Ecological Engineering 75 (2015) 208–216

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Restoration of acidified and eutrophied rich fens: Long-term effects of traditional management and experimental liming

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ARTICLE INFO

Article history:
Received 5 August 2014
Received in revised form 26 November 2014
Accepted 1 December 2014
Available online xxx

Keywords:
Rich fens
Successional stages
Management measures
Liming
Mowing
Burning
Acidification
Eutrophication

ABSTRACT

Rich fens are known for their high botanical diversity encompassing many endangered species. For decades, several management measures, including mowing and burning, have been applied to maintain a high biodiversity by means of slowing down the natural succession from calcareous rich fens to acidic poor fens or woodland. In this study, we assessed the long-term effects of these traditional management measures, and explored the effectiveness of liming as a measure to restore rich fen vegetation. Effects of summer mowing, and of burning after winter mowing, were assessed by comparing current (2013) and historical (1967) vegetation data. Effects of experimental liming, using different levels of lime addition (0, 1000, 2000, and 4000 kg Dolokal/ha), were monitored in the field during 7.5 years. Summer mowing led to more acidic and nutrient-poor conditions as indicated by a shift from rich to poor fen vegetation, including a well-developed bryophyte cover dominated by *Sphagnum* with some threatened species. Burning (after winter mowing) counteracted acidification but increased nutrient availability, as indicated by dominance of vascular species characteristic of productive tall-herb grasslands and a sparse bryophyte cover with common species. We conclude that the traditional measures were unable to maintain rich fen composition in the long term. Given the fact that the restoration of hydrological conditions, favouring rich fens, is not always feasible, liming could be an alternative to counteract acidification and improve rich fen conditions in the short term. This measure, however, appeared to be unsustainable as the re-establishment and dominance of *Sphagnum* spp. seriously complicated the development of rich fen vegetation in the longer term.

1. Introduction

Fens show a high habitat and species diversity, and are home to many rare and endangered plant species (Bootsma et al., 2002; Bedford and Godwin, 2003). As they show a natural terrestrialisation from open water into different successional stages of vegetation composition, fens often comprise a myriad of vegetation types. The formation of floating mats and the subsequent increase in peat thickness leads to increased influence of base-poor rainwater, and reduced influence of base-rich surface water and/or groundwater, which still remains dominant in the margins and deeper in the peat mat. This process creates a biogeochemical gradient that enhances the development of different successional stages from rich fen (dominated by *Cyperaceae* and brown mosses), via poor fen (with or without hummock forming *Sphagnum* species), towards eventually carr woodland (Verhoeven and Bobbink, 2001; Grootjans et al., 2006). Rich fens are generally more species-rich than poor fens or woodlands. These earlier successional stages are, however, seriously threatened and biodiversity has strongly declined in many rich fens as a result of fast succession to either poor fens or woodlands (Beltman et al., 2001,b; Middleton et al., 2006a,b; Lamers et al., 2002, 2014).

Due to anthropogenic influences including major changes in hydrology, agricultural pollution of groundwater and surface water, and increased atmospheric deposition of sulphur and nitrogen, many fens have degraded as a result of concomitant desiccation, acidification and eutrophication (Hogg et al., 1995;

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http://dx.doi.org/10.1016/j.ecoleng.2014.12.006
0925-8574/

Kooijman and Paulissen, 2006; Klimkowska et al., 2007; Lamers et al., 2002, 2014). This has significantly changed the rate, course and outcome of succession, resulting in accelerated transition of Brownmoss dominated rich fens to *Sphagnum* dominated poor fens (van Diggelen et al., 1996; Kooijman and Paulissen, 2006; Bobbink et al., 2010; Lamers et al., 2014). If *Sphagnum* spp. become dominant, acidification is accelerated by their high rain water retention, cation exchange and active excretion of uronic and phenolic acids, enhancing peat accumulation (Hemond, 1980; Verhoeven and Liefveld, 1997; Bootsma et al., 2002). In addition, eutrophied fens often show a low species diversity as slow-growing vascular plant- and bryophyte species, adapted to low nutrient concentrations, are outcompeted by tall-growing, highly productive species (Hogg et al., 1995; Bobbink et al., 1998, 2010; Cusell et al., 2014a).

To counteract these anthropogenic effects, and in particular to maintain the original lifespan of early successional vegetation, such fens depend on active management including mowing, grazing or burning (Hogg et al., 1995; Middleton et al., 2006a). For decades, mowing has been a traditional management tool in European fens. The removal of biomass and resulting increase of light availability is thought to increase biodiversity, but only if species are still present or able to disperse or germinate (Middleton et al., 2006a). However, few studies have tried to explore long-term effects of mowing management on vegetation development in fens (van Diggelen et al., 1996; van Belle et al., 2006). Burning after winter mowing can be useful to remove litter, and fire is also thought to slightly raise the soil pH and base-cation concentrations (Raison, 1979). However, not much is known about the potential role of burning in maintaining rich fen biodiversity (Middleton et al., 2006a).

Acidification is recognised as an important issue in fens nowadays. More intrusive measures, such as top-soil removal have enhanced acidification due to stagnation of rainwater, re-establishment of *Sphagnum* (Beltman et al., 1996b; Beltman et al., 1996b), and the exposure of the formerly reduced peat soil to oxygen that may oxidise reduced sulphur (Mylona, 1996). A more recent measure to counteract acidification is the application of lime, which may improve base-rich conditions by increasing acid buffering, and preventing *Sphagnum* spp. from becoming dominant (Beltman et al., 2001; Dorland et al., 2004). In this way, base-rich conditions may be restored, enabling minerotrophic rich fen species to re-establish (Beltman et al., 1996a, 2001; Patzelt et al., 2001). However, an increase in soil pH may at the same time stimulate peat decomposition and increase mineralisation (Ono, 1991; Smolders et al., 2002). As only few studies have explored the effectiveness of liming on vegetation and biogeochemistry, in our study we experimentally tested this measure to restore rich fen vegetation from *Sphagnum*-dominated poor fen vegetation, by applying different levels of lime and monitoring the development over a period of 7.5 years. In addition, we assessed the long-term effects of traditional management measures aimed at maintaining species richness in fens. Effects of summer mowing, and of burning after winter mowing, were assessed by comparing current (2013) with historical (1967) vegetation data. Our results will be discussed with respect to their implications for future management to restore rich fen vegetation in fens.

