon inundation with P-rich water in the first period, when vegetation biomass was low. In ILP, o-PO₄ concentrations were already much higher than in ST and BPT, and increased considerably upon inundation. High values of around 130 $\mu\text{mol L}^{-1}$ were reached with both clean and P-rich water. However, subsequent immobilization of P upon drought resulted in a decrease to, or even below, initial concentrations in all fen types.

Overall, there was no effect of water quality on NH₄ and NO₃ concentrations. However, in BPT, NH₄ concentrations increased upon inundation with P-rich water in the first period, when above-ground biomass was still low (Appendix A.4:b,c). This was indicated by a water level $\times$ water quality interaction (Appendix B.2). The effect of water level on NH₄ and NO₃ concentrations was again more important than that of water quality. While the reference cores with water levels at 0 cm showed no significant changes in NH₄ and NO₃ over time, the effects of drought and inundation were highly significant. Generally, drought led to decreased NH₄ and increased NO₃ concentrations due to ammonium oxidation (nitrification) by intruding O₂, while inundation led to increased NH₄ and decreased NO₃ concentrations as a result of decreased nitrification, increased denitrification, and dissimilatory nitrate reduction to ammonium. These effects were most obvious in BPT and ILP, where inundation with both clean and P-rich water during the first period led to a severe increase of NH₄. As already indicated, NH₄ concentrations further increased in BPT to values known to be phytotoxic of over 600 $\mu\text{mol L}^{-1}$ when inundation was applied with P-rich water in the first period, accompanied by a strong increase in DOC (Appendix A.3:c). Inundation with P-rich water during period 2, when vegetation biomass had already increased, did not have this strong effect.

Fig. 3. (A–C) Fluorescence yields for the dominant bryophytes for each fen type. The water level turning point is indicated by the dashed line. Means with S.E. are shown ($n = 20$). Different symbols above each pair of bars indicate significant differences ($P < 0.05$) between water level treatments.

Furthermore, the increase of NO_3 concentrations by nitrification during drought in ST and ILP was much stronger when preceded by inundation, accompanied by a stronger decrease in alkalinity.

3.3. Moss vitality

Fluorescence yields in the reference situation with water levels at 0 cm were lower in all fen types after period 2 than after period 1, indicating that the experimental conditions in general were not optimal for the mosses. There was no general effect of water quality on the vitality of any of the mosses (BPT: $F_{1,228} = 0.9^{\text{NS}}$, ST: $F_{1,228} = 1.0^{\text{NS}}$, ILP: $F_{1,228} = 3.2^{\text{NS}}$). However, there was a clear effect of water level for the two rich-fen species. Drought generally led to lower fluorescence yields of *S. scorpioides* in ST ($F_{5,228} = 38.6^{***}$) and *C. giganteum* in BPT ($F_{5,228} = 29.4^{***}$) (Fig. 3). During subsequent inundation in period 2, vitality of *S. scorpioides* remained low, but *C. giganteum* showed a clear recovery. Drought after inundation, however, led to very low fluorescence yields for both rich fen moss spp. Vitality of *S. palustre* in ILP was, in contrast, not affected by drought or inundation ($F_{5,228} = 0.1^{\text{NS}}$).

4. Discussion

The main objective of this study was to test the effects of water level fluctuation and water quality in fens differing in biogeochemical characteristics, under controlled conditions and for the combination of plant and soil (mesocosm). In all fens, effects of water level fluctuation were the most imminent, and general risks and benefits of drought and inundation could be observed, depending on the vegetation development.

4.1. Risks and benefits of higher drought incidence

Direct effects on plants, such as water shortage, and indirect effects such as acidification and N-eutrophication by increased mineralization are generally considered to be major potential constraints on vegetation development in relation to drought in mesotrophic fens (e.g. Lamers et al., 2015). However, temporary drought may also be beneficial for P-limited vegetation, since Fe-oxidation can lead to rapid binding of phosphate in the soil (Richardson, 1985), temporarily reducing P-availability in porewater. The potential risks and benefits need to be weighed up for different fen types separately.

Generally, vascular plant growth was not inhibited by drought, which we attribute to sufficiently deep rooting preventing water shortage. In BPT and ILP, vascular plant growth was even stimulated by drought directly from the start (similar to early spring

conditions shortly after winter). This stimulation is, however, not necessarily favorable for mesotrophic peatlands, since high biomass production may lead to a less diverse species composition due to competition, and may offer less room and light for mosses.

