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Impacts of short-term droughts and inundations in species-rich fens during summer and winter: Large-scale field manipulation experiments

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ABSTRACT

For the conservation and restoration of biodiverse rich fens, base-rich and nutrient-poor conditions are vital. In wetlands with artificially stable surface water levels, the re-introduction of temporary water level fluctuations has been postulated to restore the acid neutralizing capacity (ANC) of fens during inundation and to reduce surface water P-input during episodes with drought. This is the first study testing this hypothesis in large-scale field manipulation experiments in rich fens with threatened rich fen mosses, rich fens with *Calliergonella*, and poor fens with *Sphagnum*. Five different experiments were conducted: 2 weeks of raised levels (+10 cm) in a floating and a non-floating fen during winter, 2 weeks of high levels in a non-floating fen during summer, and 2 weeks of lowered levels (−15 cm) in a floating and a non-floating fen during summer. For floating fens, both lowered and raised surface water levels in adjacent ditches did not show any effect on water tables, soil ANC or nutrient levels in fens. For non-floating fens, raised surface water levels led to inundation in all vegetation types, without affecting nutrient concentrations or vegetation. Although redox potentials decreased immediately in upper soils, ANC was generally not enhanced in winter due to limited infiltration into the waterlogged soils. In summer, in contrast, ANC increased because accelerated evapotranspiration led to enhanced infiltration of inundation water and higher temperatures resulted in microbial alkalinity generation. Short-term lowering of surface water levels in summer led to lower water tables in non-floating fens, but only when precipitation rates were low. Vegetation, ANC and nutrient concentrations were, however, not affected. The effectiveness of short-term surface water level fluctuation to restore ANC strongly depends on peat buoyancy, water saturation of soils, season and weather conditions. This explains why short-term inundation in winter is often inadequate, while short-term inundation in summer does increase ANC. Short-term droughts do not affect the ANC or nutrient availability. Our results are not only important for the hydrological management of fens, but also have implications for future management since short-term extreme weather events will occur more frequently due to climate change.

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1. Introduction

Rich fens are well-buffered and nutrient-poor peatland habitats that occur at a pH of 5.5–7.5 (e.g., Sjörs, 1950; Wheeler and Proctor, 2000). These species-rich fens are protected under

the European Habitats Directive (transition mires, type H7140) and harbor many threatened vascular plants and bryophytes. In recent decades many rich fens have been lost in Europe due to land use change (Kooijman, 1992; JNCC, 2007; Paulissen et al., 2013; Lamers et al., 2014). Part of this decline can be attributed to natural succession to *Sphagnum*-dominated fens (e.g., Clapham, 1940), but anthropogenic forcing, including high nitrogen deposition rates, have presumably accelerated this succession (Gorham et al., 1987; Gunnarsson et al., 2000). In addition, P-eutrophication has accelerated succession of P-limited rich fens

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to *Sphagnum*-dominated fens (Kooijman, 1993; Kooijman and Paulissen, 2006).

In wetlands with strongly regulated surface water levels as a result of adjacent agricultural water management, one of the proposed management tools to counteract acidification and P-eutrophication is the re-introduction of fluctuating surface water levels. Raised surface water levels may lead to increased alkalinity, pH, and/or Ca-concentrations in soil pore waters (Loeb et al., 2008a,b; Cusell et al., 2013a). Additionally, the acid neutralizing capacity (ANC) may be increased during inundation by microbial reduction of Fe(III), SO_4 and/or NO_3 (Gambrell and Patrick, 1978; Baker et al., 1986), or, more permanently, infiltration of base-rich surface water (Cusell et al., 2013a). Inundation may, however, also result in eutrophication due to higher P- and N-inputs (Wassen et al., 1996) or internal P-mobilization (Patrick and Khalid, 1974; Lamers et al., 1998a).

Allowing lowered water levels means a reduced input of external water, which will presumably result in a reduction of nutrient inputs since surface waters in Europe often contain high nutrient concentrations due to intensive agricultural land use around wetlands (Coops and Hosper, 2002; Lamers et al., 2014). At the same time, however, drought may lead to increased oxygen availability, increased microbial decomposition and thus increased mineralization of nutrients (Grootjans et al., 1986; Bridgham et al., 1998; Olde Venterink et al., 2002; Mettrop et al., 2014). Furthermore, water level drawdown may result in acidification (Lamers et al., 1998b; Lucassen et al., 2002), as a consequence of aerobic oxidation processes by which protons are released (Stumm and Morgan, 1996).

Although all these water-level related processes have been studied intensively in mesocosm and incubation experiments, none of these studies examined their net effect in a field experiment. We present the first study in which the physical and biogeochemical responses to short-term (2 weeks) raising (during winter and summer), and draw-down (during summer) of the surface water level were tested for several years in large-scale field experiments in base-rich fens, and *Sphagnum*-dominated poor fens. The questions addressed in this study were: (1) what are the changes in water table and biogeochemical responses as a result of short-term (2 weeks) changes in surface water level, (2) do these responses differ between floating and non-floating fens, and (3) do the responses to raised surface water levels in non-floating fens differ between winter and summer conditions? Answers to these questions will not only be important for the hydrological management of fens, but are also likely to show future implications for the conservation of fens since short-term periods with intense precipitation or drought are predicted to occur more frequently due to climate change (e.g., Bronstert, 2003; Kundzewicz et al., 2006). Our expectation for (1) was that raised surface water levels lead to increased ANC, but also to P-eutrophication. In contrast, lowered surface water levels were expected to lead to acidification and eutrophication due to increased mineralization rates. For (2), we expected that the effects on biogeochemistry are larger in non-floating fens due to stronger water table fluctuations. For (3), we expected that the increase in ANC upon inundation is stronger in summer, because of higher infiltration and/or higher microbial alkalinity generation.