2. Methods

2.1. Research area

The research was carried out in the wetland reserve and Natura 2000 area the 'Nieuwkoopse Plassen' in The Netherlands (52°9′N, 4°49′E). This area is characterised by alternating ridges of peat and peat extraction ponds, with an extensive network of canals and ditches throughout the reserve, as well as several large shallow fen lakes (den Held et al., 1992). The current vegetation types, representative of different successional stages found on peat mats, can only be maintained by human interference, as areas without management have all developed into carr woodland (Wiegers, 1992). The surface level is ± 1.5 m below sea level, which is 0.4–4 m higher than surrounding agricultural areas that have subsided due to drainage. As a result, the Nieuwkoopse Plassen reserve has become an infiltration area dependent on precipitation and relatively nutrient-rich, buffered surface water from the river the Oude Rijn to maintain sufficiently high surface water levels.

2.2. Comparing current with historical vegetation data

2.2.1. Sampling strategy

The vegetation of the Nieuwkoopse Plassen was investigated by den Held in 1967 (den Held, 1970), by recording the cover and composition of bryophytes and vascular plant species in randomly selected plots throughout the reserve. In 2013, 49 of these historic fen sites were reassessed. The selection was based on their current management type (23 summer-mown, and 26 winter-mown and burned), the vegetation composition in 1967 (equal distribution of the different successional stages) and the accuracy by which the sites could be found again. Selected sites ranged in size from 2 to 30 m^2 (average size of 10 m^2). It was not known exactly how long summer mowing and burning after winter mowing had been carried out since 1967. We do know, however, that the measures had been carried out annually for at least 10 years before the start of this part of the research.

2.2.2. Vegetation assessment

Composition and cover of bryophytes (April–May, 2013) and vascular plants (June–July, 2013) were assessed using the ordinal scale used by den Held (1970): codes 1–4 represent <5% cover with 1: 1 individual, 2: 2–5 individuals; 3: 6–50 individuals, 4: >50 individuals; 5: 5–12% cover; 6: 13–25% cover; 7: 26–50% cover; 8: 51–75% cover; 9: 76–100% cover. The numbers of individuals for categories 1–4 were adjusted to account for the differences in size between the relevés by multiplying them with a factor calculated as the log of the area of the relevé, divided by the log of the standard relevé area (4 m^2). The nomenclature follows van der Meijden (2005) for vascular plants and Siebel and During (2006) for bryophytes, but *Sphagnum capillifolium* and *Sphagnum rubellum* were considered one species. Additional information about red-list status and common habitats was gained from Synbiosys (version 2.5.8. Alterra, Wageningen).

2.3. Liming experiment

2.3.1. Experimental set up

In October, 2006, 12 plots of 3 m × 3 m were created on a thick, (formerly) floating mat, from which the top soil (10–30 cm) had been removed in the winter of 2000–2001. At start of the experiment, the mat had been (re-) acidified and become dominated by *Sphagnum* species. Vegetation was mown during summer every year, which continued during the experimental period. Liming treatments were randomly distributed over these plots (three replicates for each treatment): control, 1000 kg/ha lime (1 k), 2000 kg/ha lime (2 k), and 4000 kg/ha lime (4 k). The amount of lime for each treatment was equally spread over the plots as a powder (Dolokal; $CaCO_3$ 84%, $MgCO_3$ 10%, MgO 5%, <0,16 mm).

To assess treatment effects on soil chemistry, a pooled soil sample (2–3 subsamples) of the upper 10 cm was collected from each plot just before the treatment ($t = 0$), and at $t = 0.5$, 1, 2, 2.5, 4.5, and 7.5 years. Additionally, at $t = 4.5$ and 7.5 years, soil pore water was collected anaerobically, using vacuum syringes (60 mL) connected to ceramic soil moisture samplers (Eijkelkamp Agrisearch Equipment) that were placed in-situ. Soil samples and pore water samples were stored overnight at 4 °C until further analysis. The composition of the bryophytes in the plots was assessed at $t = 0.5$, 1.5, 2.5, 4.5, and 7.5 years, the vascular plant composition at $t = 0.5$, 1.5, 2.5, and 4.5 years, using the Londo method (Londo, 1975). Afterwards, this scale was converted to the scale used by den Held (1970).

2.3.2. Chemical analysis

The bio-available amount of phosphorus (P) in the soil was measured by water extraction using 17.5 g of fresh soil shaken (2 h) with 50 mL MilliQ. To determine the bio-available amount of nitrate (NO_3^-), ammonium (NH_4^+) and potassium (K^+), a soil extraction was performed using 50 mL of 0.2 M NaCl shaken (2 h) with 17.5 g fresh soil. The soil pH was determined in the latter extract, using a combined pH electrode (radiometer) and a TIM840 pH meter. The amounts of calcium (Ca^{2+}) and magnesium (Mg^{2+}) bound to the soil adsorption complex were determined by extracting fresh soil (amount equal to 2.5 g dry weight) with 200 mL of $SrCl_2$ solution (0.2 M, 1 h). Digestates and soil extracts were diluted where necessary and analysed for cation- and nutrient concentrations by ICP and AA (see below).