While growth of vascular plants was not negatively affected by drought, vitality of rich fen bryophytes severely decreased. Most probably, water shortage is the main factor causing this decrease in vitality, because biogeochemical effects such as changes in pH or toxicity (Paulissen et al., 2004) did not occur. However, the effects of specific moss spp. characteristics, and the biogeochemical characteristics of the fen type in which they occur, cannot be teased apart. Although *C. giganteum* was able to recover during subsequent inundation, the decrease in vitality of *S. scorpioides* upon drought could not be restored within 7 weeks of subsequent inundation, due to reduced growth rates (Kooijman and Whilde, 1993). In contrast, vitality of *S. palustre* was not affected by drought at all, presumably due to the efficient capillary water transport and water storage of *Sphagnum* spp. (Clymo and Hayward, 1982), and to the fact that *Sphagnum* spp. are able to tolerate acid conditions (e.g. Rochefort et al., 1990). These findings confirm the considerable competitive advantage of *Sphagnum* over rich fen bryophytes during drought, explaining drought-induced vegetation shifts from certain brown mosses to peat mosses.

Lowering of the water table led to subsidence of the peat soil surface in all fen types, but only when preceded by inundation. This suggests that subsidence is not solely due to reduced buoyancy by release of entrapped gas bubbles (Strack et al., 2006), or increased decomposition rates as a result of aeration (e.g. Mettrop et al., 2014). Presumably, subsidence was further affected by the reduced vegetation development during prior inundation, which led to inhibited root growth and lower stability of the peat soil.

Drought generally led to decreased porewater Ca-concentrations, and especially decreased porewater alkalinity due to acidification. In the Fe-rich BPT, acidification seemed mainly be due to iron oxidation (Stumm and Morgan, 1996). In the Ca-rich ST, which contained slightly more S in the soil, and particularly in the S-rich ILP, the oxidation of sulfides may have been more important (Lamers et al., 1998a; Lucassen et al., 2002). Interestingly, prior inundation modified these drought effects. In all fen types, drought-induced acidification was accelerated when preceded by inundation, which may be due to increased concentrations of reduced components that could readily be oxidized during subsequent drought.

Despite the decrease in alkalinity upon drought, ANC remained sufficiently high to prevent a severe drop in pH in all fen types to values below 6.0, considered a critical value for rich fens dominated by brownmosses (Kooijman, 2012). Unexpectedly,

pH values even increased to pH values of 7.0 upon drought in BPT, presumably due to degassing of CO₂-charged porewater, as demonstrated in previous studies in Fe-rich fens (Zak et al., 2004). A release of CO₂ to the atmosphere can lead to increased pH values ($\text{pH} = 6.4 + \log([\text{HCO}_3^-]/[\text{CO}_2])$) (Stumm and Morgan, 1996). The combined effect of decreased alkalinity and increased pH during drought in BPT may have induced Ca-mineral precipitation (Boyer and Wheeler, 1989), possibly explaining the decrease in porewater Ca-concentrations, despite a concentration effect by evapotranspiration.

In previous experimental studies, increased decomposition rates with drought are generally reported to result in increased N-mineralization in peat soils (Olde Venterink et al., 2002; Mettrop et al., 2014). However, in terms of the actual porewater N-concentrations, increased plant uptake may compensate for this N-release. In all fen types, we found that drought at an early stage led to lower total porewater N-availability (NO₃ + NH₄) than early inundation, because vascular plant development was stimulated by this water level regime and thereby N-uptake by plants was enhanced.

In contrast to that of N, the availability of P in porewater decreased upon drought in all fen types. In the Ca-rich ST, we presume that mainly co-precipitation of P with calcite was involved (Boyer and Wheeler, 1989), which explains the relatively small response to oxic conditions. In the Fe-rich BPT, high rates of Fe-oxidation and subsequent Fe-P precipitation were involved (Patrick and Khalid, 1974; Richardson, 1985), explaining the more obvious decrease in P-availability. In the S-rich ILP, oxidation of FeS_x has presumably increased the reactive Fe³⁺ concentration, stimulating substantial P-binding in the topsoil (Roden and Edmonds, 1997). The binding of P to Fe temporarily reduces P-availability in porewater (e.g. Patrick and Khalid, 1974), but the question is whether this is really an advantage to P-limited vegetation. Fe-related P precipitation may be less relevant in terms of reducing P-availability to plants as generally assumed, an idea that was already reported by Pawlikowski et al. (2013). Many vascular plants are still capable of taking up P from accumulated Fe-phosphates in soils (Marschner, 1995).

All in all, the direct drought effects were not negative for vascular plants, but vitality of protected rich fen bryophytes severely decreased, giving *Sphagnum* a competitive advantage. Drought-induced acidification did not lead to considerable lowering of pH during 7 weeks, because of sufficient buffering in all fen types. In terms of nutrient-availability there were no considerable effects.

4.2. Risks and benefits of higher inundation incidence

Formation of potential toxins and increased P-mobilization are generally considered major constraints on vegetation development in relation to inundation in mesotrophic fens (e.g. Lamers et al., 2015). However, inundation may also be beneficial, since inundation with base-rich water in summer promotes buffering against acidification (Cusell et al., 2015). Also the potential risks and benefits of inundation need to be weighed up with a critical eye for different fen types separately.