2. Materials and methods

2.1. Experimental design

Three fen sites in the Dutch Ramsar area and National Park “Weerribben–Wieden” were chosen for the experiments: a floating fen in “De Weerribben” (WEE) and two non-floating

fens in “De Kiersche Wiede” (KW) and “De Veldweg” (VW) (Fig. 1). All fen sites are annually mown with a brush cutter by the end of August to prevent the development of alder carr, and the hay is harvested.

The floating WEE had a buoyant 70–90 cm thick peat layer, floating above a sandy substrate 250 cm below soil surface. It comprised three vegetation types: (1) rich fen with *Calliergonella cuspidata* (Hedw.) Loeske dominating the moss layer, a pore water pH of 5.9 and an average water table at –8.8 cm (Call; *Caricion nigrae*–*Carex nigra*–*Agrostis canina* type), (2) poor fen type with *Sphagnum palustre* (L.) and *Sphagnum fallax* (H. Klinggr.) dominating the moss layer, a pore water pH of 5.0 and an average water table at –12.2 cm (Sph; *Caricion nigrae*–*Pallavicinio*–*Sphagnetum typicum* type), and (3) moor type dominated by ericaceous shrubs (*Erica tetralix* L.) with a *S. palustre* moss layer, a pore water pH of 4.8 and an average water table at –16.7 cm (Moor; *Oxycocco-Ericion*–*Sphagno palustris*–*Ericetum* type).

In contrast, the non-floating KW- and VW-fens were firmly connected to the sandy substrate located at a depth of 60–90 cm. These KW- and VW-fens included all three vegetation types that were mentioned for WEE, and additionally comprised rich fens with a pore water pH of 5.7 and an average water table at –3.0 cm (Scor) with *Hamatocaulis vernicosus* (Mitt.) Hedenäs (*Caricion nigrae*–*Carex nigra*–*Agrostis canina* type) or *Scorpidium cossonii* (Schimp.) Hedenäs (*Caricion davallianae*–*Scorpidium*–*Carex diandra* type), respectively.

The present surface water level of the National Park fluctuates slightly between 0.73 and 0.83 m below mean sea level (BMSL) from March to November and is maintained at 0.83 m BMSL from December to February. The Park includes many historical, man-made ditches with a maximum depth of 1 m in order to be able to regulate the water table for reed harvesting and hay-making. At all fen sites, the vegetation types were located within a maximum distance of 50 m from adjacent ditches.

Fig. 1. The three different experimental fen sites in The Netherlands: ‘De Weerribben’ (WEE; 52°47’N, 5°55’E), and ‘De Kiersche Wiede’ (KW; 52°42’N, 6°08’E) + ‘De Veldweg’ (VW; 52°42’N, 6°07’E).

Five different experiments were conducted to evaluate the biogeochemical effects of surface water level changes on the four different vegetation types, in the three different fen sites mentioned (Table 1). In WEE and KW, raising and lowering of the water level was realized by the construction of dams around the areas (about 5 and 35 ha, respectively) and the use of pumps. Surface water levels were raised by 10 cm for 2 weeks in November to 0.63 m BMSL in the floating WEE-fen (experiment 1) and non-floating KW-fen (experiment 2). These raised levels were applied in 2009 and 2010 for WEE and between 2008 and 2011 for KW. In addition, the effects of high surface water levels in summer were examined in the non-floating VW-fen (experiment 3) during wet periods in July 2009 and 2010. During these periods, about 50 mm of rain in 2 weeks (3.5–4 mm/day) resulted in surface water levels of 0.73 m BMSL. In this case, therefore, surface water levels were not manipulated by pumps but equalled the levels in the entire National Park. Finally, surface water levels were lowered by 15 cm for 2 weeks in July 2009–2011 to about 0.98 m BMSL in the floating WEE-fen (experiment 4) and non-floating KW-fen (experiment 5).

2.2. Sampling

At all three fen sites, five homogenous plots of 2×2 m were selected for each of the vegetation types present. At each plot, water tables in the fen were manually recorded (a) 2 days before, (b) during and (c) 2 days after each experimental manipulation of the surface water level.

Before and after the treatments, soil pore water samples of the upper 10 cm were collected anaerobically with soil moisture samplers (Rhizons SMS 10 cm, Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands), connected to vacuumed plastic syringes (50 ml). The first 10 ml of each sample was discarded to exclude stagnant sampler water. Similar samples were collected in July 2008 to determine the initial biogeochemical conditions for all fen sites.

In experiment 2 (inundation of KW), we also collected inundation water above the vegetation in iodated polyethylene bottles of 100 ml after 1 week of inundation in 2009, 2010 and 2011, and in five adjacent ditches that supplied the inundation water. Concentrations of Cl in inundation water and pore water were used as indicator of infiltration, because of its suitability as an inert tracer.