The pH values of pore water samples were measured within 24 h after sampling as explained above. Dissolved total inorganic carbon (TIC) was measured within 24 h after sampling by injecting 0.2 mL pore water or surface water in a closed chamber containing 0.2 M H_3PO_4 solution, converting all dissolved TIC into CO_2. A continues gas flow (N_2) directly transports the CO_2 to an ABB advance optima infrared gas analyzer (IRGA) to measure TIC. The pore water pH was used to calculate the partition of dissolved CO_2 and HCO_3^- concentrations in the pore water prior to storage at 4 °C until further elemental analysis by ICP, 0.1 mL 65% HNO_3^- was added to 10 mL of each pore water sample to prevent metal precipitation. The remaining pore water samples were stored at −20 °C until measurement of nutrient concentrations by AA (see below).

To determine concentrations of Ca^{2+}, Mg^{2+}, P and other cations an inductively coupled plasma spectrophotometer (ICP; Thermo Electron corporation IRIS Intrepid II XDL) was used. The following ion concentrations were determined colourimetrically on Auto Analyzer 3 systems (Bran and Luebbe): NO_3^- (Kamphake et al., 1967), NH_4^+ (Grasshoff and Johannsen, 1972), and phosphate (PO_4^{3-}; Henriksen, 1965). K^+ concentrations were determined with a Technicon Flame Photometer IV Control (Technicon Corporation).

2.4. Statistical analyses

2.4.1. Vegetation survey

Changes in vegetation in relation to the traditional management types were investigated using the indirect gradient analysis detrended correspondence analysis (DCA). This analysis was performed for bryophytes and vascular plants separately, using CANOCO (Version 4.55; ter Braak and Šmilauer, 1998). The relevés were classified based on their species composition using WinTwins (Version 2.3; Hill, M.O.). Default settings were used, except that cut levels were set to 1–9, according to the ordinal cover and abundance scale used for the vegetation assessments. Clusters up to third division were taken into account. A similar analysis was performed for investigating the changes in vegetation caused by the different liming treatments. However, instead of a DCA, a principal components analysis (PCA) was performed as the maximum length of gradient was close to 3.0 (Table 1; ter Braak and Šmilauer, 1998).

Table 1
Statistical analyses of the effects of traditional management measures on vegetation development over 46 years (DCA; Fig. 1 and Supplementary data) and the effects of experimental liming on vegetation development (PCA; Fig. 5 and Supplementary data).

	Summer mowing and Burning		Liming	
	Bryophytes	Vascular plants	Bryophytes	Vascular plants
Length of gradient (DCA)	5.428	4.322	2.977	1.336
	DCA		PCA	
Total variation (SD)	5.345	6.127	1.031	0.735
Axis 1 variation	12.9%	10.0%	42.3%	34.1%
Axis 2 variation	6.3%	5.1%	15.3%	22.2%

2.4.2. Biogeochemical analyses

For statistical analysis of the chemical results from the liming experiment, SPSS Statistics for Windows (Version 21.0; IBM Corp.) was used. Differences among treatments were tested using a GLM mixed model. Time was used as repeated measure and treatment as fixed factor, with AR(1) heterogeneous as the covariance type. A Bonferroni post-hoc test was used to test for differences between treatments. Differences between treatments at a fixed moment were analysed with ANOVA, using Tukey's-b posthoc test. Data was transformed with logarithm or square root when residuals were not normally distributed.

3. Results

3.1. Historical references

In 1967, different successional fen stages were present, ranging from young successional stages with species characteristic of rich fens, to older stages with a dominance of *Sphagnum* characteristic of poor fens. In 46 of the historic relevés *Sphagnum palustre* or *Sphagnum fallax* was the dominant bryophyte species (avg. code 6; Supplementary data), but additional species indicated differences in abiotic conditions. The first group of historic relevés ($n = 6$) contained bryophytes characteristic for more buffered conditions such as *Pellia* species (avg. code 5) or *Brachythecium rutabulum* (codes 2–3). Vascular plants of rich fens such as *Hammarbya paludosa* and *Liparis loeselii* were present in five of these relevés (codes 1–3). The second, large group of historic relevés ($n = 26$) contained species of moderately acidic conditions such as the bryophyte species *Pallavicinia lyellii* (codes 2–3), and vascular plant species such as *Dryopteris carthusiana* (codes 1–3), *Succisa pratensis* (codes 1–7), and *Platanthera bifolia* (code 1). This group includes four relevés that contained an intermediate composition between rich and poor fen. The last group (16 historic relevés) contained bryophytes such as *Sphagnum magellanicum* (code 2), *Sphagnum rubellum* (codes 1–2), *Kurzia pauciflora* (codes 3–7) and *Cladopodiella fluitans* (code 3), which are all characteristic for acidic conditions (poor fens including typical ombrotrophic hummock species, in this paper referred to as bogs).

3.2. Vegetation changes due to traditional management

Succession and summer mowing induced a shift towards bryophytes indicating acid and nutrient-poor conditions (Fig. 1 for bryophyte composition; vascular plants in Supplementary data). The bryophyte composition of 15 (out of 23) of the relevés was characteristic for poor fens or bogs. *Sphagnum palustre* was the most abundant bryophyte species (22 relevés; avg. code 7), and the

