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Recovery of target bryophytes in floating rich fens after 25 yr of inundation by base-rich surface water with lower nutrient contents

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Nomenclature

Van Tooren & Sparrius (2007)

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Introduction

Mineral-rich fens are threatened in Europe by acidification and eutrophication (Kooijman 1992; Gunnarson et al. 2000; Heino et al. 2005; Juutinen 2011; Lamers et al. 2015), and are protected by the EU Habitat directive (European Union 1992). Mineral-rich fens have become very rare, and well-developed fens with *Scorpidium* spp. may cover less than 10 ha in the Netherlands (Cusell et al. 2013a). Mineral-rich fens are characterized by high plant diversity, including EU habitat directive species such as

Liparis loeselii, and many brown moss species (Sjörs 1950; Succow & Jeschke 1986; Hallingbäck & Hodgetts 2000; Vitt & Wieder 2009). Bryophytes are not only important in terms of biomass dominance, but also good indicators of environmental conditions, because they have no roots and are only one cell layer thick (Proctor 1982). In fact, the bryophyte layer is a sensitive indicator of environmental change in rich fen ecosystems (Sjörs 1950; Gorham et al. 1987).

Many rich fens are threatened by acidification (e.g. Clapham 1940; Koerselman et al. 1990; Van Wirdum

Abstract

Question: What are the changes in mineral-rich fens (H7410A) after 25 yr of improved surface water quality in a national park?

Location: Stobbenribben floating-fen complex in National Park Weerribben-Wieden, the Netherlands.

Methods: Bryophyte species composition, peak above-ground biomass and vascular plant nutrients, as well as electrical conductivity of various layers in the peat were measured between 1988 and 2013.

Results: The eutrophic moss *Calliergonella cuspidata* clearly decreased in aerial extent over the 25-yr study, especially near the ditch supplying base-rich surface water to the fen. In contrast, the characteristic rich fen species *Scorpidium scorpioides* expanded locally near the ditch. In the rich fen zone, peak above-ground biomass decreased from ca. 1000 to 250 g·m⁻². Also, foliar N:P ratios in vascular plant tissues increased from 16 to more than 22 g·g⁻¹, which clearly point to lower P availability over time. Improved surface water quality probably also promoted persistence of rich fen habitats in a different way. A large part of the rich fen peatland in 1988 changed into *Sphagnum* peatland by 2013, probably due to the reduction of base-rich water from below the floating root mat. This mat had become ca. 35 cm thicker in the past 50 yr. However, in areas closer to the ditch, rich fen species persisted, due to inundation with base-rich water during high water periods. Base-rich water probably no longer comes to the surface through the floating root mat, but more likely from the ditch.

Conclusions: Water quality improvement can be important in the long-term re-establishment of target fen species. Also, local inundation can be helpful if regional groundwater access becomes limited. In the national park, rich fens are more threatened than *Sphagnum* peatlands. This study suggests that the rich fen stage can be maintained, and succession towards *Sphagnum* peatland prevented, with occasional inundation with high pH, nutrient-poor water.

1991; Van Diggelen et al. 1996; Soudzilovskaia et al. 2010; Lamers et al. 2015). To maintain sufficient acid neutralization capacity and ensure survival of rich fen species, input of calcium and bicarbonate-rich water is needed (Hajek & Adamec 2009; Soudzilovskaia et al. 2010). When access of base-rich water to the fen surface is reduced, rich fen mosses are replaced by *Sphagnum* species, and these mosses actively acidify these wetlands (Clymo 1963; Kooijman & Paulissen 2006). In many industrialized countries, high atmospheric deposition also contributes to acidification (De Haan et al. 2008). This process may result in approximately 1.5 times higher amounts of buffer components needed to sustain a suitable pH (Kooijman 2012). However, in many fens, supply of base-rich water has become limited. Groundwater input has been reduced in many areas, due to extraction for drinking water and agriculture (Schot & Molenaar 1992; Van Loon 2010).

Many rich fens are also threatened by eutrophication, which is a problem in densely populated countries with intensive agriculture (Lamers et al. 2015). Many rich fens are P-limited (Wassen et al. 2005). Eutrophication generally leads to an increase in biomass production and changes in plant species composition, especially in the bryophyte layer. In many rich fens, characteristic brown-moss species such as *Scorpidium scorpioides* and *S. cossoni* have been replaced by more eutrophic species, such as *Calliergonella cuspidata* (Kooijman 1992, 1993). In the 1980s, even the most biodiverse rich fens of the Netherlands contained moss species of more eutrophic habitats (Verhoeven et al. 1988; Van Wirdum 1991). Meanwhile, measures have been taken to improve water quality and decrease eutrophication in many wetland nature reserves, especially eutrophication with P (Lamers et al. 2015). In Weerribben-Wieden National Park, such measures included wastewater treatment and redirection of regional and local water flows, to reduce input of nutrients to natural systems. Although concentrations of total P did not change between 1982 and 2000, phosphate concentrations in the main channels decreased from 1–2 to 0.5–1.0 $\mu\text{mol}\cdot\text{L}^{-1}$ (Cusell et al. 2013a).

The goal of this study was to evaluate 25 yr of changes in bryophyte species composition, nutrient availability and base status in response to water quality improvement, in one of the largest and best-preserved rich fen complexes in the Netherlands. Rich fen studies over such periods are becoming more common (Van Diggelen et al. 1996, 2015; Gunnarson et al. 2000; Juutinen 2011), but are not always conducted by the same researcher, and only address environmental changes in e.g. base status and nutrient availability, to a limited extent. In our study, we compared detailed surveys of the bryophyte layer in 5 m \times 5 m grid cells in one of the fens, undertaken by the first author in 1988 and 2013. To analyse changes in

nutrient status, peak above-ground biomass and vascular plant nutrient concentrations were measured in the rich fen zone in 1984, 1990, 2005, 2010, 2011 and 2012. Changes in base status in various peat layers were studied in various years using measurements of electrical conductivity as a proxy.

Methods

Study area

The Stobbenribben fens are located in Weerribben-Wieden National Park (eastern Netherlands), in one of the largest wetland areas in NW Europe (Fig. 1). The climate is temperate-humid, with 800 mm rainfall, evenly distributed over the year. The national park is surrounded by low-lying agricultural polders; during wet periods, water is pumped from these polders into the park to ensure constant water levels in the agricultural areas. Inside the park, water levels are also maintained more or less constant through water control structures, but are allowed to fluctuate 10 cm between 0.83 and 0.73 m below mean sea level (Cusell et al. 2013a).

The Stobbenribben consists of a few adjacent rectangular ponds of ca. 20–40 m width and 200 m length, created by cutting the *Carex* peat around AD 1900 (Van Wirdum 1991). Depth of the ponds to the Pleistocene sandy underlayer is ca. 2.5–3.0 m. Kuiper & Kuiper (1958) mentioned the site as a good example of floating fens, with many characteristic rich fen species, such as *S. scorpioides* and the EU Habitat directive species *Liparis loeselii*. The fens are annually mown with small machines to prevent establishment of shrubs and trees (Cusell et al. 2013a).