2.3. Chemical analyses of water samples

The pH-values of all water samples were measured, and alkalinities were determined by titration to pH 4.2, using 0.01 M HCl. Surface water samples were filtered (GF/C glass-fibre filters, $\phi = 1.2 \mu\text{m}$; Whatmann, Brentford, UK). All samples were divided into two subsamples, and 1% HNO_3 was added to one subsample to avoid metal precipitation. Total concentrations of soluble Ca, Fe and S were measured in the acidified subsamples by ICP-OES (Optima 3000 XL, PerkinElmer, Waltham, USA). In the non-acidified subsamples, concentrations of NH_4 ,

NO_3 , O-PO_4 and Cl were analyzed colorimetrically by continuous flow auto-analyzers (Skalar Analytical BV, Breda, The Netherlands).

2.4. Continuous redox measurements

Continuous measurements of the redox potential (E_h) were conducted in VW between September 2010 and July 2012. Two fiberglass probes with platinum sensor tips (PaleoTerra, Amsterdam, The Netherlands) were permanently installed in patches with Scor-, Sph- and Moor-vegetation, and these six probes were connected to a HYPNOS III data logger (MVH Consult, Leiden, The Netherlands; Vorenhout et al., 2011). Each probe contained seven sensor tips to record the E_m (measured potential) at -1 , -3 , -5 , -10 , -15 , -20 and -50 cm below the soil surface every 15 min. E_m was measured as the potential between a sensor tip and a 3 M Ag/AgCl reference probe. The E_h was calculated by adding a standard reference voltage and correcting for differences in pH, since pH indirectly modifies the Nernstian effect of the redox electrode:

$$E_h = E_m + E_{\text{ref}} - 59 \times (7 - \text{pH}),$$

with E_{ref} being the potential of the reference probe.

2.5. Statistical analyses

Statistical analyses were performed in SPSS for Windows (SPSS 20.0.0, IBM, Armonk, USA). A two-way ANOVA with LSD post-hoc test was used to determine significant differences in initial water tables (relative to the fen surface) and biogeochemical conditions between fen sites and vegetation types in July 2008. Since fen sites differed in terms of biogeochemistry and the ability to float, subsequent analyses were performed separately for the five different experiments. Since measurement plots were fixed, hence not independent over the years, a linear mixed model with year as repeated effect was used to determine the response to the fixed factors vegetation type and year (West et al., 2007). Within each year, the differences between measurements directly before and after the treatment were used as response variables. Significant differences between vegetation types and years were further examined by comparing their estimated marginal means in a LSD post-hoc test. P -values in the text are indicated as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

In experiment 2, where raised surface water level led to inundations in KW, two additional linear mixed models, each with year as repeated effect and a single predictor variable, were used. The first model used vegetation type as fixed factor to evaluate if the inundation water had a homogenous composition or differed between the vegetation types. The second model used a categorized value for the start water table as fixed factor to evaluate the effect of this start water table on the increase of Cl-concentrations in soil pore waters during inundation.

Table 1
Overview of the five experiments.

	Fen site	Fen type	Season	Treatment of 2 weeks
Experiment 1	Weerribben (WEE)	Floating	November	Raised surface water level
Experiment 2	Kiersche Wiede (KW)	Non-floating	November	Raised surface water level
Experiment 3	Veldweg (VW)	Non-floating	July	Raised surface water level
Experiment 4	Weerribben (WEE)	Floating	July	Lowered surface water level
Experiment 5	Kiersche Wiede (KW)	Non-floating	July	Lowered surface water level

Fig. 2. Water table (a), pH (b), alkalinity (c) and concentrations of Ca (d), Cl (e), o-PO₄ (f), NO₃ (g) and NH₄ (h) in soil pore water of four vegetation types (Scor: fen dominated by *Scorpidium cossonii* or *Hamatocaulis vernicosus*, Call: fen dominated by *Calliergonella cuspidata*, Sph: fen dominated by *Sphagnum palustre*, Moor with *Erica tetralix* and *Sphagnum palustre*) in three fens. Sample means are shown with their standard deviations ($n=5$). KW: non-floating fen in Kiersche Wiede, VW: non-floating fen in Veldweg, WEE: floating fen in Weerribben. Statistical information is provided in Table S1.

3. Results

3.1. Initial conditions

Water tables were significantly higher in base-rich Scor- and Call-vegetation than in Sph- and Moor-vegetation, with mean depths of 5–10 cm and 15–23 cm below the surface in July ($F_{3,43} = 13.5^{***}$; Fig. 2 and Table S1). As expected, initial pH-values of 5.6–6.3 in soil pore waters for Scor- and Call-vegetation were also significantly higher than in Sph- and Moor-vegetation, where mean pH-values of about 4.7 were measured ($F_{3,42} = 29.4^{***}$). Scor- and Call-vegetation also showed significantly higher alkalinities, Ca- and Cl-concentrations than Sph- and Moor-vegetation, with initial alkalinities of about 1000 and 200 $\mu\text{mol}_c \text{L}^{-1}$ ($F_{3,40} = 21.5^{***}$), Ca-concentrations of around 500 and 200 μmolL^{-1} ($F_{3,41} = 17.5^{***}$) and Cl-concentrations of around 900 and 500 μmolL^{-1} ($F_{3,41} = 10.5^{***}$). It was remarkable that VW showed significantly higher pH, alkalinities and Ca-concentrations than the other two fen sites, especially in base-rich vegetation types as indicated by interaction effects of area and vegetation type (pH: $F_{5,42} = 2.6^*$, alkalinity: $F_{5,40} = 2.6^*$, Ca: $F_{5,41} = 4.3^{**}$). In contrast, concentrations of o-PO_4 , NO_3 and NH_4 did not differ between vegetation types or fen sites, and were low in the soil pore waters of all vegetation types, with concentrations below 1, 3 and 10 μmolL^{-1} , respectively.