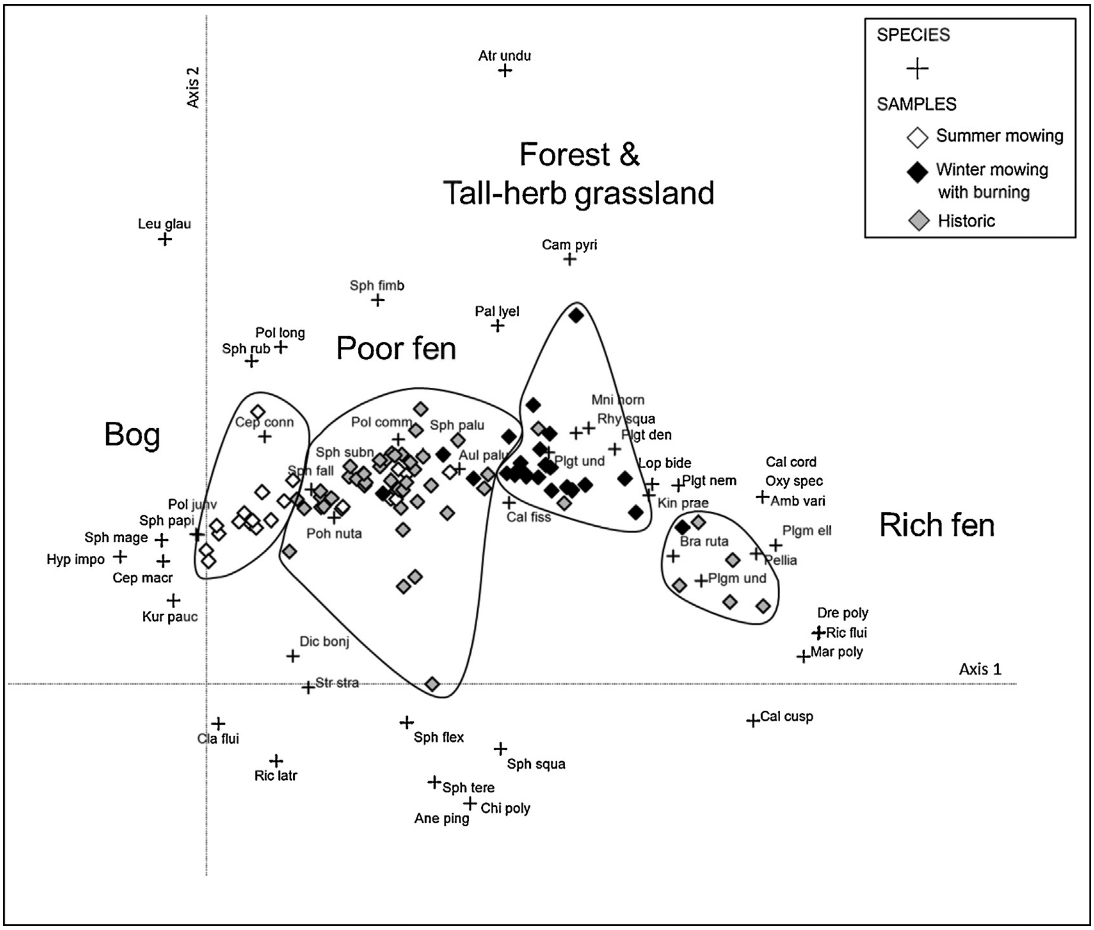

Fig. 1. Indirect ordination diagram (DCA) of bryophyte species occurring in 49 historic relevés (1967), which were re-assessed in 2013 after a management regime of 'summer mowing' (23 relevés) or 'burning after winter mowing' (26 relevés) in the Dutch fen reserve 'Nieuwkoopse plassen'. The total variation is 5.345, axis 1 explains 12.9% and axis 2 explains 6.3% of this variation (see Table 1). A cluster analysis (WinTwins) was used to define different vegetation groups (indicated by delineated areas).

ombrotrophic species *Sphagnum magellanicum* the second most abundant (14 relevés; avg. code 5). The red-list liverwort species *Cephalozia macrostachya* (4 relevés, codes 3–7) and *K. pauciflora* (14 relevés, codes 3–8) often showed an equally high cover as the *Sphagnum* species. Furthermore, *S. fallax* (avg. code 4), *S. papillosum* (avg. code 5) and *S. rubellum* (avg. code 3) each occurred in half of the relevés. While the summer-mown relevés were still quite species-rich and contained rare and red-list species, the burned relevés generally only contained common species (Supplementary data). Burning after winter mowing induced a shift to vegetation of more nutrient-rich, but still buffered conditions (Fig. 1). In a total of 26 relevés, *S. palustre* (20 relevés, avg. code 6) and *S. fallax* (3 relevés, code 5) were abundant, but more eutrophic species such as *B. rutabulum* (avg. code 3), *Plagiothecium denticulatum var. undulatum* (avg. code 3), and *Kindbergia praelonga* (avg. code 4) were also present in 19 relevés. In only 3 relevés a closed bryophyte cover was present (code 9). In addition, relevés contained vascular plants rooting in the deeper, well buffered soil such as *Phragmites australis* (26 relevés; avg. code 5), *Molinia caerulea* (20 relevés; code 8), *Peucedanum palustre* (13 relevés; code 2), *Juncus subnodulosus* (9 relevés; code 3), and *Valeriana officinalis* (8 relevés; code 4), indicating a shift towards more eutrophic, tall-herb grasslands (Supplementary data).

3.3. Liming to counteract acidification

After liming, soil pH increased for all treatments from pH 3.5 to pH 6 within a year, unlike the control (Fig. 2; upper panel). After this period, however, only the 4 k treatment remained stable for another 2 years, while for the other lime treatments pH gradually decreased and reached intermediate values. Except for the 1 k treatment, all lime treatments still showed significantly higher ($p = 0.005$) pH values over time than the control (Fig. 2; upper panel). The exchangeable Ca^{2+} and Mg^{2+} concentrations of the soil matrix increased strongly ($p < 0.005$) for all lime treatments with, as expected, the highest concentrations for the highest lime treatment (4 k) (Fig. 2; lower panel). The 1 k treatment showed a strong drop after 4.5 years, while in all other lime treatments exchangeable Ca^{2+} and Mg^{2+} concentrations showed a gradual decrease over time but were still significantly higher ($p < 0.001$). After 7.5 years, concentrations were still significantly higher ($p < 0.01$) in the 4 k treatment. Accordingly, the buffer capacity of the pore water, as reflected in dissolved HCO_3^- concentrations, were shown to be significantly ($p < 0.01$) increased for the 4 k treatment after 4.5 years, while after 7.5 years no differences between treatments were found anymore. CO_2 concentrations in the pore water showed no clear differences between lime treatments after both 4.5 and 7.5 years (data not shown).