Plant growth was hampered when inundated directly from the start (similar to early spring conditions shortly after winter), especially in BPT and ILP, which was probably due to anoxic conditions and formation of toxins in the first period. In BPT, inundation with P-rich water led to porewater Fe-concentrations over 1000 μmol L⁻¹, reported as toxic to *J. subnodulosus* (Snowden and Wheeler, 1993), which is confirmed by our results for development per group of species. In this fen type, NH₄ concentrations also considerably increased with inundation shortly after winter. Particularly with P-rich water, NH₄ concentrations increased well over 100 μmol L⁻¹, a level above which toxic effects can seriously

damage bryophyte vegetation under summer conditions (Paulissen et al., 2004; Verhoeven et al., 2011), and toxic effects may be expected for plants (Lamers et al., 2015). When subjected to inundation after a period of drought (when plants already had the opportunity to grow), however, ammonium toxicity did not seem to be a severe problem anymore. Increased plant activity probably led to increased radial oxygen loss (ROL) from roots (Lamers et al., 2012), stimulating nitrification in the rhizosphere, and increased uptake of N. In the S-rich ILP, the decline in vegetation, especially of *P. australis*, upon inundation with both clean and P-rich water shortly after winter may very well be caused by sulfide toxicity (Armstrong et al., 1996). When subjected to inundation after drought however, when plants already had had the opportunity to grow, sulfide toxicity did not seem to be a problem anymore. Although sulfide concentrations in bulk soil still increased to toxic values, increased plant activity probably led to increased ROL, stimulating sulfide oxidation in the rhizosphere. Additionally, inundation in itself is a significant stress factor, both for above-ground plants and moss species. Direct effects such as decreased growth rates and mortality are expected because CO₂ and light availability are strongly reduced under water. Just like for drought, effects of specific species characteristics, and the biogeochemical characteristics of the fen type in which they occur, cannot be entirely separated.

Otherwise, a wet period in spring, with reduced vegetation development, is not necessarily detrimental for mesotrophic peatlands. Competition by fast growing species may be limited this way, eventually resulting in increased biodiversity.

For rich-fen mosses, inundation, or at least waterlogging, turned out to be vital, not only to prevent water shortage, but partly also to restore direct effects of prior drought. *S. palustre* however, turned out to be well able to endure periods of inundation as well, regardless of the water quality. Even with base-rich inundation water, which was assumed to cause problems since *Sphagnum* spp. are generally associated with and adapted to acidic conditions, *S. palustre* thrived remarkably well.

Generally, inundation resulted in increased Ca-concentrations and alkalinity in porewater, but only when preceded by drought. This suggests that a prior period of drought promoted infiltration of base-rich water during inundation. In this way, inundation with base-rich water may contribute to a lasting increase in the ANC, as this is not only determined by the amount of bicarbonate in porewater, but also by the amount of Ca attached to the adsorption complex (Stumm and Morgan, 1996). Moreover, the increase in porewater alkalinity during inundation after drought in the rich fens ST and BPT may point to additional alkalinity generation, resulting from anaerobic microbial reduction processes (Stumm and Morgan, 1996). An increased ANC by inundation, both by infiltration and by internal alkalinity generation, was previously demonstrated by field inundation experiments in similar fen types in summer (Cusell et al., 2015). In addition, anaerobic decomposition may have resulted in increased partial pressure of CO₂ in porewater (Estop-Aragonés et al., 2012), causing calcite to dissolve (Komor, 1994).

In ST, a period of 7 weeks of inundation seemed favorable to improve and/or conserve the porewater ANC, as desired from a management perspective. In BPT, the absence of an increase in porewater ANC in this experiment was primarily related to the dilution by supply-water with a lower alkalinity than the original porewater. This would, however, also be the case in the field situation, since alkalinity in surface water close to the sampled plots in BPT did not exceed 0.5 meq L⁻¹ (I. Mettrop, unpublished data). Interestingly, in ILP, porewater alkalinity and Ca-concentrations remained lower than in the supply-water, which may indicate that buffer capacity was consumed. An important factor may be the exchange of Ca²⁺ for H⁺ between supply-water and the H⁺-rich

adsorption complex of *Sphagnum*-mosses in the mineral-poor ILP (Clymo, 1963). In contrast, adsorption complexes of *S. scorpioides* in the rich fen ST and *C. giganteum* in the rich fen BPT may already have been saturated with Ca, as expected for minerotrophic moss species.

In the P-limited fens ST and BPT, P-availability remained relatively low. The high internal P-mobilization in ILP however, where the soil Fe:P ratio was low, is in accordance with previous findings for fen soils with high P-content (e.g. Zak et al., 2010). Furthermore, the high S-concentrations in ILP may have induced additional release of Fe-associated P during inundation. Since reduction of Fe and SO_4 leads to formation of FeS_x , the P-binding capacity of the peat sediment strongly decreases (Smolders and Roelofs, 1993; Caraco et al., 1989; Lamers et al., 1998b).