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3.2. Experiment 1: raised surface water levels in a floating fen during winter

Raising surface water levels by 10 cm had almost no effect on the water tables in the floating fens (Fig. 3 and Table S2). Along with this limited change in water tables, none of the biogeochemical variables was changed for any of the vegetation types, nor did vegetation suffer from flooding.

3.3. Experiment 2: raised surface water levels in a non-floating fen during winter

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Raising surface water levels by 10 cm in a non-floating fen in November led to inundation in all vegetation types during all 4 years through flooding and lateral flow from adjacent ditches (Fig. 3 and Table S2), without visual effects of flooding on vegetation. Water table rises were largest in 2011 ($F_{2,14.6} = 116.0^{***}$) when initial water tables were lowest with 5–15 cm below the surface ($F_{2,15.5} = 157.4^{***}$), and smallest in 2009 when initial water tables were highest with levels around the soil surface. In 2009, most Scor- and Call-vegetation was already inundated at the start of the treatment. Furthermore, water tables rose more in Scor- and Call-vegetation than in Sph- and Moor-vegetation ($F_{3,15.1} = 8.3^{**}$).

Fig. 3. Effect of five surface water level treatments on the water table (cm above/below the fen surface) in four vegetation types, as measured 2 days before (black lines at the left of each triplet), during (grey lines) and 2 days after the treatments (black lines at the right of each triplet). Sample means (white centres of a line) are shown with their standard deviations ($n = 5$). See the caption of Fig. 2 for a description of the vegetation abbreviations. Statistical information is provided in Table S2.

In inundation waters, concentrations of Cl as an inert tracer did not differ between vegetation types during any of the monitored years, and were equal to those in the adjacent ditches that supplied the water (Fig. 4). Concentrations of o -PO₄, NH₄ and NO₃ were also

similar for all vegetation types and low with values of 0.05, 3 and 2 $\mu\text{mol L}^{-1}$, respectively. In contrast, alkalinities and Ca-concentrations of inundation water differed for Scor- and Call-vegetation versus Sph- and Moor-vegetation, with alkalinities of around

Fig. 4. pH (a), alkalinity (b) and concentrations of Ca (c), Cl (d), S (e), o -PO₄ (f), NH₄ (g) and NO₃ (h) in the surface water of adjacent ditches and in the inundation water above four vegetation types in the KW-fen (experiment 2). See the caption of Fig. 2 for abbreviations. Sample means for 2009–2011 are shown with their standard deviations ($n = 15$). Different letters indicate significant differences between vegetation types ($P \leq 0.05$).

Fig. 5. Effects of five surface water level treatments on the Cl-concentrations ($\mu\text{mol L}^{-1}$) in four vegetation types, as measured 2 days before (black lines at the left of each triplet), during (grey lines; only in experiment 2) and 2 days after the treatments (black lines at the left of each triplet). See the caption of Fig. 2 for abbreviations. Sample means (white centres of a line) are shown with their standard deviations ($n=5$). Statistical information is provided in Table S2.

900 versus $500 \mu\text{mol}_c \text{L}^{-1}$ ($F_{4,17.3} = 80.6^{***}$) and Ca-concentrations of about 500 versus $200 \mu\text{mol L}^{-1}$ ($F_{4,20.1} = 68.0^{***}$). Also, pH decreased significantly from about 7.0 in ditches to 6.4 in the inundation water above Scor- and Call-, and to 5.4 above Moor-vegetation ($F_{4,19.4} = 36.0^{***}$).

In all years, Cl-concentrations in the inundation water were higher than the initial Cl-concentrations in the soil pore waters (Fig. 5). However, inundation only led to increased pore water Cl-concentrations in Scor- and Call-vegetation in 2011 and in Sph- and Moor-vegetation in 2010 and 2011 (Table S2). Additional analysis showed that pore water Cl-concentrations only increased when initial water tables were lower than 5 cm below the soil surface ($F_{4,17.1} = 9.1^{***}$; Table 2).