3.4. Effects of liming on nutrient availability

The amount of bio-available P became slightly, but not significantly, higher for the lime treatments compared to the control over time (Fig. 3; upper panel). Plant available nitrogen (N) became significantly ($p < 0.05$) higher in the 4 k treatment over time, when compared to the control (Fig. 3; lower panel), with

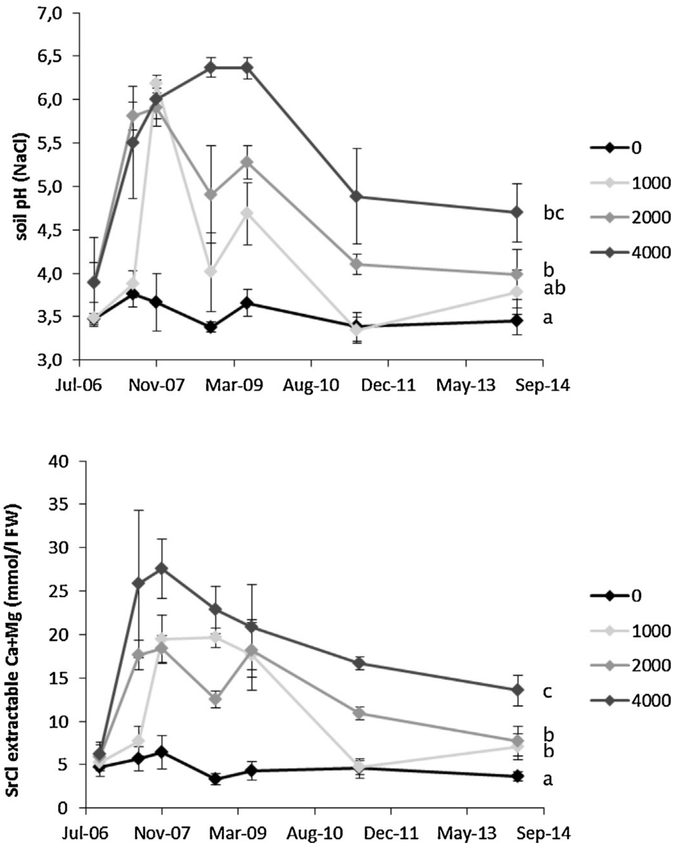

Fig. 2. Long-term effects of lime addition (0, 1000, 2000, 4000 kg/ha) on soil pH and Ca + Mg concentrations in the soil of the experimental plots (mmol/L FW). Error bars indicate SEM values, different letters indicate significant differences between treatments.

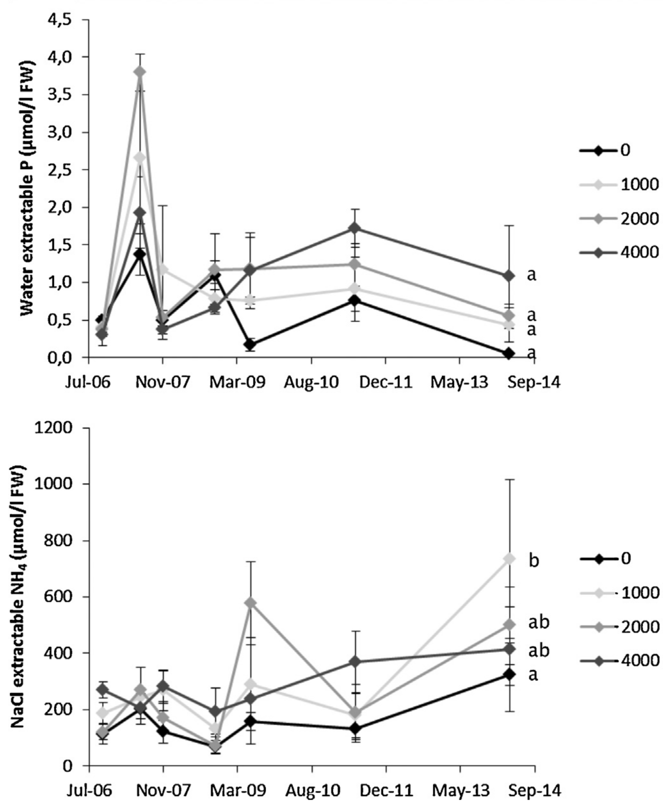

Fig. 3. Long-term effects of lime addition (0, 1000, 2000, 4000 kg/ha) on available nutrient concentrations in the soil of the experimental plots (P and N). Error bars indicate SEM values, different letters indicate significant differences between treatments.

NH_4^+ accounting for more than 81% of the available N. The much lower plant available NO_3^- concentrations in the soil showed no differences between treatments. Moreover, plant available K^+ concentrations showed no significant differences between lime treatments over time (data not shown). Similarly, PO_4^{3-}, NO_3^-, NH_4^+ and K^+ concentrations in pore water did not differ among treatments after 4.5 and 7.5 years either, and all remained relatively low (data not shown).