Hydrology of the fen complex was studied in 1970–1980s by Van Wirdum (1991). To the southeast, this fen complex borders an agricultural polder, which was drained in the 1950s and is several meters lower than the fens themselves (Fig. 1). As a result of their relative elevation, the fens are subject to downward water movement (infiltration) of ca. 1–2 $\text{m}\cdot\text{yr}^{-1}$. The water loss is far larger than the precipitation surplus, and compensated by lateral inflow of surface water from a ditch at the NE side of the fens. This water flows beneath and through the floating root mat. Towards the SW end, the fens are hydrologically isolated with peat ridges, and base-rich ditch water becomes increasingly mixed with rain-water. As a result, the fens generally show a vegetation gradient from brown moss communities with *S. scorpioides* closer to the ditch to *Sphagnum*-dominated vegetation in the more isolated parts of the fen (Van Wirdum 1991).

In the 1980s, base-rich (ditch) water, needed to sustain the rich fen vegetation, was probably mainly supplied to

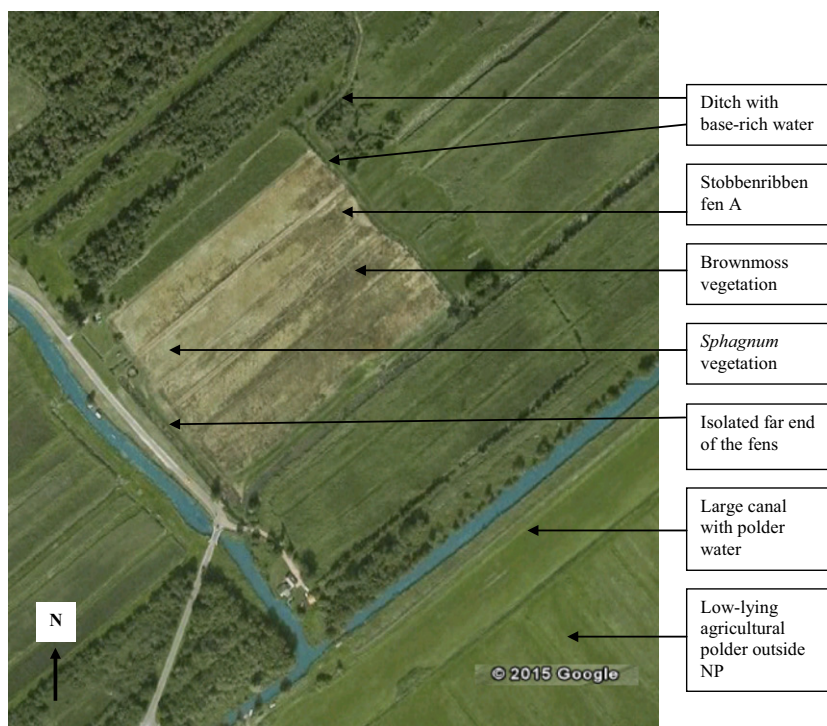


Fig. 1. Location of the Stobbenribben Fen complex in National Park (NP) Weerribben-Wieden. The dark brown colours in the fen complex indicate rich fen (brownmoss) vegetation dominated by *Scorpidium scorpioides*, the lighter areas are *Sphagnum* peatland dominated by *S. palustre*. The length of the fens is 200 m.

the fen surface from below the floating root mat, through gaps in the young layer of bryophyte vegetation (Van Wirdum 1991). However, occasional flooding with ditch water after heavy rain was reported, especially in areas close to the ditch (Bergmans 1975; Van Wirdum 1991; Kooijman 1993). The chemical composition of ditch water varies between seasons and years, depending on the amount of rain and input of water pumped in from the surrounding agricultural polders. Water moving out of the polders usually has relatively high calcium and bicarbonate content (Cusell et al. 2014a). However, polder water is also rich in nutrients, especially P.

Various measures have been applied to improve water quality since the 1970s. The major surface water inlet of the national park has been shifted from relatively eutrophic rivers to the much cleaner Lake Vollenhoven. Also, water purification facilities have been constructed, and P input from urban areas has decreased (Cusell et al. 2013a). Local measures to improve water quality and increase supply of base-rich ditch water were taken in 1992 (Schouwenberg & Van Wirdum 1997). The flow of water to the ditch in the Stobbenribben fen complex was redirected, leading to a longer pathway for nutrient removal. Also, within this project, the local ditch at the NE side of the fen complex was cleaned and enlarged.

Survey of the bryophyte layer

In one of the fens (Fen A), a detailed survey of the bryophyte layer was conducted in Oct 1988. The fen was divided in 200 grid cells of 5 m × 5 m, in 40 rows of five grid cells each. Unfortunately, in the last rows close to the ditch, six grid cells with unmown reed swamp, dominated by *C. cuspidata*, were inaccessible and thus not studied. In each grid cell, all bryophyte species present were noted; the total number of bryophyte species was 47. Bryophyte nomenclature is according to Van Tooren & Sparrius (2007). Cover values were adapted from Tansley (1946) and estimated on a scale from 1–5 (rare, frequent, common, co-dominant and dominant, respectively). The survey of the bryophyte layer was repeated in May 2013, within all 200 grid cells.

Peak above-ground biomass and foliar N:P ratios in vascular plants

Living vascular plant biomass growing above the fen surface was measured in the rich fen zone at 25–50 m from the ditch in Jul in 1984, 1990, 2005, 2010, 2011 and 2012. The number of replicates varied between sampling years from three in 1984, to three to five in later years. In 1984,

the three replicates consisted of ten different subplots of 20 m × 20 cm (Verhoeven et al. 1988). In later years, above-ground living phanerogam biomass was collected in plots of 25 cm × 25 cm. Samples were collected, dried and weighed. After weighing, samples were ground and used for analysis of foliar N and P. In 1984–1990, N and P content were determined with a method using H₂SO₄ destruction with salicylic acid, and in 2005–2012 with a CNS analyser and microwave destruction with HNO₃ (Westerman 1990) followed by element concentration analysis with ICP-OES (Optima 3000 XL, PerkinElmer, Waltham, MA, US). Foliar N:P ratios were calculated as g·g⁻¹. Foliar N:P ratios are a well-established proxy to estimate whether N or P could be a limiting factor (Koerselman & Meuleman 1996; Güsewell 2004; Cusell et al. 2014a). N:P ratios of 14–16 indicate more or less balanced conditions, while values above 20 clearly suggest P limitation (Koerselman & Meuleman 1996; Güsewell 2004). For 2010, however, P content was negligible so that these ratios were not analysed.

Surface EC values

Electrical conductivity (EC) values in the peat are related to calcium and bicarbonate concentrations in the water (Van Wirdum 1991; Cusell et al. 2014b), so that EC values may be used as a proxy for base status. EC values also help to determine the origin of base-rich water. EC at 25 °C and surface pH were measured during the bryophyte survey in Nov 1988, with a field meter at the fen surface near the centre of each 5 m × 5 m grid cell.

The EC measurements were repeated four times under various hydrological conditions, three of them characterized by high inundation of the rich fen zone (Jul 2012, May 2013 and Oct 2014), and one by low inundation throughout the fen (Nov 2012). Redox sensors in the rich fen zone showed low redox potentials during measurements with high water, and high values during low water (see Appendix A in Mettrop et al. 2014).