In line with the absence of infiltration in 2008 and 2009, inundation had almost no biogeochemical effect in these years. However, during the inundation of 2011, when infiltration occurred in all vegetation types, biogeochemical effects were observed. Redox potentials (E_h) decreased almost immediately in Sph- and Moor-soils from about +600 to -100 mV in the upper 12 and 18 cm of the soils (Fig. 6). On the other hand, E_h was only

slightly affected in Scor-soils, because nearly the entire profile already showed anaerobic conditions before inundation, with E_h values of around -200 mV . In these soils, E_h only changed slowly from around 300 to -200 mV in the upper 2 cm of the soil. In contrast, pore water alkalinities and Ca-concentrations only increased significantly in Scor- and Call-vegetation, with $350 \mu\text{mol}_c \text{L}^{-1}$ and $150 \mu\text{mol L}^{-1}$, and remained equal in Sph- and Moor-vegetation, as indicated by the interaction vegetation type*year (alkalinity: $F_{9,8.4} = 7.8^{**}$, Ca: $F_{9,15.0} = 3.5^{*}$; Figs. 7 and 8, and Table S2). Finally, inundation in 2011 had no effect on Fe-, S-, $o\text{-PO}_4$, NH_4 - and NO_3 -concentrations in soil pore waters of any vegetation type (Fig. S1 and Table S2).

Supplementary material related to this article found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2015.01.025>.

3.4. Experiment 3: raised surface water levels in a non-floating fen during summer

Before the start of the treatment, water tables were significantly lower in July 2010 than July 2009 ($F_{2,16.0} = 290.0^{***}$; Fig. 3 and

Table 2

Effect of water table on Cl-infiltration into soil pore water of the KW-fen during inundations in 2009–2011 (experiment 4). Data shown are mean differences between the Cl-concentrations just after and before the inundations, and their standard deviations. Different letters indicate significant differences between water level categories ($P \leq 0.05$).

	Initial water table				
	Above the surface	0–2 cm below surface	3–5 cm below surface	6–9 cm below surface	More than 9 cm below surface
Cl ($\mu\text{mol L}^{-1}$)	$-64 (81)^A$	$53 (134)^A$	$46 (111)^A$	$282 (167)^B$	$185 (107)^B$

Fig. 6. Redox potentials (E_h) in the upper 20 cm of the soil (vertical scale) in three vegetation types of the KW-fen (Scor: fen dominated by *Hamatocaulis vernicosus*, Sph: fen dominated by *Sphagnum palustre*, Moor with *Erica tetralix* and *Sphagnum palustre*) between June 16 and July 31 (2011; left), and November 1 and December 16 (2011; right). The vertical white lines indicate the initiation and end of the treatment period. For interpolation, ordinary kriging was applied in ArcGIS (ArcMap 10.0, ESRI, Redlands, USA).

Table S2), with tables of 20–30 cm below the surface in 2010 (when the treatment was preceded by a very dry period) and tables of 3–20 cm below the surface in 2009. Rather heavy rainfall of $10\text{--}20\text{ mm day}^{-1}$ during the first treatment week of 2009 and 2010 led to a rise of water tables by 10–15 cm. In 2009, this rise resulted in inundation with surface water in Scor- and Call-vegetation, while lower initial water levels in 2010 prevented inundations.

The raised surface water levels in 2009 and 2010 had no visual flooding effect on vegetation, and no effect on pH or o-PO_4 , NH_4^- and NO_3^- concentrations in soil pore waters, but alkalinities and Ca-concentrations increased (Fig. S1 and Table S2). These effects were stronger in 2009 than in 2010 and differed between vegetation types, as indicated by the interaction vegetation type*year (alkalinity: $F_{3,10.9} = 4.0^*$, Ca: $F_{3,12.8} = 3.9^*$; Figs. 7 and 8). In 2009, alkalinities and Ca-concentrations increased more (about $1900\text{ }\mu\text{mol}_c\text{ L}^{-1}$ and $450\text{ }\mu\text{mol}_c\text{ L}^{-1}$) in the inundated Scor- and Call-vegetation than in the non-inundated Sph- and Moor-vegetation (about $300\text{ }\mu\text{mol}_c\text{ L}^{-1}$ and $80\text{ }\mu\text{mol}_c\text{ L}^{-1}$). Non-inundated Scor- and Call-vegetation in 2010 showed significantly smaller increases in alkalinities (about $600\text{ }\mu\text{mol}_c\text{ L}^{-1}$) and Ca-concentrations (about $150\text{ }\mu\text{mol}_c\text{ L}^{-1}$) than in 2009, while Sph- and Moor-vegetation showed similar increases in alkalinities (about $250\text{ }\mu\text{mol}_c\text{ L}^{-1}$) and Ca-concentrations (about $80\text{ }\mu\text{mol}_c\text{ L}^{-1}$). Furthermore, Cl-concentrations increased by about $300\text{ }\mu\text{mol}_c\text{ L}^{-1}$ in soil pore waters of all vegetation types during the non-inundated situation in 2010, but remained unaltered in 2009.

In 2009 and 2010, raised surface water levels led to decreased S-concentrations and increased Fe-concentrations in soil pore waters of all vegetation types (Fig. S1 and Table S2). In all vegetation types, S-concentrations decreased with

$50\text{--}150\text{ }\mu\text{mol}_c\text{ L}^{-1}$ in both years, while Fe-concentrations increased significantly more in 2009 than 2010 ($F_{1,13.7} = 25.6^{***}$), with $50\text{--}115\text{ }\mu\text{mol}_c\text{ L}^{-1}$ and $15\text{--}25\text{ }\mu\text{mol}_c\text{ L}^{-1}$, respectively.