3.5. Effects of liming on vegetation development

In all lime treatments, *Sphagnum* spp. died and reached the lowest cover 1.5 years after liming (<10% cover; Fig. 4). From this moment on, re-growth of *Sphagnum* started in accordance with the lime treatment, resulting in the lowest cover in the 4 k treatment and the highest cover in the 1 k treatment. Liming did, however, not have a clear effect on vascular plant composition (Supplementary data). The bryophyte composition in the limed plots over 7.5 years could be divided into four main groups (Fig. 5). The first group (n = 13) mainly consisted of 4 k lime plots, characterised by a low cover of *S. palustre* (11 relevés; codes 2–4) and *Polytrichum commune* (10 relevés; codes 1–2), and the presence of rich fen species like *Aneura pinguis* (10 relevés; code 2), *Bryum pseudotriquetrum* (9 relevés; code 2) and *Riccardia chamaedryfolia* (4 relevés, code 2) (rich fen; Fig. 5). Moreover, *L. loeselii*, a characteristic rich fen orchid, was found after 4 k lime addition in 3 relevés (code 1–2). The second group (poor fen with *P. commune*; Fig. 5) consisted of 9 relevés that were all characterised by *S. palustre* (avg. code 5) and *P. commune* (avg. code 3), and the presence of *S. fallax* in 6 relevés (code 2). In three of these relevés, only these three bryophyte species were present. The 26 relevés of the third group (poor fen with liverworts; Fig. 5) were all dominated by *S. palustre* (avg. code 7) with a co-dominance of *S. fallax* in 24 relevés (avg. code 4), *S. rubellum* (18 relevés; avg. code 4) and the liverworts *C. connivens* (15 relevés; avg. code 3) and *K. pauciflora* (14 relevés; avg. code 2). The last group (bog; Fig. 5) was again dominated by *S. palustre* (11 relevés; avg. code 8), *S. fallax* (9 relevés; avg. code 3), and *S. rubellum* (10 relevés; avg. code 3), and a relatively high abundance of *C. macrostachya* (7 relevés; avg. code 3), *K. pauciflora* (4 relevés; avg. code 3), and the ombrotrophic hummock species *S. papillosum* (6 relevés; avg. code 4) and *S. magellanicum* (8 relevés; avg. code 3).

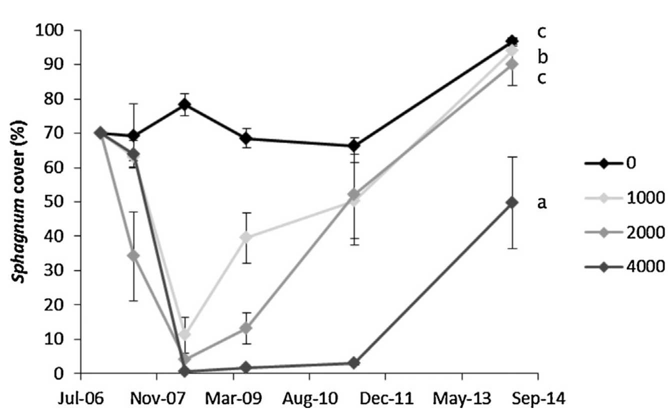

Fig. 4. Cover of *Sphagnum* species (%) over time in the experimental plots with different amounts of lime addition (0, 1000, 2000, 4000 kg/ha). Error bars indicate SEM values, different letters indicate significant differences between treatments.