Net internal P-mobilization was lower upon inundation after drought than upon inundation directly from the start in BPT and ILP, which seemed to be related to P-consumption by plants. As mentioned, drought followed by inundation resulted in much higher plant biomass in these fen types. As reflected by the total amount of P in above-ground phanerogams per m^2 at the end of the experiment, the increase in biomass resulted in increased P-consumption, resulting in reduced net P-mobilization. In ST, the above-ground biomass did not differ between water level treatments, and net P-mobilization with inundation was relatively low. This can be explained by the fact that most P is bound to Ca, which is not sensitive to oxidation-reduction processes (Stumm and Morgan, 1996). Therefore, the link between net P-mobilization and P-consumption by plants seems to be less important in the Ca-rich ST.

All in all, the formation of toxins most likely results in significantly reduced vegetation development, especially with inundation in early spring. In addition, inundation increases the risk of internal P-mobilization, especially for fen soils with high P-content. On the other hand, inundation with base-rich water, especially after a period of drought, may contribute to an increased ANC.

4.3. Supply of P-rich water

In general, P-enrichment did not lead to increased above-ground biomass in any fen type, which was unexpected given the P-limitation of biomass production (as indicated by vegetation N:P ratios), and contrary to our hypothesis. Inundation with P-rich water only led to enhanced P-consumption by plants when preceded by a period of drought, when the vegetation had had the opportunity to develop, but this did not lead to higher production rates.

In the Ca-rich ST and the Fe-rich BPT, P-enrichment did not result in increased porewater P-availability either. In ST, most of the added P seemed to be mainly immobilized within calcium phosphate in the soil (Boyer and Wheeler, 1989), while in BPT, most of the added P was presumably immobilized in soil Fe-P complexes (Patrick and Khalid, 1974; Richardson, 1985). However, overall plant N:P ratios in the Fe-rich BPT were considerably lower than in the Ca-rich ST, which may imply that Fe-related P precipitation may be less relevant in terms of reducing P-availability than generally assumed, an idea that was already reported by Pawlikowski et al. (2013). Many vascular plants are still capable of taking up P from accumulated Fe-phosphates in soils (Marschner, 1995). In ILP, where P-binding elements such as Ca and Fe are sparse, P-enrichment seemed to primarily result in increased porewater P-concentrations, which is not relevant for plants as the P-availability was already high in this fen type. In addition, a small portion of the added P could be adsorbed by mosses in all fen types, but we assume that this way of P-immobilization is of minor importance.

Unexpectedly, P-rich inundation shortly after winter even had a negative effect on plant growth in BPT, in an indirect way. The strongly increased NH_4 , DOC and Fe-concentrations upon inundation with P-rich water during period 1 indicate increased microbial activity with P-enrichment (Amador and Jones, 1995; White and Reddy, 2000), which may have resulted in toxic concentrations of NH_4^+ , Fe(II) and/or organic acids to plants. When preceded by drought however, inundation with P-rich water did not have these extreme effects in BPT, probably because in this case vegetation had the chance to develop. Increased plant activity probably led to increased ROL (Lamers et al., 2012), and in the case of P-rich water also to enhanced P-consumption. Enhanced plant development by a favorable water regime may thus have mitigated the stimulating effect of P-enrichment on anaerobic microbial activity later in the growing season.

4.4. Conclusions and implications for management

We here show that chemical properties of peat soils, as determined by the geohydrological setting in the landscape, strongly determine the responses to water level fluctuation and P-enrichment during flooding. In general, fluctuating water levels turn out to be much more important in terms of biogeochemical responses than P-enrichment, and the stage of vegetation development appears to be very important for its response. In Fig. 4, we have summarized the potential benefits and drawbacks of the re-introduction of water table fluctuation in rich fens for decision support in water and nature management. The decision will largely depend on the geohydrological setting of the specific fen area.

In rich fens with Ca-rich soils due to groundwater and/or surface water supply, drought episodes up to 7 weeks will lead to a decline of characteristic rich fen bryophytes such as *S. scorpioides*. Vascular plant development, however, was not considerably affected by changes in the water level. Further, drought in these fens does not lead to a considerable risk of lowering of pH due to their high ANC. Accelerated decomposition and N-mineralization, on the other hand, are serious reasons for concern. Increased N-availability may eventually promote the degradation of rich fens because of increased encroachment of graminoid species at the expense of characteristic brown moss and slow-growing vascular species (Verhoeven et al., 2011; Cusell et al., 2014). These adverse drought effects should therefore be prevented by inundation with surface water, especially late in the growing season after a period with high water levels. Moreover, periods of inundation with base-rich water in summer, especially when preceded by a period of drought, seem to be favorable in order to structurally improve the porewater ANC by supply of Ca and internal soil alkalization. Short-term summer inundations as a management measure have been postulated previously to restore the ANC in the top soil of Ca-rich fens that lack sufficient HCO_3^- and Ca-buffering to prevent acidification (Cusell et al., 2013a, 2015), and our findings confirm this idea. Finally, inundation does not result in severe P-mobilization, and in case of supply of P-rich water, short-term inundation does not seem to be very harmful, presumably due to Ca-related precipitation of P.