Electrical conductivity depth profiles

The EC depth profiles are very suitable to track the flow of water in and below the floating root mat (Van Wirdum 1991), and may help to determine the origin of the base-rich water. EC depth profiles were measured with a metal stick of 2 m with EC and temperature sensors in the top, which was pushed through the peat for measurements at different depths (Van Wirdum 1991). EC measurements were automatically corrected for temperature, standardized at 25 °C, and transformed to standard values in μS·cm⁻¹. EC depth profiles were measured to 100 cm depth, which is in the zone of open water below the float-

ing root mat. Surface EC values could often not be measured with the stick, and were measured with a field EC meter.

The EC depth profiles were measured along transects in the centre of the fen in Jun 1973 (Touber 1973) and in Jun 1990, Jul 2012, May 2013 and Oct 2014. EC depth profiles were also measured in Nov 2012, but in only in the half of the fen closest to the ditch; the plots in this case included all 5 m × 5 m grid cells as well as all wet hollows not in the centre of the grid cells.

In 1973, unfortunately, only five EC depth profiles were available, partly because parts of the floating fen were inaccessible (Touber 1973; Bergmans 1975). In 1990 and 2012–2014, each transect consisted of 16–28 measurement points, divided over the entire length of the fen. For comparison, the fen was divided in ten zones of 20-m length, and mean EC values for each zone were calculated.

In Jun 1973, the EC depth profiles started at 10-cm depth, and in Jun 1990 at 20-cm depth. Also, in Jun 1990, EC was measured every 20- rather than 10-cm intervals. In 2012–2014, however, EC depth profiles were measured from 0–100-cm depth, at intervals of 10 cm. In addition to the actual EC values, the data were used to calculate a rough proxy for the relative contribution of ditch water.

Statistical analyses

For most statistical analyses, the fen was divided into four zones of 50-m length, which more or less followed the zonation patterns of the fen in 1988. Differences in the number of grid cells containing particular bryophyte species between 1988 and 2013 were tested with Pearson's chi-squared tests, with 1988 values as the expected frequency (Mason et al. 1994). Differences were considered significant with *P*-values below 0.05.

Since the original biomass data of 1984 could not be retrieved, peak living above-ground phanerogam biomass and foliar N:P ratios were assessed using only the mean values and SD (Verhoeven et al. 1988). It was thus not possible to test differences between measurement periods directly with GLM. Instead, the changes over time were tested with linear regression analysis, with year and mean value per sampling period as input values.

Differences in surface EC values were tested with two-factor GLM, with fen zone and measurement series (time) as independent factors using SAS (Cody & Smith 1987). Differences between individual mean values were *post-hoc* tested with LSMeans tests. In zone 3, the zone at 100–150 m from the ditch, rich fen species still occurred in 1988, but became dominated by *Sphagnum* in 2013. In this zone, surface EC values were generally lower than in other zones, which masked potential differences between 1988 and 2012–2014 in the two-factor GLM. To further test such

differences, a one-factor GLM was applied for this fen zone separately, with time as independent factor.

Differences in EC depth profiles were tested for the three periods with complete profiles and inundation in the rich fen zone: Jul 2012, May 2013 and Oct 2014. Three-factor GLM were used, with the 50-m fen zones, time and depth as independent factors. Each factor turned out to be highly significant, as well as some of their interactions. However, general patterns with depth and fen zone were the same in all periods, as shown by the insignificant interactions between time \times depth and time \times zone. For a more general analysis of EC differences with depth and between fen zones, data from different periods were combined. Potential differences were tested with two-factor GLM, with fen zone and depth as independent factors, and *post-hoc* LSMeans tests. For the sake of clarity, this analysis was also done for each fen zone separately.

In June 1973 and June 1990, EC depth profiles were unfortunately incomplete, which made a direct comparison with the values of 2012–2014 impossible. For a rough estimate, five 20-m fen zones were selected for which data were available for 1973, 1990, 2012, 2013 and 2014 at 0–20, 20–40, 120–140, 160–180 and 180–200 m from the ditch. The data of 2012–2014 were combined to one mean value per fen zone per depth, to give the present situation equal weight to 1973 and 1990. We used the 20- and 40-cm depth measurements, partly because EC values in 1990 were only measured every 20 cm, but also because changes in water transport from below the root mat to the fen surface could be better detected in the upper layers, especially because inflow patterns below the floating root mat seemed more or less the same. Differences in EC values were tested with three-factor GLM, with time, depth and fen zone as independent factors.

Results

Vegetation changes between 1988 and 2013

In 1988, the moss layer of the Stobbenribben Fen consisted of a mosaic of rich fen hollows interspersed with poor fen hummocks (Fig. 2). The fen had a zonation pattern characterized by dominant bryophyte vegetation near the ditch including eutrophic species such as *C. cuspidata*, *Brachythecium rutabulum* and *Calliergon cordifolium* (Table 1). By 2013, these eutrophic bryophytes had decreased, with *C. cuspidata* dominant only in a small zone directly adjacent to the ditch. *B. rutabulum* and *C. cordifolium* also decreased.

In 1988, a large part of the fen, up to 100-m distance from the ditch, was dominated by the mesotrophic rich fen species *Scorpidium scorpioides*. Other rich fen bryophytes were also present, such as *Campylium stellatum*, *Fissidens adianthoides* and *Calliergon giganteum*. In 2013, the rich fen species more or less completely disappeared from the

central part of the fen. However, *S. scorpioides* increased closer to the ditch, and partly replaced the eutrophic *C. cuspidata*. The rich fen species *C. stellatum* also disappeared from the central fen, but increased near the ditch, albeit in lower numbers.

In 1988, the central part of the fen, the area of 50–150 m from the ditch, was dominated by the intermediate fen species *Sphagnum subnitens*, together with *S. contortum*. By 2013, both of these species were replaced by the poor fen species *S. palustre*, which by then dominated almost 70% of the area. Other poor-fen species also increased, such as *S. magellanicum*, *S. capillifolium* and *Polytrichum commune*.

Decrease in biomass production and P availability over the past 25 yr

The decrease in eutrophic bryophytes after 1988 was accompanied by a decrease in above-ground vascular plant biomass production (Table 2). In 1984, peak standing crop amounted to more than 1000 g·m⁻² in the rich fen zone dominated by *S. scorpioides* and *C. cuspidata*. In 1990, values in this area had decreased to ca. 500 g·m⁻², and further decreased to ca. 250 g·m⁻² in the last few years. Value of foliar N:P ratios increased. In 1984, foliar N:P ratios were about 16, but gradually increased over time to above 22.

Electrical conductivity values at the fen surface

In July 2012 (high-water period), water levels in the national park ranged around the maximum for several weeks, due to a prolonged wet period, and the rich fen zone was completely inundated, with water levels of 3–12 cm above the surface. At the time of these measurements, an open connection existed between the surface water of the ditch and the fen, over a length of ca. 10 m. In Nov 2012 (low-water period), water levels had gradually dropped after Sept to the minimum. Water levels in the ditch and fen were also low and the surface water in the ditch and fen was not connected. In May 2013 (high-water period), measurements were conducted 2 wk after the first rise to maximum water levels since Sept 2012, which lasted for about 1 wk. Water levels in ditch and fen were still relatively high, and the open connection between ditch and fen was ca. 0.5-m wide. In Oct 2014 (high-water period), measurements were conducted 10 d after the first rise to maximum water levels after a dry period of 2 mo. During the measurements, the rich fen zone was still partially inundated and anoxic, but the open connection between ditch water and fen surface was not more than a few cm. Mean EC of the ditch was 517 $\mu\text{S}\cdot\text{cm}^{-1}$ in Jul 2012, 353 $\mu\text{S}\cdot\text{cm}^{-1}$ in Nov 2012, 627 $\mu\text{S}\cdot\text{cm}^{-1}$ in May 2014 and 572 $\mu\text{S}\cdot\text{cm}^{-1}$ in Oct 2014.