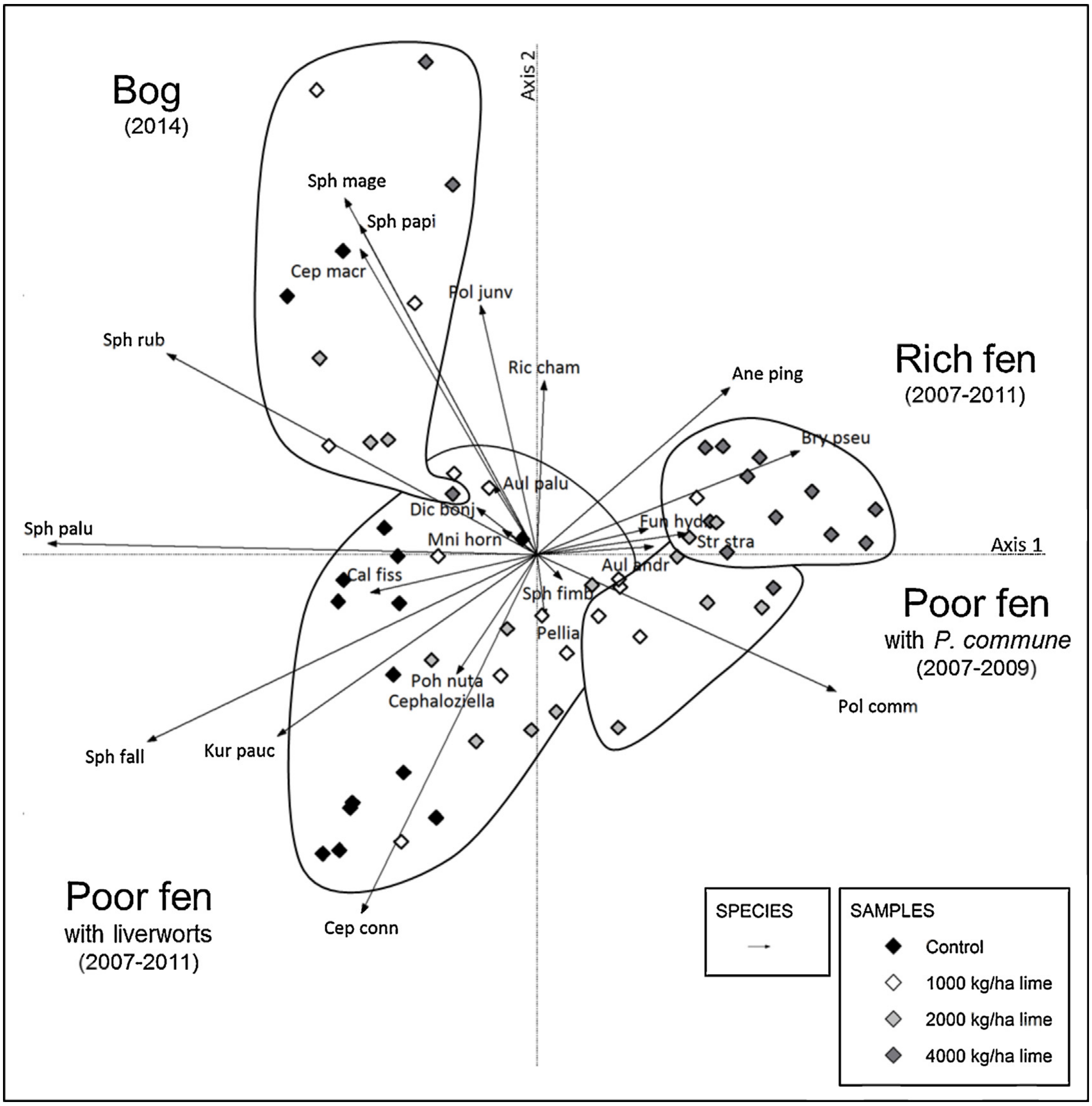

Fig. 5. Indirect ordination diagram (PCA) of bryophyte species found in control and lime treated plots at 0.5, 1.5, 2.5, 4.5 and 7.5 years after treatment. The total variation is 1.031 (SD), axis 1 explains 42.3% and axis 2 explains 15.3% of the variation (see Table 1). A cluster analysis (WinTwins) was used to define different vegetation groups (indicated by delineated areas); the years represent the time range in which these vegetation groups were present.

The vegetation composition in the plots changed during the time-span of the experiment. All plots, including the control, were characterised by poor fen vegetation just after the start of the experiment (0.5 years). The control plots, two 1 k and one 2 k limed plots maintained a poor fen vegetation throughout 4.5 years. However, one 1 k plot, and two 2 k plots were characterised by a rich fen composition after 1.5 years, and subsequently returned into a poor fen composition. The 4 k plots had developed into a rich fen vegetation after 1.5 years, which remained throughout 4.5 years of monitoring. After 7.5 years, however, all control and limed plots were characterised by a *Sphagnum* bog composition.

4. Discussion

4.1. Summer mowing stimulates Sphagnum *development*

The effects of traditional management measures on vegetation development appeared to be strongly determined by the development of *Sphagnum* cover. Summer mowing enhanced *Sphagnum* dominance, resulting from decreased buffered conditions in the top soil by ongoing peat formation and succession, and frequent biomass removal leading to decreased nutrient and base-cation availability (Olde Venterink et al., 2002). Tall growing vascular plants such as *P. australis* (Güsewell et al., 2000) and *Molinea caerulea* (Hogg et al., 1995) are known to decrease with respect to aboveground biomass production and cover in response to summer mowing. This enhances light availability in the growing season, stimulating bryophyte growth (van Diggelen et al., 1996; Kotowski et al., 2001; Middleton et al., 2006a; Grootjans et al., 2006). Although conservation of early successional vegetation was not achieved by summer mowing, the large number of rare and red-list bog-species that had established as a result can still be considered a positive effect. Although this management measure seems perfect to develop species-rich poor fens with *Sphagnum* hummocks, the question remains whether this will lead to raised bog development in the long term.

4.2. Burning leads to graminoid dominance

In contrast to summer mowing, litter burning after winter mowing led to a reduction in *Sphagnum* growth. Shaw et al. (1996) showed that bryophytes often die off as a result of heat exposure, but on the longer term especially shading by vascular plants (Middleton et al., 2006a) and perhaps also enhanced base-cation concentrations by remaining ashes (Raison, 1979) might have played a role. The enhanced growth of tall-growing, ruderal vegetation and dominance of grasses in combination with a decreased bryophyte cover indicates increased nutrient availability (Bobbink et al., 1998; Gryseels, 1989). The ashes remaining after burning can cause a temporarily increased nutrient availability (Raison, 1979), which grasses might utilise very effectively (Hobbs, 1984; Aerts, 1990). The formation of tussocks by grass species might have aided their expansion as well. Tussocks protect the meristems of new leaves and shoots against fire, causing species such as *M. caerulea* to be hardly affected by burning management (Shaw et al., 1996). Although burning (after winter mowing) seems to counteract *Sphagnum* growth and acidification, species diversity decreased and the remaining vegetation lacked rare and endangered species. For this reason, this does not seem to be the most preferable management measure to maintain different successional stages in fens.

4.3. *Liming temporarily tackles acidification and* Sphagnum *growth*

Liming immediately counteracted acidification by increasing pH and base saturation of the top soil. We showed that, in the short term, this measure effectively decreased *Sphagnum* cover and enhanced the development of poor fen towards rich fen bryophyte vegetation, in particular when using high doses (up to 4000 kg/ha). Although Beltman et al. (2001) only found a raised pH after *Sphagnum* had been removed before lime application (up to 1500 kg/ha), we showed that this also held when *Sphagnum* was still present. Increased buffering was expected to have a strong negative effect on the growth and establishment of *Sphagnum* (Beltman et al., 1996b; Clymo and Hayward, 1982), and to effectively improve survival and cover expansion of rich fen bryophytes (Mälson and Rydin, 2007; Mälson et al., 2010). However, only common rich fen pioneer bryophytes established in our experiment, without reaching high covers. In addition, typical vascular rich fen species hardly established.