In rich fens with Fe-rich soils (caused by current or former discharge of Fe-rich groundwater), short-term drought will also result in a decline of characteristic rich fen bryophytes such as *C. giganteum*. In contrast, a period of drought shortly after winter stimulates vascular plant development. In addition, drought results in an even higher degree of acidification than in Ca-rich fens due to Fe-oxidation, and increased decomposition and N-mineralization are considered detrimental in this fen type as well. Therefore, inundation with surface water is recommended. Inundation, however, should be prevented shortly after winter, when vegetation

Fig. 4. A summarizing overview of potential benefits and drawbacks of lowered and increased surface water levels, and hence changes in water tables in fen peat soils, at the level of site conditions.

development, hence P-consumption by plants, is still limited. Especially inundation with P-rich water seems to stimulate microbial activity, despite Fe-related precipitation of P, resulting in NH_4^+ and/or Fe(II) toxicity. In agricultural areas, this may well generate a friction between preventing acidification and N-eutrophication during drought on the one hand, and preventing external eutrophication and accumulation of toxins during inundation on the other hand.

In mineral-poor fens with P- and S-rich soils, inundation in an early stage of the growing season leads to significantly reduced plant biomass. In this case, sulfide toxicity induced by inundation is presumed to limit plant growth, which may be beneficial in terms of preventing outcompetition by fast growing species, eventually resulting in increased biodiversity. On the other hand, inundation (even with relatively base-rich water) will not be favorable, given the strong internal P-mobilization. Since the *Sphagnum* mosses already predominate and there are no chances for base-rich bryophytes anyway, it is better to occasionally allow low water levels than to engender inundation in these S-rich fen types.

Given the outcomes of this study, the risks and benefits of the re-establishment of fluctuating water levels, with either clean or P-rich water, need to be considered for different fen types separately in water management and nature management plans before its implementation.

Acknowledgements

The authors wish to thank Peter Serné and Jelle Eygensteyn for their analytical work, and Peter Cruijnsen for assistance with sampling in the field. This research was financially supported by Kennisnetwerk Ontwikkeling en Beheer Natuurkwaliteit (O+BN) of the Dutch Ministry of Economic Affairs, Agriculture and Innovation.

Appendices A and B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2015.09.077>.

References

- Amador, J.A., Jones, R.D., 1995. Carbon mineralization in pristine and phosphorus-enriched peat soils of the Florida Everglades. *Soil Sci.* 159, 129–141.
- Armstrong, J., Afreen-Zobayed, F., Armstrong, W., 1996. Phragmites die-back: sulphide- and acetic acid-induced bud and root death, lignifications, and blockages within aeration and vascular systems. *New Phytologist* 134, 601–614.
- Baker, C., Thompson, J.R., Simpson, M., 2009. Hydrological dynamics i: surface waters, flood and sediment dynamics. In: Maltby, E., Barker, T. (Eds.), *The Wetlands Handbook*. Wiley-Blackwell, Oxford, pp. 120–168.