Calliergonella cuspidata 1988

5	3	2	2						2	3	3	2	2	2	2	2	3	2	2	2	2	1	1	2	2	2	3	2	3	4	4	4	4	3	3	4	4	5	5
3					2	2	2	1	1	1		1	1		1	2	2	1	1	1		2	1	1	1	1	1	1	2	2	2	2	3	4	4	4	4	5	5
3							2	3	1			1	1			1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	3	3	3	3	3	4	5	5	5
3					2	2	4	3	1							1	1					1	1	1	1	2	1	2	2	3	3	3	3	5	4	5	5	5	
3	2	2	3	3	3	2	1	2	1	1					1	2						3	1	1	1	1	1	2	2	3	2	3	3	3	4	4	4	5	

Calliergonella cuspidata 2013

5	1	1	1	1					1																1			1	2	1	2	2	3	4	4	4	5	5
3																									1	1	1	2	2	2	2		1	1	1	2	5	4
2																										1		2	2		1			1	5	3		
2	1		1																								2	1							2	5	2	
3		1	1	1	2	1	2	1																				1	1	2		1		1	1	5		

Scorpidium scorpioides 1988

													1		2	2	4	4	5	3	4	4	4	4	4	4	5	4	4	4	5	4	4	3	2	1				
					2	2	2	1	2	2	2	2	2	3	2	4	2	2	3	4	4	4	4	4	5	4	4	5	5	5	5	5	2	5	5	4	4	1		
							2	3	2	1	2	2	2	1		1	1	1	2	3	4	4	3	2	4	4	2	3	5	4	5	5	4	5	4	5	4	1		
					2	2	4	3	3	3	2	1				1	1	2	1	2	2	3	4	4	3	2	2	4	5	4	3	4	5	3	2	2				
			3	4	3	3	2	1	2	1	1	2	1	2	1		1	1	1	2	2	3	4	4	3	2	2	4	5	4	3	4	5	3	2	2				

Scorpidium scorpioides 2013

		1	2																					1	2	2	5	5	5	5	5	5	5	5	5	5	4	4	5	3	
					1	1																				2	4	5	4	5	4	5	5	5	5	5	5	5	4	5	2
																												1	2		3	5	5	5	5	5	5	5	5	2	
						1																						1	2	1		3	5	4	5	5	5	5	5	2	
2	5	5	4	2	2	2	2	1																		1	2	2	1	1	1	2	4	5	5	5	5	5	5	5	

Sphagnum subnitens 1988

		2		1		3	2	4	5	5	3	3	3	3	3	4	3	4							1	2	3	2	2	2		2	2	3	1		1	1
					1	2	2	3	3	3	3	3	2	3	4	4	4	2	4	4	4	3	2	4	2	2	2	2	1	1		2	3	2		1	1	
2				1		2	2	2	2	2	2	3	4	4	5	5	5	4	3	4	5	4	5	5	4	4	5	4	1	3	2	1	2	1	1			
					1	3	3	3	3	3	4	3	3	5	4	5	5	5	5	5	5	5	5	4	4	5	5	5	3	2	4	3	2		1	2	1	
2			3	3	2	2	2	3	2	2	4	4	5	5	5	5	5	4	5	5	4	4	5	5	4	5	5	4	5	5	2	1	1	3				

Sphagnum subnitens 2013

1	1			1		1	1	1																												3		1	1		
2					1	2	1																		1	1		2		3	1	1	2		1			2	2	2	
																												1		1	2	2	3	1	2	2					
1			1				1	2																							1	2	1	1	2	3	3	2	2	2	2
1			1	1	2	2	1		2																	1	2	1	1	1	1	2	2	3	1	2				1	

Sphagnum palustre 1988

2	4	4	4	4	4	4	3	2	1	4	4	2	2	2		1	1	3	2																	1		3	1	3	1	1
3	4	5	4	4	4	3	3	5	3	3	3	2	2	1	1	2	2	4	5	2	1	1																1	1	3	2	1
2	3	4	4	3	2	4	2	4	4	3	5	5	3	4	2	2	2	3	5	2																						
2	3	4	4	3	3	3	5	3	3	1	3	4	3	2		1	2	2	2	2	1								1											1	2	
1	3	2	1	4	3	3	4	5	3	5	5	4	3	2	2	2	1	1	3	2							1	1		1												

Sphagnum palustre 2013

3	4	4	4	4	5	5	5	4	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
4	4	4	4	4	5	4	3	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
5	5	5	4	4	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
3	5	5	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
2	2	3	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	

Fig. 2. Comparison of selected bryophyte species within the Stobbenribben Fen in 1988 and 2013 in 200 5 m × 5 m grid cells. The ditch, which supplies base-rich water to the grid cells, is represented toward the right of the figure. Z1 = zone 1, 0–50 m from the ditch at the right of the figure; Z2 = zone 2, 50–100 m from the ditch; Z3 = zone 3, 100–150 m from the ditch and Z4 = zone 4, 150–200 m from the ditch. 1 = rare (light grey); 2 = frequent (light grey); 3 = common (grey); 4 = co-dominant (dark grey) and 5 = dominant (dark grey).

In general, EC values at the fen surface decreased from the ditch to the more isolated end of the fen (Fig. 3, Table 3). High EC values above 400 μS·cm⁻¹ were mostly

present near the ditch in zone 1, where rich fen vegetation prevailed. However, temporal and spatial variation was rather large. In Nov 1988 and Jul 2012, EC values above

Table 1. Presence (in percentage) of characteristic bryophyte species in the Stobbenribben in 1988 and 2013, in total or in particular fen zones of 50-m length, starting from the ditch at the NE side of the fen. Z1 = zone 1, 0–50 m from the ditch; Z2 = zone 2, 50–100 m from the ditch; Z3 = zone 3, 100–150 m from the ditch and Z4 = zone 4, 150–200 m from the ditch.