The failed establishment was likely due to dispersal constraints from local remnant populations (Donath et al., 2007; van Duren et al., 1998; Beltman et al., 1996a,b). Moreover, even with small distances, the absence of flooding events in the area may have prevented the seeds from dispersing, as hydrochory is an important dispersal mechanism in fens (Vogt et al., 2004). Thus, although the right abiotic conditions had been achieved after liming, the seeds did not arrive, missing the window of opportunity created by liming. To obtain a well-developed rich fen vegetation after restoring base-rich site conditions in heavily fragmented landscapes, it may therefore be necessary to aid species in their dispersal by spreading propagules (Mälson et al., 2010; Hedberg et al., 2012; Middleton et al., 2006b), for instance by application of hay (Patzelt et al., 2001).

4.4. *Liming effects in the longer term*

Lime addition, especially high amounts, might stimulate decomposition processes and mineralisation of the peat soil as a result of increased pH buffering (Ono, 1991). We found a slightly increased NH_4^+ availability following liming, indicating that mineralisation may indeed have been enhanced (Geurts et al., 2010). Lucassen et al. (2006) suggested that increasing Ca concentrations might decrease binding of NH_4^+ to the soil complex, thereby increasing NH_4^+ solubility and removal via flowing groundwater. In our experiment, however, available NH_4^+ increased with liming which suggests that accumulation by mineralisation may be higher than its removal by dissolution. Although atmospheric N input can be partly removed by hay removal after mowing (Olde Venterink et al., 2002) or burning (Raison, 1979), extra N input by mineralisation enhances its accumulation. The observed increase of P availability was not significant, however, this might be due to the small number of replicates in our experiment as a trend was visible. Increased nutrient availability might be unfavourable for plant composition and biodiversity of rich fens in the long term, since it may enhance dominance of highly competitive species (Boeye et al., 1997; Bobbink et al., 1998; Olde Venterink et al., 2002; Cusell et al., 2014b), and accelerate succession towards *Sphagnum*-dominated poor fens (Kooijman and Paulissen, 2006). Even though the soil still showed buffered conditions after 7.5 years, *Sphagnum* became dominant again in the 4 k lime treatment, which provided a strong positive feedback due to its active peat formation and acidification, raising the soil surface and decreasing the buffering of the top soil (Malmer and Wallen, 2005; Lamers et al., 2000; Fritz et al., 2014). Increasing dominance of *Sphagnum* species may therefore have interfered with the germination and establishment of rich fen species.

4.5. *Implications for future management of rich fens*

Even without management, vegetation changes will occur due to natural succession, but these will be strongly influenced by atmospheric N deposition, eutrophication and/or climatic change (Hogg et al., 1995; Malmer and Wallen, 2005; Kooijman and Paulissen, 2006; Bobbink et al., 2010; Lamers et al., 2014). Changes in succession rate have been found to be related to management (Bakker et al., 1994), with an accelerated development of old successional stages at the expense of early successional rich fen vegetation (van Diggelen et al., 1996; Kooijman and Paulissen, 2006; Bobbink et al., 2010; Lamers et al., 2014). Although terrestrialisation can take decades, the transformation of one successional fen stage into the next can take only 11–12 years (Bakker et al., 1994; Verhoeven and Bobbink, 2001), depending on the level of eutrophication. Moreover, the development of late successional stages is often indirectly correlated with increasing thickness of the peat mat, due to a changing hydrology. This raises the question whether it is feasible to restore early successional rich fen stages on thick, old peat mats.

In our study, none of the traditional management measures were able to maintain or re-establish the historic (1967) successional vegetation gradient, nor similar species richness. We indeed found that changes in vegetation over the last 46 years were strongly driven by eutrophication and acidification, but also that they could be clearly linked to the effects of different management options. Although liming, as an alternative, was found to enhance rich fen development in the very short term, *Sphagnum* showed a rapid expansion accelerating succession towards poor fen and bog vegetation. In our experiment, re-establishment of *Sphagnum* may have been favoured by the use of relatively small plots and the fact that *Sphagnum* had not been removed before lime application. When liming is used at a larger scale and directly after top-soil removal, dominance of *Sphagnum* might be postponed. Repeated addition of lime might be another option, although the effectiveness and possible negative effects are yet to be tested. Newly formed floating mats might be favourable to promote development of rich fen vegetation. However, given the fact that terrestrialisation is a significant problem faced in the conservation of fens (Geurts et al., 2009; Lamers et al., 2014), management will still call for management and restoration measures to restore rich fen vegetation on older peat mats. Alternatively, management goals could be adapted to the condition, targeting for the development of a bryophyte-rich poor fen vegetation, as developed in our summer mowing regime.

Slightly acidic conditions and the presence of *Sphagnum* species not necessarily inhibit the occurrence of rich fen vegetation per se, as we already found a vertical soil gradient with slightly acidic conditions in the top soil and buffered conditions deeper in the soil in 1967.

However, *Sphagnum* dominance and (re-) acidification, and thereby accelerated succession from rich fen to poor fen, has to be slowed down. The only sustainable option to achieve this seems to lie in the restoration of original hydrological conditions in the top soil, for example by allowing buffered groundwater or surface water to infiltrate the top soil (van Diggelen et al., 1996; Beltman et al., 2001; Lamers et al., 2014), or by regular inundation with base-rich surface water, although possible eutrophication issues should be taken into account (Cusell et al., 2013). In conclusion, we found that the management measures summer mowing, burning after winter mowing, and liming were all unable to restore rich fens in the long term.

Acknowledgements

The authors would like to thank Hanneke den Held for her support during the study and assessments of the traditional management measures. We would like to thank Jeroen Geurts and Rick Kuiperij for their practical assistance during the liming experiment, Jeroen Graafland, Jelle Eygensteyn, Paul van der Ven and Sebastian Krosse for their help with chemical analyses, and Leon van den Berg for his help with statistical analyses. We are grateful to the nature management authority 'Natuurmonumenten' for the facilitation and permission to perform this research in their reserve.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2014.12.006.

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