- Bettinelli, M., Baroni, U., Pastorelli, N., 1989. Microwave oven sample dissolution for the analysis of environmental and biological materials. *Anal. Chim. Acta* 225, 159–174.
- Boyer, M.L.H., Wheeler, B.D., 1989. Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. *J. Ecol.* 77, 597–609.
- Caraco, N.F., Cole, J.J., Likens, G.E., 1989. Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. *Nature* 341, 156–158.
- Clymo, R.S., 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot.* 27, 309–324.
- Clymo, R.S., Hayward, P.M., 1982. The ecology of *Sphagnum*. In: Smith, A.J.E. (Ed.), *Bryophyte Ecology*. Chapman & Hall, London, pp. 333–381.
- Cusell, C., Kooijman, A.M., Mettrop, I.S., Lamers, L.P.M., 2013a. Natura 2000 knowledge gaps in De Wieden & De Weerribben. 2013/OBN171-LZ. Directie Agrokennis, Ministerie van Economische Zaken, Den Haag (in Dutch with English summary).
- Cusell, C., Lamers, L.P.M., Van Wirdum, G., Kooijman, A., 2013b. Impacts of water level fluctuation on mesotrophic rich fens: acidification vs. eutrophication. *J. Appl. Ecol.* 50, 998–1009.
- Cusell, C., Kooijman, A., Lamers, L.P.M., 2014. Nitrogen or phosphorus limitation in rich fens? – Edaphic differences explain contrasting results in vegetation development after fertilization. *Plant Soil* 384, 153–168.
- Cusell, C., Mettrop, I.S., Van Loon, E.E., Lamers, L.P.M., Vorenhout, M., Kooijman, A.M., 2015. Impacts of short-term droughts and inundations in species-rich fens during summer and winter: large-scale field manipulation experiments. *Ecol. Eng.* 77, 127–138.
- Estop-Aragón, C., Knorr, K.-H., Blodau, C., 2012. Controls on in situ oxygen and dissolved in organic carbon dynamics in peats of a temperate fen. *J. Geophys. Res.* 117, G02002.
- Koerselman, W., Bakker, S.A., Blom, M., 1990. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *J. Ecol.* 78, 428–442.
- Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* 33, 1441–1450.
- Komor, S.C., 1994. Geochemistry and hydrology of a calcareous fen within the Savage Fen wetlands complex, Minnesota, USA. *Geochim. Cosmochim. Acta* 58, 3353–3367.
- Kooijman, A.M., 1992. The decrease of rich fen bryophytes in the Netherlands. *Biol. Conserv.* 59, 139–143.
- Kooijman, A.M., Whilde, J., 1993. Variation in growth rates between populations of *Scorpidium scorpioides* with different habitats. *J. Bryol.* 17, 567–577.
- Kooijman, A.M., 2012. 'Poor rich fen mosses': atmospheric N-deposition and P-eutrophication in base-rich fens. *Lindbergia* 35, 42–52.
- Lamers, L.P.M., Van Roozendaal, S.M.E., Roelofs, J.G.M., 1998a. Acidification of freshwater wetlands: combined effects of non-airborne sulfur pollution and desiccation. *Water Air Soil Pollut.* 105, 95–106.
- Lamers, L.P.M., Tomassen, H.B.M., Roelofs, J.G.M., 1998b. Sulfate-induced eutrophication and phytotoxicity in freshwater wetlands. *Environ. Sci. Technol.* 32, 199–205.
- Lamers, L.P.M., van Diggelen, J.M.H., Op den Camp, H.J.M., Visser, E.J.W., Lucassen, E.C.H.E.T., Vile, M.A., Jetten, M.S.M., Smolders, A.J.P., Roelofs, J.G.M., 2012. Microbial transformations of nitrogen, sulfur, and iron dictate vegetation composition in wetlands: a review. *Frontiers Microbiol.* 3, 156.
- Lamers, L.P.M., Vile, M.A., Grootjans, A.P., Acreman, M.C., van Diggelen, R., Evans, M.G., Richardson, C.J., Rochefort, L., Kooijman, A.M., Roelofs, J.G.M., Smolders, A.J.P., 2015. Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. *Biol. Rev.* 90, 182–203.
- Lucassen, E.C.H.E.T., Smolders, A.J.P., Roelofs, J.G.M., 2002. Potential sensitivity of mires to drought, acidification and mobilisation of heavy metals: the sediment S/(Ca+Mg) ratio as diagnostic tool. *Environ. Pollut.* 120, 635–646.
- Marschner, H., 1995. *Mineral Nutrition of Higher Plants*. Academic Press, New York.
- Mettrop, I.S., Cusell, C., Kooijman, A.M., Lamers, L.P.M., 2014. Nutrient and carbon dynamics in peat from rich fens and *Sphagnum*-fens during different gradations of drought. *Soil Biol. Biochem.* 68, 317–328.
- Mettrop, I.S., Kooijman, A.M., Lamers, L.P.M., Cusell, C., 2015. Peilfluctuaties in het laagveenlandschap: relaties tussen hydrologie, ecosysteemdynamiek en Natura 2000-habitattypen, rapport fase 2. Vereniging van Bos- en Natuureigenaren, Driebergen.
- Olde Venterink, H., Davidsson, T.E., Kiehl, K., Leonardson, L., 2002. Impact of drying and re-wetting on N, P and K dynamics in a wetland soil. *Plant Soil* 243, 119–130.
- Patrick, W.H., Khalid, R.A., 1974. Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science* 186, 53–55.
- Paulissen, M.P.C.P., van der Ven, P.J.M., Dees, A.J., Bobbink, R., 2004. Differential effects of nitrate and ammonium on three fen bryophyte species in relation to pollutant nitrogen input. *New Phytologist* 164, 451–458.
- Pawlikowski, P., Abramczyk, K., Szczepaniuk, A., 2013. Nitrogen:phosphorus ratio as the main ecological determinant of the differences in the species composition of brown-moss rich fens in north-eastern Poland. *Preslia* 85, 349–367.
- Richardson, C.J., 1985. Mechanisms controlling phosphorus retention capacity in freshwater wetlands. *Science* 228, 1424–1427.
- Rochefort, L., Vitt, D.H., Bayley, S., 1990. Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* 71 (5), 1986–2000.
- Roden, E.E., Edmonds, J.W., 1997. Phosphate mobilization in iron-rich anaerobic sediments: microbial Fe(III) oxide reduction versus iron-sulfide formation. *Arch. Hydrobiol.* 139, 347–378.
- Stumm, W., Morgan, J.J., 1996. *Aquatic Chemistry. Chemical Equilibria and Rates in Natural Waters*, 3rd edn. John Wiley & Sons, Inc., New York.
- Smolders, A.J.P., Roelofs, J.G.M., 1993. Sulphate-mediated iron limitation and eutrophication in aquatic systems. *Aquat. Bot.* 46, 247–253.
- Snowden, R.E.D., Wheeler, B.D., 1993. Iron toxicity to fen plant species. *J. Ecol.* 81, 35–46.
- Strack, M., Kellner, E., Waddington, J.M., 2006. Effect of entrapped gas on peatland surface level fluctuations. *Hydrol. Process.* 20, 3611–3622.
- Van Wirdum, G., (Dissertation) 1991. *Vegetation and Hydrology of Floating Rich-fens*. University of Amsterdam, Datawayse, Maastricht.
- Verhoeven, J.T.A., Beltman, B., Dorland, E., Robat, S.A., Bobbink, R., 2011. Differential effects of ammonium and nitrate deposition on fen phanerogams and bryophytes. *Appl. Vegetat. Sci.* 14, 149–157.
- Wassen, M.J., Van Diggelen, R., Wolejko, L., Verhoeven, J.T.A., 1996. A comparison of fens in natural and artificial landscapes. *Vegetatio* 126, 5–26.
- White, J.R., Reddy, K.R., 2000. Influence of phosphorus loading on organic nitrogen mineralization of Everglades soils. *Soil Sci. Soc. Am. J.* 64, 1525–1534.
- Zak, D., Gelbrecht, J., Steinberg, C.E.W., 2004. Phosphorus retention at the redox interface of peatlands adjacent to surface waters in northeast Germany. *Biogeochemistry* 70, 357–368.
- Zak, D., Wagner, C., Payer, B., Augustin, J., Gelbrecht, J., 2010. Phosphorus mobilization in rewetted fens: the effect of altered peat properties and implications for their restoration. *Ecol. Appl.* 20, 1336–1349.