Bryophyte Species	1988					2013				
	Total	Z1	Z2	Z3	Z4	Total	Z1	Z2	Z3	Z4
Eutrophic Rich Fen Species										
<i>Calliergonella cuspidata</i>	78	25	21	15	12	32*	18*	5*	1*	10
<i>Sphagnum squarrosus</i>	68	11	21	24	12	1*	0*	1*	0*	0*
<i>Brachythecium rutabulum</i>	21	11	1	1	8	4*	4*	0	0	0*
<i>Calliergon cordifolium</i>	12	2	1	2	8	1*	1	0	0*	0*
<i>Rhytidiadelphus squarrosus</i>	9	3	0	0	6	3*	2	0	0	1*
<i>Plagiomnium affine</i> s.l.	8	4	1	0	4	6	2	0	0	1*
<i>Drepanocladus aduncus</i>	7	7	1	0	0	1*	1*	0	0	0
Mesotrophic Rich Fen Species										
<i>Sphagnum subnitens</i>	76	16	23	25	14	41*	12	17	1*	11
<i>Campylium stellatum</i>	72	16	24	21	11	46*	21	15*	0*	10
<i>Scorpidium scorpioides</i>	71	17	24	21	9	44*	22	16*	0*	7
<i>Sphagnum contortum</i>	64	7	21	22	15	23*	3*	6	2	12
<i>Bryum pseudotriquetrum</i>	50	14	14	15	8	42	24*	9*	0*	10
<i>Fissidens adianthoides</i>	39	18	16	4	3	14*	11*	3*	0*	1
<i>Calliergon giganteum</i>	23	10	3	7	4	15*	8	3	0*	4
Poor Fen Species										
<i>Polytrichum commune</i>	63	5	12	23	24	72	5	18*	25	25
<i>Sphagnum palustre</i>	62	7	7	24	25	83*	12	22*	25	25
<i>Sphagnum fallax</i>	58	7	4	24	43	69*	10	21*	22	16*
<i>Aulacomnium palustre</i>	40	4	3	18	15	22*	4	0*	5*	13
<i>Sphagnum papillosum</i>	17	0	0	6	11	19	0	0	5	14
<i>Sphagnum capillifolium</i>	5	0	0	2	4	20*	1	5*	12*	3
<i>Sphagnum magellanicum</i>	1	0	0	0	1	11*	0	0	2	10*

*Significant increase or decrease in number of grid cells between 1988 and 2013 in total or in a particular fen zone (chi-square tests; $P < 0.05$).

Table 2. Peak above-ground living vascular plant biomass and foliar N:P ratios in July in Stobbenribben in the rich fen zone with *S. scorpioides*, close to the ditch. Values are mean and SD in parentheses. The decrease in phanerogam biomass and increase in N:P ratio with time was significant for both factors ($R^2 = 0.79$ and 0.90 , respectively).

Year	Vascular Plant Biomass (g·m ⁻²)	Foliar N:P Ratio (g·g ⁻¹)
1984	1123 (241)	16.0 (1.8)
1990	512 (73)	19.1 (3.1)
2005	212 (136)	22.4 (2.2)
2010	187 (110)	
2011	229 (96)	23.7 (1.5)
2012	287 (74)	22.1 (1.1)

400 $\mu\text{S}\cdot\text{cm}^{-1}$ were relatively common in zone 1, but in Nov 2012, when water levels had been low for several months, lower values prevailed. In contrast, in May 2013 and Oct 2014, when the rich fen zone became inundated after a prolonged dry period, high EC values also occurred in zone 2. In May 2013, 82% of the grid cells with *S. scorpioides* had EC values above 400 $\mu\text{S}\cdot\text{cm}^{-1}$.

While temporal variation was rather large, there were no indications that the distribution of base-rich water near

the ditch drastically changed between 1988 and 2012–2014. Near the ditch, the 1988 values actually fell within the range of values for 2012–2014, although we had only one set of measurements in 1988 and do not know whether EC values were high or low for that period. Also, in both periods, high EC values were only found near the ditch. However, in the central part of the fen, base status of the fen surface water probably fell. In 1988, many surface EC values ranged between 100–300 $\mu\text{S}\cdot\text{cm}^{-1}$, and values below 100 $\mu\text{S}\cdot\text{cm}^{-1}$ were measured in only 9% of the grid cells. These relatively high values point to at least some contact with base-rich water. In 2012–2014, however, EC values below 100 $\mu\text{S}\cdot\text{cm}^{-1}$ were very common. Also, in *S. palustre* vegetation, EC could often not be measured, due to lack of surface water. In the overall statistical analysis, differences in zone 3 between 1988 and 2012–2013 were not significant, due to much higher EC values in zone 1. However, when zone 3 was analysed separately, 1988 showed significantly higher values than all other years. These results suggest that contact of the peat surface with base-rich water is no longer common, and has actually diminished compared to the situation in 1988.

Table 3. Mean pH and EC values ($\mu\text{S}\cdot\text{cm}^{-1}$) and SD at the fen surface in different measurement periods and different fen zones, starting from the ditch at the NE side. Zone 1–4 are each progressively 50 m more distant from the ditch, with zone 1 0–50 m from the ditch. Different letters indicate significant differences between fen zones and/or times ($P < 0.05$).

	Zone 1: 0–50 m from Ditch	Zone 2: 50–100 m from Ditch	Zone 3: 100–150 m from Ditch	Zone 4: 150–200 m from Ditch
pH				
Nov 1988	6.2 (0.3) ^c	6.1 (0.4) ^c	5.0 (1.0) ^b	4.7 (0.7) ^a
EC				
Nov 1988	342 (109) ^c	177 (100) ^{ab}	140 (50) ^a	171 (41) ^a
July 2012	396 (85) ^c	184 (122) ^{ab}	43 (-) ^a	123 (48) ^a
Nov 2012	264 (100) ^b	95 (44) ^a	-	118 (37) ^a
May 2013	555 (59) ^d	369 (224) ^c	71 (33) ^a	263 (176) ^b
Oct 2014	530 (66) ^d	226 (224) ^{ab}	107 (19) ^a	166 (75) ^a