3.5. Experiment 4: lowered surface water levels in a floating fen during summer

2 weeks of lowered surface water levels ($\sim 15\text{ cm}$) had no clear effect on the water tables in the floating soils (Fig. 3 and Table S2), nor on vegetation. In July 2010 and July 2011 water tables were hardly affected, which may be attributed to a precipitation surplus of $1.0\text{--}1.5\text{ mm day}^{-1}$ at the end of the treatment period (weather station Marknesse: KNMI, 2014). In July 2009, when there was an evaporation surplus of about 2.5 mm day^{-1} , water tables lowered in all soils upon treatment ($F_{2,9.9} = 15.9^{**}$), but only 4 cm. In addition, there were no biogeochemical changes in any of the vegetation types (Fig. S1 and Table S2), except that pore water Cl- and S-concentrations decreased in 2011 (Cl: $F_{2,7.6} = 17.1^{**}$, S: $F_{2,7.5} = 5.2^*$), presumably due to dilution with rainwater.

3.6. Experiment 5: lowered surface water levels in a non-floating fen during summer

Before the start of the treatments, water tables clearly differed among the 3 years ($F_{2,15.8} = 209.5^{***}$; Fig. 3 and Table S2), with lowest levels of 20–30 cm below the surface in 2010 (when the treatment was preceded by a very dry period) and significantly higher levels in 2009 (0 to $\sim 25\text{ cm}$) and 2011 (~ 5 to $\sim 10\text{ cm}$). In 2011, most Scor-vegetation was already inundated at the start of the treatment.

Fig. 7. Effects of five surface water level treatments on the alkalinities (mmol L^{-1}) in four vegetation types, as measured 2 days before (black lines at the left of each triplet), during (grey lines; only in experiment 2) and 2 days after the treatments (black lines at the left of each triplet). See the caption of Fig. 2 for abbreviations. Sample means (white centres of a line) are shown with their standard deviations ($n = 5$). Statistical information is provided in Table S2.

Lowering of surface water levels by 15 cm only led to lower field water tables in July 2011 ($F_{2,16.0} = 167.0^{***}$; Fig. 3 and Table S2), while water tables in the fens raised in July 2009 and 2010 due to heavy rainfall. These raised water tables in 2009 and 2010 had no effect on pH and Fe- , o-PO_4 , NH_4^- and NO_3^- -concentrations in soil pore waters (Fig. S1 and Table S2). The inundated locations with Scor- and Call-vegetation did, however, show significantly increased alkalinities (about $500 \mu\text{mol L}^{-1}$) in their soil pore waters in 2009, as indicated by the interaction effect vegetation type*year ($F_{5,14.4} = 3.1^*$; Fig. 7), while Ca-concentrations did not change (Fig. 8) and Cl-concentrations even decreased during this treatment (Fig. 5). There were no visual effects of flooding on vegetation survival.

Although surface water levels were also raised by 4–6 cm after the treatment in July 2011 due to 2 days of rainfall (about 25 mm day^{-1}) after the end of the treatment, the lowered surface water levels did still lead to lower water tables during the treatment (Fig. 3 and Table S2). Water tables decreased by 10–15 cm in all vegetation types, leading to an increase of the redox potential (E_h) from around -200 to $+500 \text{ mV}$ in the upper 5 cm of Scor-soils (Fig. 6). In contrast, E_h did not change in the upper 10 cm of Sph- and Moor-soils, since the initial E_h was already above $+600 \text{ mV}$. However, none of the vegetation types showed significant changes in pH, alkalinity, Ca-concentrations or nutrient concentrations (Fig. S1 and Table S2). E_h decreased immediately in all vegetation types upon the 2 days of rainfall after the end of the treatment.

4. Discussion

4.1. Water table dynamics in floating fens hardly depend on surface water levels

As hypothesized, fluctuations in surface water levels had almost no effect on water tables in floating fens dominated by *Calliergonella* or *Sphagnum*, since the buoyant peat followed the surface water levels. This was not only the case during short-term experiments of 2 weeks, but also occurred during a similar surface water level rise of 3 months (field observation C. Cusell). As a result of the limited change in water tables, ANC and nutrient concentrations in soil pore waters did not change during the field experiments, not even after 3 months of lowered or raised surface water levels (Cusell et al., 2013b).

It has, however, been reported that lowered surface water levels can still lead to lower water tables in floating fens, especially when soil thickness increases (e.g., van Wirdum, 1993). Similarly, it has also been shown that raised surface water levels may lead to inundations in floating fens (O'Connell, 1981; Koerselman, 1989; van Wirdum, 1991), especially on rich fens with *Scorpidium* species (Cusell et al., 2013b). Such rich fens are usually located at or below, instead of clearly above the water table. Although there is still debate about the origin of this water above soil surface, which may be seepage of water from beneath the floating mat (van Wirdum, 1991) or flooding by surface water (Cusell et al., 2013b), it is clear that floating rich fens may get inundated when surface water levels

Fig. 8. Effects of five surface water level treatments on the Ca-concentrations ($\mu\text{mol L}^{-1}$) in four vegetation types, as measured 2 days before (black lines at the left of each triplet), during (grey lines; only in experiment 2) and 2 days after the treatments (black lines at the left of each triplet). Sample means (white centres of a line) are shown with their standard deviations ($n=5$). See the caption of Fig. 2 for abbreviations. Statistical information is provided in Table S2.

get sufficiently high. The absence of inundation in the floating fens we studied may thus mainly be caused by the limited water level rise of only 10 cm and their high buoyancies, but may also reflect the absence of rich fens with *Scorpidium* species in the floating fens that were studied.