Supplementary data in addition to:
Mettrop et al.: The ecological effects of water level fluctuation and phosphate enrichment in mesotrophic peatlands are strongly mediated by soil chemistry (Ecological Engineering)

APPENDIX A.1 - 4

Appendix A.1. Height of the peat soil surface just below the living moss layer in relation to the inner core. The water level turning point in between period 1 and period 2 is indicated by the dashed line. Means with S.E. are shown (n=4).

Appendix A.2. Porewater Ca-concentrations (A), alkalinity (B) and pH (C). The water level turning point in between period 1 and period 2 is indicated by the dashed line. Means with S.E. are shown ($n=4$). Note that for Ca the scales on the y-axis differ between graphs.

Appendix A.3. Fe (A), S (B), and DOC (C) concentrations in soil porewater. The water level turning point in between period 1 and period 2 is indicated by the dashed line. Means with S.E. are shown ($n=4$). Note that for Fe the scales on the y-axis differ between graphs.

Appendix A.4. o-PO_4 (A), NH_4 (B) and NO_3 (C) concentrations in soil porewater. The water level turning point in between period 1 and period 2 is indicated by the dashed line. Means with S.E. are shown ($n=4$). Note that for o-PO_4 the scales on the y-axis differ between graphs.

Supplementary data in addition to:

Mettrop et al.: The ecological effects of water level fluctuation and phosphate enrichment in mesotrophic peatlands are strongly mediated by soil chemistry (Ecological Engineering)

APPENDIX B.1 - 2

Appendix B.1. Total N- and P-contents and N:P ratios of above-ground vascular plant tissue upon different treatments, as measured at the end of the experiment. Means with standard deviations are shown (n=4).

Treatment	Plant P (g kg ⁻¹)	Plant N (g kg ⁻¹)	Plant N:P (g g ⁻¹)
Stobbenribben (ST)			
0 cm	0.27 (0.06)	12.3 (1.2)	46.9 (7.7)
0 cm P-rich	0.30 (0.08)	13.2 (2.1)	45.7 (10.8)
-15 cm to +15 cm	0.33 (0.12)	12.5 (3.0)	39.2 (5.4)
-15 cm to +15 cm P-rich	0.73 (0.18)	14.0 (2.4)	18.7 (2.9)
+15 cm to -15 cm	0.37 (0.20)	14.9 (3.8)	44.6 (11.1)
+15 cm to -15 cm P-rich	0.57 (0.29)	22.5 (5.9)	43.0 (10.6)
Binnenpolder Tienhoven (BPT)			
0 cm	0.82 (0.24)	21.1 (2.4)	26.7 (5.3)
0 cm P-rich	0.59 (0.13)	17.4 (2.5)	29.6 (2.0)
-15 cm to +15 cm	0.51 (0.08)	12.9 (1.7)	25.6 (5.9)
-15 cm to +15 cm P-rich	1.09 (0.27)	16.3 (4.3)	15.0 (1.7)
+15 cm to -15 cm	0.49 (0.08)	16.9 (0.9)	35.0 (4.6)
+15 cm to -15 cm P-rich	0.57 (0.05)	18.7 (2.0)	32.6 (1.9)
Ilperveld (ILP)			
0 cm	0.80 (0.09)	11.6 (2.3)	14.4 (1.3)
0 cm P-rich	0.91 (0.24)	11.9 (2.1)	13.5 (2.4)
-15 cm to +15 cm	0.56 (0.10)	11.7 (5.7)	20.2 (6.4)
-15 cm to +15 cm P-rich	0.78 (0.18)	11.4 (2.9)	14.7 (3.0)
+15 cm to -15 cm	0.91 (0.29)	13.5 (2.4)	15.4 (2.8)
+15 cm to -15 cm P-rich	0.85 (0.16)	15.7 (5.5)	18.5 (4.2)