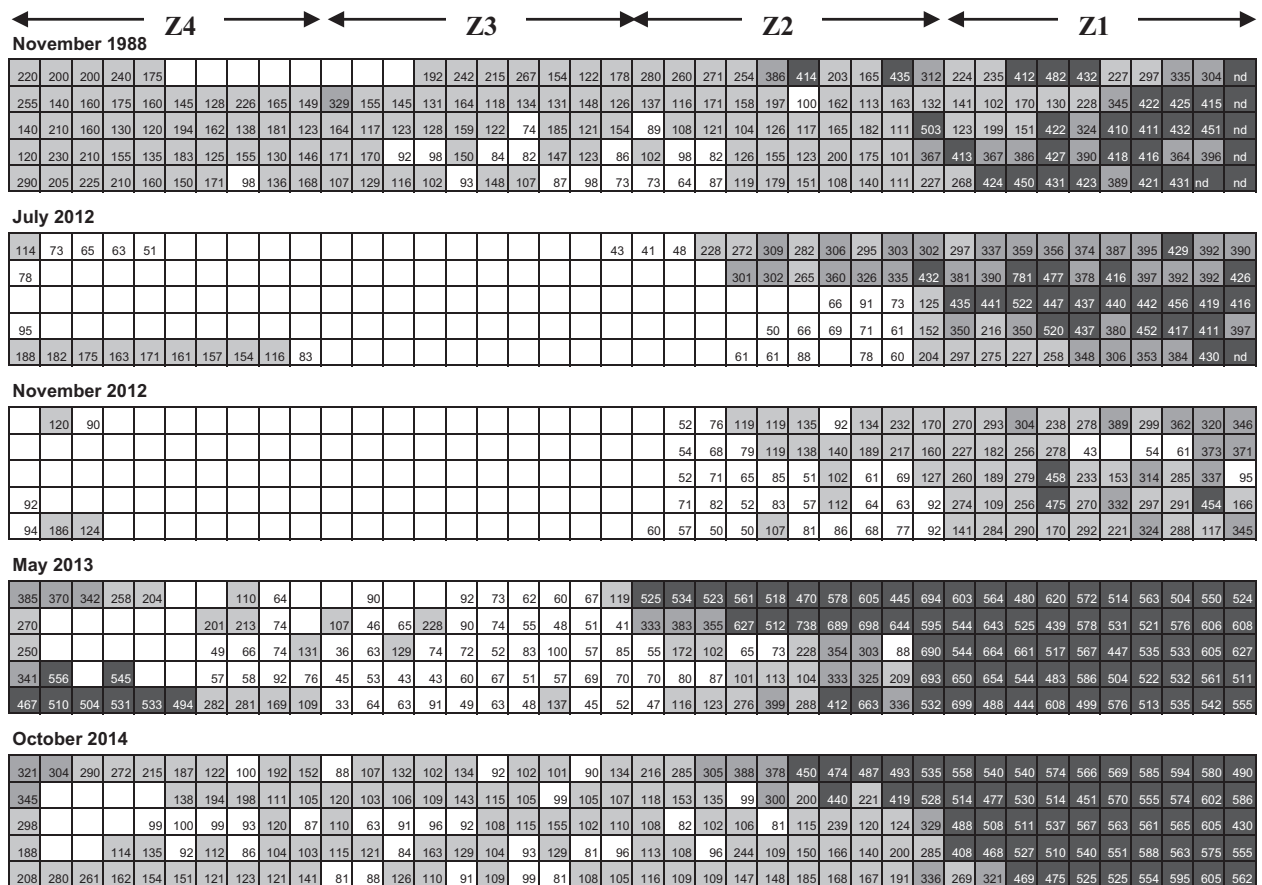


Fig. 3. EC values ($\mu\text{S}\cdot\text{cm}^{-1}$) at the fen surface in the 200 5 m \times 5 m grid cells in the Stobbenribben Fen in Nov 1988, Jul 2012, Nov 2012 and May 2013. Z1 = zone 1, 0–50 m from the ditch; Z2 = zone 2, 50–100 m from the ditch; Z3 = zone 3, 100–150 m from the ditch and Z4 = zone 4, 150–200 m from the ditch. If no values are given, EC could not be measured due to lack of surface water. Grid cells are classified as very low (white; $EC < 100 \mu\text{S}\cdot\text{cm}^{-1}$), low (light grey; $100-300 \mu\text{S}\cdot\text{cm}^{-1}$), intermediate (grey; $300-400 \mu\text{S}\cdot\text{cm}^{-1}$) and high (dark grey; $>400 \mu\text{S}\cdot\text{cm}^{-1}$). July 2012 was a period with high rainfall and high water table, Nov 2012 a period with low rainfall and low water table, and in May 2013 water table had increased after heavy rain to maximum levels for the first time since autumn 2012. EC values in the ditch were $517 \mu\text{S}\cdot\text{cm}^{-1}$ for July 2012, $353 \mu\text{S}\cdot\text{cm}^{-1}$ for Nov 2012, $627 \mu\text{S}\cdot\text{cm}^{-1}$ for May 2013, and $572 \mu\text{S}\cdot\text{cm}^{-1}$ for Oct 2014.

Electrical conductivity depth profiles

In 1973 and 1990, the EC depth profiles did not include the depths 60–120 cm (Fig. 4). Also, it is not clear whether

the values were relatively low or high during these time periods. Nevertheless, they can be used to trace inflow patterns of base-rich water from the ditch. The basic inflow patterns below the floating fen have probably not changed

since 1991 (Van Wirdum 1991). Inflow below the root mat may seem higher in 1973 than in 2012–2014, but that may be due to relatively high EC values in the ditch. In terms of

ditch water contribution, values at 100-cm depth were ca. 51–56% in the zone furthest from the ditch in Jun 1973 and 45–52% in Oct 2014.