4.2. Short periods of lowered surface water levels do not lead to acidification or eutrophication

Non-floating fens did not respond uniformly to surface water level draw-downs of 2 weeks in summer, due to weather conditions. Water tables only dropped during an evapotranspiration surplus. Under these conditions, water tables dropped 10–15 cm in non-floating fens, while levels only dropped 4–6 cm in floating fens. The lowered water tables did not affect redox potentials (E_h) in the upper soil layers of non-floating fens with Sph- and Moor-vegetation, which were already above +600 mV. In contrast, a strong increase of E_h (from –200 to +500 mV) upon water level draw-down was found in the upper 5 cm of Scor-soils, indicating oxygen intrusion into these soils (e.g., Gambrell and Patrick, 1978). This short-term intrusion of oxygen did not lead to acidification or eutrophication, but it is well known that longer episodes of drought can stimulate net mineralization rates (Grootjans et al., 1986; Bridgham et al., 1998; Olde Venterink et al., 2002; Mettrop et al., 2014) and acidification by aerobic oxidation processes (Lamers et al., 1998a; Lucassen et al., 2002; Mettrop et al., 2014).

4.3. Inundation of non-floating fens

In non-floating fens, high water tables clearly led to inundation due to fixation of these fens to the sandy substrate, as is supported by diver data (Cusell et al., 2013b). High Cl-concentrations in inundation waters compared to soil pore waters showed that the inundation water originated from the adjacent ditches. Plots with highest water tables before the treatment, which were often dominated by *Scorpidium* species or *H. vernicosus*, showed the largest rise in water tables during inundation. This is presumably because they were situated in depressions that were 5–10 cm lower than the surface of *Sphagnum*-dominated vegetation, where water tables often bulge somewhat.

4.4. Effect of winter inundation on the ANC depends on infiltration rates

The absence of change in Cl-concentrations in soil pore waters during most winter inundations, despite higher Cl-concentrations in the inundation water, indicated that there was hardly any infiltration into the waterlogged soils. Infiltration only occurred where initial water tables were lower than 5 cm below soil surface. This is in accordance with Hooijer (1996) and Banach et al. (2009), who also found limited infiltration of inundation water in waterlogged riverine floodplain fens.

In the case in which 2 weeks of inundation during winter had no effect on the infiltration of HCO_3^- , Ca and Mg (ANC input), anaerobic

reduction rates in the peat (internal ANC generation) did not occur either. However, longer-term inundations during winter can lead to both forms of ANC-increase in waterlogged rich fen soils, as demonstrated in a mesocosm experiment (Cusell et al., 2013a).

2 weeks of winter inundation in 2011 did lead to an increase in alkalinity and Ca-concentration in soil pore water by 50–100%, but only in Scor- and Call-soils. Since alkalinity and Ca-concentration increased at a ratio of 2:1 in these plots, we attribute this increase only to infiltration of Ca- and HCO_3^- -rich inundation water, and not to anaerobic microbial reduction processes. Despite E_h values below -200 mV in Scor-vegetation, at which Fe(III)- and SO_4^- -reduction may lead to internal alkalinization (e.g., Ponnamperna, 1984), unchanged Fe- and SO_4^- -concentrations in soil pore waters support the idea of limited alkalinity generation. This is most probably caused by the low temperatures and subsequent low microbial activity in winter (Loeb et al., 2008a,b).

For Sph- and Moor-vegetation, inundation led to an immediate decrease of E_h from $+600$ mV to -100 mV, but these anaerobic conditions did not result in internal alkalinity generation. Unlike in Scor-vegetation, infiltration of inundation water did not lead to an increase of alkalinity and Ca-concentrations in soil pore waters, which was related to lower alkalinity and Ca-concentrations in the water layer above Sph- and Moor-vegetation compared to Scor- and Call-vegetation. This striking difference in inundation water composition at a relatively short distance (10–20 m) can only be explained by the exchange of Ca^{2+} for H^+ between inundation water and the adsorption complex of living mosses and their peat. This exchange process has also been described for non-inundated conditions in *Sphagnum*-dominated fens (Clymo, 1963; Kooijman and Bakker, 1994). Acidification (alkalinity consumption) of inundation water may have mainly occurred at *Sphagnum*-dominated sites, because adsorption complexes of *Scorpidium* spp. and *C. cuspidata* were probably already saturated with Ca before inundation, while those of *Sphagnum* spp. often contain high concentrations of H^+ .

4.5. Effect of inundation on the ANC depends on season

The increase of alkalinity and Ca-concentrations in soil pore waters upon 2 weeks of inundation of non-floating fens with Scor- and Call-vegetation was much stronger in summer than in winter. This clear seasonal difference may be explained by higher evapotranspiration in summer, which facilitates the infiltration of base-rich inundation water (Cusell et al., 2013a).