Appendix B.2. Effects of water level, water quality and their interaction on porewater chemistry, as tested by a linear mixed model with LSD post hoc analyses for each location separately. F-ratios including denominator d.f. in parentheses are shown with their level of significance: *P≤0.05, **P≤0.01. Different letters indicate significant differences (P≤0.05) between water level treatments.

Variable	Quality (d.f.=1)	Level (d.f.=5)	Level*Quality (d.f.=5)	Period 1			Period 2		
Stobbenribben (ST)				0 cm	-15 cm	+15 cm	0 cm	-15 cm	+15 cm
Soil height	0.07 (58.6)	53.98** (55.4)	4.78** (55.4)	b	b	c	b	c	a
pH	0.03 (76.8)	15.56** (76.8)	1.46 (76.8)	b	b	b	b	b	a
Alkalinity	0.61 (57.3)	30.88** (57.3)	0.71 (57.3)	d	b	c	d	e	a
Ca	0.27 (52.9)	25.41** (32.1)	1.47 (32.1)	b	a	bc	a	c	a
Fe	2.14 (67.9)	35.54** (55.5)	1.45 (55.5)	cd	b	d	c	e	a
S	0.47 (39.4)	43.82** (31.7)	0.79 (31.7)	b	c	b	b	a	d
o-PO ₄	0.25 (75.1)	26.44** (46.0)	0.74 (46.0)	b	ab	b	b	c	a
NO ₃	0.06 (30.7)	39.03** (18.9)	0.08 (18.9)	a	a	a	a	a	b
NH ₄	0.03 (44.0)	25.39** (43.5)	2.11 (43.5)	c	b	cd	c	d	a
DOC	0.00 (94.1)	9.45** (70.7)	2.22 (70.7)	b	b	a	c	ab	b
Binnenpolder Tienhoven (BPT)				0 cm	-15 cm	+15 cm	0 cm	-15 cm	+15 cm
Soil height	0.41 (48.9)	28.16** (45.8)	1.42 (45.8)	b	b	c	b	c	a
pH	2.45 (77.7)	45.71** (73.3)	1.40 (73.3)	b	c	b	bc	a	d
Alkalinity	3.93 (73.3)	66.86** (71.2)	1.63 (71.2)	c	a	b	c	d	b
Ca	1.13 (50.0)	115.80** (33.9)	1.16 (33.9)	d	a	b	d	e	c
Fe	0.12 (63.9)	99.21** (44.6)	1.16 (44.6)	d	b	d	c	d	a
S	0.00 (59.2)	121.87** (42.1)	1.70 (42.1)	b	c	b	b	a	c
o-PO ₄	0.32 (49.9)	46.37** (44.0)	3.11* (44.0)	c	b	d	b	c	a
NO ₃	0.31 (37.2)	21.00** (34.2)	0.67 (34.2)	a	b	a	a	a	b
NH ₄	0.99 (52.0)	54.52** (38.9)	21.17** (38.9)	c	b	d	c	bc	a
DOC	0.17 (41.7)	89.50** (37.6)	152.44** (37.6)	b	b	c	b	b	a
Ilperveld (ILP)				0 cm	-15 cm	+15 cm	0 cm	-15 cm	+15 cm
Soil height	7.04* (50.2)	75.01** (50.1)	2.66* (50.1)	c	c	d	b	bc	a
pH	0.00 (64.9)	23.84** (64.0)	7.14** (64.0)	bc	c	c	b	b	a
Alkalinity	0.08 (70.6)	60.27** (68.1)	4.13** (68.1)	c	b	d	cd	e	a
Ca	0.00 (76.9)	4.64** (61.4)	0.41 (61.4)	b	a	c	b	d	a
Fe	2.77 (63.6)	32.84** (41.8)	1.30 (41.8)	b	a	b	b	c	a
S	0.03 (74.9)	109.54** (48.8)	0.71 (48.8)	b	c	b	b	a	c
o-PO ₄	0.75 (55.9)	45.14** (41.8)	1.20 (41.8)	c	b	e	c	d	a
NO ₃	1.20 (59.8)	6.59** (44.1)	0.46 (44.1)	a	b	a	a	a	c
NH ₄	0.51 (55.6)	12.12** (35.2)	1.21 (35.2)	b	a	c	b	b	a
DOC	0.23 (80.1)	3.42** (65.5)	2.50 (65.5)	ab	ab	b	b	a	b