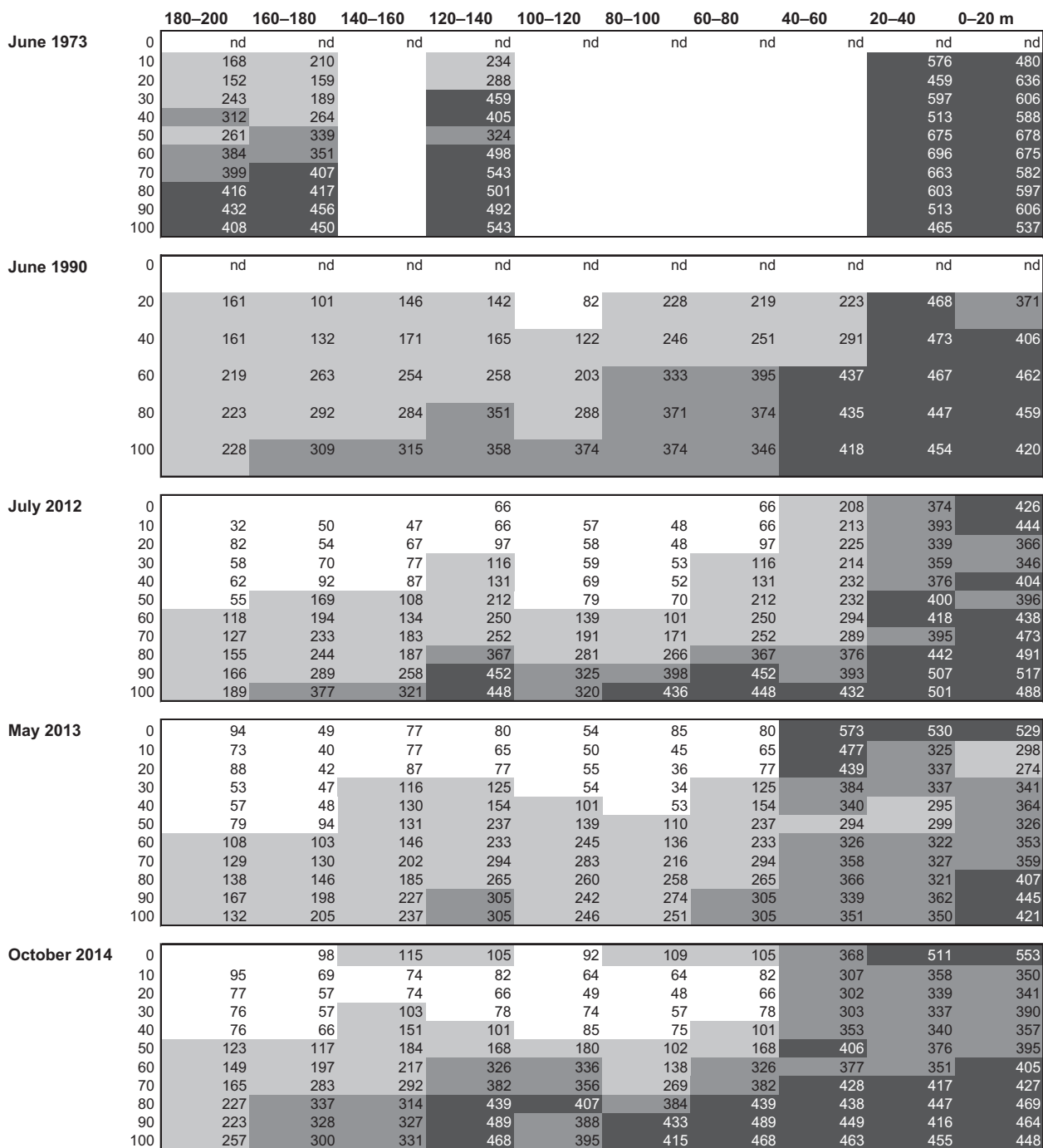


Fig. 4. EC values ($\mu\text{S}\cdot\text{cm}^{-1}$) at the surface and at different depths (cm) in the floating root mat, in different parts of a transect through the centre of the Stobbenribben Fen. Distances are given in meters from the ditch, which is positioned to the right of the plots in the figure. Grid cells are classified as very low (white; $\text{EC} < 100 \mu\text{S}\cdot\text{cm}^{-1}$), low (light grey; $100\text{--}300 \mu\text{S}\cdot\text{cm}^{-1}$), intermediate (grey; $300\text{--}400 \mu\text{S}\cdot\text{cm}^{-1}$) and high (dark grey; $>400 \mu\text{S}\cdot\text{cm}^{-1}$). In June 1973, EC depth profiles were only measured in five parts of the fen, partly because the central part was inaccessible, and not at the surface. In July 1990, EC values were only measured at every 20-cm depth and not at the surface. In July 2012, May 2014 and Oct 2014, the rich fen zone was inundated. (Mean) EC values in the ditch were $800 \mu\text{S}\cdot\text{cm}^{-1}$ for 1973, $516 \mu\text{S}\cdot\text{cm}^{-1}$ for 1990, $517 \mu\text{S}\cdot\text{cm}^{-1}$ for 2012, $627 \mu\text{S}\cdot\text{cm}^{-1}$ for 2013, and $572 \mu\text{S}\cdot\text{cm}^{-1}$ for 2014.

In the upper layers of the floating root mat, the water was probably more base-rich in 1973 than in 2012–2014 (Fig. 5). At 20–40-cm depth, EC values were significantly higher in zones closer rather than farther from the ditch, but also significantly higher in the overall fen in 1973 and 1990 than in 2012–2014. Differences were also significant when expressed as percentage ditch water. In 2012–2014, EC values at 20–40-cm depth were always lower than in 1973 and 1990.

The EC values were examined to determine the source of the water at the fen surface. In zone 1, closest to the ditch, EC values were significantly higher at the fen surface than at 10-, 20- or 30-cm depth during the three flooded surveys (Jul 2012, May 2013 and Oct 2014) during inundation of the rich fen zone (Table 4). At the surface, the average contribution of ditch water amounted to 83%, but this sharply decreased to 63–60% at 10–30-cm depth. Below the floating root mat, around 90–100-cm depth, values increased again to 77% ditch water due to open

contact with the ditch. In both May 2013 and Oct 2014, however, EC values at the fen surface were even higher than below the floating root mat.

Discussion

Water quality improvement and long-term conservation of protected area vegetation

In protected wetland areas, water quality improvement is a key aspect of maintenance and restoration of aquatic and semi-terrestrial ecosystems (Naiman et al. 1999; Nienhuis & Gulati 2002; Lamers et al. 2015). Ecosystems such as the Everglades in the USA and the Rhine River in NW Europe have been severely polluted from urban and agricultural sources, so that attention must be paid to water quality improvement as part of the restoration process (Rudnick et al. 1999; Nienhuis et al. 2002). In many countries, legislation such as the Clean Water Act in the USA and the Water Framework Directive in the EU has been

		m from ditch				
		180–200	160–180	120–140	20–40	0–20
June 1973	Depth					
	20 cm	152	159	288	459	636
	40 cm	312	264	405	513	588
June 1990	20 cm	161	101	142	468	371
	40 cm	161	132	165	473	406
2012–2014	20 cm	82	51	54	338	327
	40 cm	65	69	85	337	375

Fig. 5. Comparison of EC values at 20- and 40-cm depth in five different 20-m fen zones in 1973, 1990 and average in 2012–2014. Distances are given in meters from the ditch at the right in the figure. Grid cells are classified as very low (white; $EC < 100 \mu S \cdot cm^{-1}$), low (light grey; $100\text{--}300 \mu S \cdot cm^{-1}$), intermediate (grey; $300\text{--}400 \mu S \cdot cm^{-1}$) and high (dark grey; $>400 \mu S \cdot cm^{-1}$). Differences were not significant between depths, but highly significant ($P < 0.0001$) between fen zones and years. EC values in the ditch were $800 \mu S \cdot cm^{-1}$ for 1973, $516 \mu S \cdot cm^{-1}$ for 1990 and average $572 \mu S \cdot cm^{-1}$ for 2012–2014.

Table 4. EC values, given as percentage ditch water, and SD at different depths in different fen zones, starting from the ditch at the NE side of the fen. Measurements of July 2012, May 2013 and Oct 2014, when the rich fen zone was inundated, were combined. Different letters indicate significant differences within a particular fen zone between particular depths (i.e. within a column; $P < 0.05$).

	Zone 1: 0–50 m from Ditch	Zone 2: 50–100 m from Ditch	Zone 3: 100–150 m from Ditch	Zone 4: 150–200 m from Ditch
<i>n</i>	23	14	13	13
EC 0 cm	83 (12) ^c	22 (17) ^{ab}	16 (4) ^{ab}	15 (5) ^{ab}
EC 10 cm	63 (13) ^a	16 (12) ^a	10 (2) ^a	11 (4) ^a
EC 20 cm	60 (10) ^a	16 (12) ^a	9 (2) ^a	13 (3) ^a
EC 30 cm	60 (10) ^a	21 (13) ^{ab}	10 (4) ^a	13 (5) ^{ab}
EC 40 cm	62 (12) ^a	27 (17) ^b	12 (4) ^{ab}	16 (9) ^{ab}
EC 50 cm	65 (14) ^a	36 (15) ^b	20 (9) ^b	21 (10) ^b
EC 60 cm	67 (14) ^a	48 (16) ^c	31 (16) ^c	28 (10) ^{bc}
EC 70 cm	69 (14) ^{ab}	56 (15) ^{cd}	42 (14) ^d	36 (15) ^c
EC 80 cm	75 (15) ^b	64 (15) ^{cd}	53 (15) ^e	41 (15) ^{cd}
EC 90 cm	77 (16) ^b	72 (16) ^d	61 (15) ^{ef}	44 (14) ^d
EC 100 cm	77 (14) ^{bc}	72 (15) ^d	63 (16) ^f	48 (19) ^d

implemented recently (Naiman et al. 1999; European Union 2000). In many areas, vegetative recovery is still lagging, but some ecosystems have shown signs of renewed vitality after reduction of water pollution (Makarewics & Bertram 1991; Nienhuis et al. 2002). In small lakes, improvement of water quality may lead to restoration of functional attributes such as healthy macrophyte vegetation, including re-establishment of *Chara* species (Bootsma et al. 1999). In our rich fen study, a vegetation shift over 25 yr towards the original vegetation type indicates that some functional attributes can also be regained by reducing water pollution. In particular, low availability of P is a desirable state for rich fens (Wassen et al. 2005). The decrease in plant productivity and increase in foliar N:P ratios of vascular species to values above 22 indeed shows that P has become a limiting factor over time in our study fen (Koerselman & Meuleman 1996; Güsewell 2004). The idea that Stobbenribben Fen is currently P-limited is further supported by the results of fertilization experiments in the fen complex, which show that vascular plant biomass increases with application of P, but not with N (Cusell et al. 2014a).