Since alkalinity and Ca-concentration increased at a ratio of 4:1 instead of 2:1, the increase in alkalinity in summer is presumably not only caused by the infiltration of base-rich inundation water, but also by other processes, i.e., evaporative concentration and microbial alkalinity generation. As long as water tables became sufficiently high (between 1 and 10 cm below the surface) in summer, raised surface water levels even led to increased alkalinity, Ca- and Cl-concentrations under non-inundated conditions. These increases cannot be caused by infiltration and are probably due to evaporative concentration. In addition, alkalinity production may have been higher during inundations in summer due to increased microbial alkalinity generation in the warmer anoxic peat soil. The simultaneous decrease in SO_4^- -concentrations (SO_4^- -reduction) and increase in Fe-concentrations (mobilization of Fe(II)) support this theory.

4.6. Short inundations with P-poor water do not lead to P-eutrophication

P-eutrophication did not occur in any of the experiments. It must, however, be noted that the inundation water contained very low o-PO_4 concentrations of $0.05 \mu\text{mol L}^{-1}$. Other studies showed

that inundation with P-rich surface water may well lead to P-eutrophication in fens (e.g., Wassen et al., 1996). Although P-uptake by vegetation may somewhat mask P-eutrophication, especially in summer, our field experiments also showed no evidence of increased internal P-mobilization in waterlogged soils upon 2 weeks of inundation. Several other experiments have, however, shown that prolonged inundation may well lead to internal P-mobilization in waterlogged soils (Patrick and Khalid, 1974; Loeb et al., 2008a,b), especially in P-rich fens (Cusell et al., 2013a), with SO_4^- -rich inundation water (Lamers et al., 1998a) and at higher temperatures (Cabezas et al., 2013). In the present study, the duration of 2 weeks seems to be sufficiently short and P-concentrations in flooding water seem to be sufficiently low to prevent P-eutrophication. However, P-eutrophication can certainly occur during flooding when soil quality and/or surface water quality are insufficient.

4.7. Implications for fen management

Rich fens, comprising many threatened vascular plants and bryophytes, can only persist under well-buffered and nutrient-poor conditions (e.g., Sjörs, 1950; Wheeler and Proctor, 2000; Kooijman and Paulissen, 2006). In wetlands with fixed surface water levels, the re-introduction of fluctuating levels has recently been proposed to restore the ANC and to reduce P-eutrophication, in order to conserve or restore fen biodiversity.

We did not see any direct effects of the experimental raising or lowering of the water table on vegetation. Our large-scale field experiments suggest that 2 weeks of raised surface water levels ($+10$ cm) may counteract acidification of base-rich fens by increasing the ANC, but only under specific conditions. A rise in surface water levels should lead to actual inundation, which was not the case for the floating *Sphagnum*-dominated fens studied. In contrast, in non-floating fens, 2 weeks of raised surface water levels did lead to inundation. The ANC, however, only increased when base-rich inundation water actually infiltrated into the soil. In winter, this only occurred when initial water tables were lower than 5 cm below the surface. In summer, infiltration was facilitated by higher evapotranspiration, as supported by the results of long-term mesocosm experiments (Cusell et al., 2013a). Furthermore, higher temperatures in summer led to internal alkalinity generation in non-floating fens as a result of Fe(III)- and SO_4^- -reduction, although this effect may be temporary since aerobic oxidation during subsequent droughts can lead to acidification (Lamers et al., 1998a,b; Loeb et al., 2008a,b).

2 weeks of lowered surface water levels (-10 cm) did not have severe acidifying or eutrophying effects. However, longer periods of drought can stimulate net mineralization and acidification, and are therefore not recommended.

4.8. Suggestions for further research

The experiments in this study were of relatively short duration. In order to get a better understanding of long-term effects, future experiments during multiple weeks are suggested, focusing both on drought and inundation. These experiments should preferably be conducted under different meteorological conditions. The analysis of such measured data can be useful toward determining an essential and fundamental set of peatland processes and feedbacks (Waddington et al., 2014).

In addition, additional field manipulation experiments during fall, summer and spring are needed to gain a better understanding of the impact during different seasons. Natural extreme events, such as droughts, are generally associated with increased temperatures, altering kinetics of biogeochemical reactions or decomposition rates as drivers of dissolved nitrogen turnover in fens

(Cabezas et al., 2012). But more importantly from a management perspective, inundations with base-rich water may be much more effective in summer than in winter to restore the ANC. High temperatures are expected to result in accelerated evapotranspiration and enhanced infiltration of inundation water, but also in accelerated microbial alkalinity generation (Cusell et al., 2013a).

The absence of inundation in the floating fens we studied may be related to the limited water level rise of only 10 cm. Additional experiments with a larger rise in water level would reveal to what extent the buoyancy of floating fens is still limiting the influence of fluctuating water levels.

5. Conclusions

Short-term inundations can be profitable for rich fens as long as surface waters are nutrient-poor and infiltration does occur. This management tool is most suitable for non-floating fens and may best be applied in summer. Short-term periods with intense precipitation, which are very likely to occur more frequently in the future due to climate change, can thus have a positive effect on rich fens, especially in summer. Severe drought periods will, on the other hand, have negative direct and indirect (biogeochemical) effects on vegetation.

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APPENDIX A: FIG. S 1

The effects of five surface water level treatments on the pH, Fe, SO_4 , o-PO_4 , NH_4 and NO_3 concentrations in four vegetation types during 2 – 4 years.