Long-term hydrological, water quality and vegetation changes with peat mat development

Despite the improvement in surface water quality in the national park and rich fen area, a portion of the rich fen turned into *Sphagnum*-dominated peatland. Rich fen vegetation is generally replaced by *Sphagnum* spp. when the peat mass is exposed to less base-rich water (Clapham 1940; Clymo 1963; Soudzilovskaia et al. 2010), although this process could be altered by high atmospheric deposition of acidic precipitation (Berendse et al. 2001; Limpens et al. 2003; Kooijman 2012). Over time, peat layers grow thicker, and the surface becomes more isolated, blocking access of base-rich water from below the mat. A palaeoecological reconstruction of the succession in zone 2 of our study fen suggests that the peat layer has become 35-cm thicker in ca. 50 yr (A.H. Fabers, B. van Geel and A.M. Kooijman, unpubl. data). Such a layer may effectively reduce the flow of base-rich water from below the floating root mat to the fen surface, as suggested from the decrease in EC values in the upper part of the fen over the past decades. Weak spots in the root mat could still provide access to base-rich water, but a detailed survey of EC depth profiles in all hollows in Nov 2012 suggests that the mat no longer allows base-rich water to rise to the surface.

Despite on-going succession, rich fen bryophytes are locally expanding in the Stobbenribben. In the SE fen of the Stobbenribben complex, rich fen bryophytes even increased from ca. 60% to 90% (1973 vs 2012: Van Wirdum 1991 and this study, respectively), while *Sphagnum*

communities decreased from ca. 40% to less than 10% (1973 vs 2012: Van Wirdum 1991 and this study, respectively). Currently, the SE fen is largely occupied by dark brown *Scorpidium* vegetation (Fig. 1). While it is clear that rich fen vegetation persists in regularly inundated areas, a debate has started as to whether this situation is due to the general raising of the water table inside the fen, which has open connections with the ditch below the floating root mat, or superficial flooding with ditch water. Although occasional flooding of the Stobbenribben has been reported (Bergmans 1975; Van Wirdum 1991; Kooijman 1993), this flooding was expected to play a minor role in floating fens, which move up and down with the water table. In the past, the fen surface was probably primarily fed by base-rich water from below the floating root mat (Van Wirdum 1991). At present, however, this contact has probably become more restricted. Instead, superficial flooding may play a more important role. This idea is supported by EC values, which were higher at the fen surface than inside the floating root mat after flooding. In May 2013, EC values at the fen surface were even higher than below the floating root mat, which suggests that inflow of base-rich water from the ditch to the area below the root mat only began recently, so that high EC values did not extend further than 20 m from the ditch. At the fen surface, however, high EC values were found up to 60 m from the ditch, which supports the idea that the origin of the water is the ditch. Open connections with the adjacent ditch were indeed observed when the rich fen zone was clearly inundated. Due to downward water movement from the fen to the low-lying adjacent agricultural polders, water tables inside the fens are generally lower than in the ditch (Van Wirdum 1991), which at least allows inflow of water from the ditch into the fen. Other aspects of water dynamics in the system are still uncertain, for instance, how much of the flood water comes from the ditch, the relationship of EC values to reduction processes (Cusell et al. 2013b), and the route of base-rich water over the surface of the mat during flooding. Nevertheless, it is likely that the current source of the water in the fen is the ditch, which has recently improved in water quality.

Concluding remarks

This study shows that floating rich fens can be restored, even in industrialized countries with a high amount of human pressure, such as the Netherlands. One of the key factors is the gradual improvement of water quality over the past 25 yr, which resulted in a four-fold decrease in above-ground biomass production, a clear increase in P limitation, and replacement of eutrophic bryophytes such as *C. cuspidata* by the mesotrophic species *S. scorpioides*. The other key factors in the re-emergence of rich fen species

may be high water levels and temporary inundation of the fens with base-rich surface water from the ditch, especially after improvement in water quality. Our results clearly indicate that rich fen vegetation can persist, despite ongoing succession, when the fen surface is occasionally inundated with mineral-rich but nutrient-poor water.

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References

- Berendse, F., van Breemen, N., Rydin, H., Buttler, A.A., Heijmans, M., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H. & Wallen, B. 2001. Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Global Change Biology* 7: 591–598.
- Bergmans, W. 1975. *Synoekologisch onderzoek in enige suksessiereeksen in het C.R.M. reservaat De Weerribben (N.W.-Overijssel)*, 67 pp. MSc thesis, University of Amsterdam, Amsterdam, NL.
- Bootsma, M.C., Barendregt, A. & van Alphen, J.C.A. 1999. Effectiveness of reducing external nutrient load entering a eutrophicated shallow lake ecosystem in the Naardermeer Nature Reserve, The Netherlands. *Biological Conservation* 90: 193–201.
- Clapham, A.R. 1940. The role of bryophytes in the calcareous fens of the Oxford District. *Journal of Ecology* 28: 71–80.
- Clymo, R.S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Annals of Botany* 27: 71–80.
- Cody, R.P. & Smith, J.K. 1987. *Applied statistics and the SAS programming language*, 280 pp. Elsevier Science, Amsterdam, NL.
- Cusell, C., Kooijman, A.M., Lamers, L.P.M. & Mettrop, I. 2013a. Natura 2000 Kennislacunes in de Wieden en de Weerribben. [Rapport nr 2013/OBN171-LZ], 356 pp. Directie Agro-kennis, Ministerie van Economische Zaken, Den Haag, NL.
- Cusell, C., Lamers, L.P.M., van Wirdum, G. & Kooijman, A.M. 2013b. Impacts of water level fluctuation on mesotrophic rich fens: acidification versus eutrophication. *Journal of Applied Ecology* 50: 998–1009.
- Cusell, C., Kooijman, A.M. & Lamers, L.P.M. 2014a. Nitrogen or phosphorus limitation in rich fens? Edaphic differences explain contrasting results in vegetation development after fertilization. *Plant and Soil* 384: 153–168.
- Cusell, C., Kooijman, A.M., Fernandez, F., van Wirdum, G., Geurts, J.J., van Loon, E.E., Kalbitz, K. & Lamers, L.P.M. 2014b. Filtering fens: mechanisms explaining phosphorus-limited hotspots of biodiversity in wetlands adjacent to heavily fertilized landscapes. *Science of Total Environment* 481: 1129–1141.
- De Haan, B.J., Kros, J., Bobbink, R., Jaarsveld, J.A., De Vries, W. & Noordijk, H. 2008. Ammoniak in Nederland. [PBL-rapport 500125003], Planbureau voor de Leefomgeving, Bilthoven, NL.
- European Union 1992. *Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora*. European Commission, Brussel, BE.
- European Union 2000. *Directive 2000/60/EC establishing a framework for Community action in the field of water policy*. European Commission, Brussel, BE.
- Gorham, E., Janssens, J.A., Wheeler, G.A. & Glaser, P.H. 1987. The natural and anthropogenic acidification of peatlands. In: Hutchinson, T.H. & Meema, K.M. (eds.) *Effects of atmospheric pollutants on forests, wetlands and agricultural ecosystems*, pp. 493–512. NATO ASI Series G16. Springer, Berlin, DE.
- Gunnarson, U., Rydin, H. & Sjörs, H. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, central Sweden. *Journal of Vegetation Science* 11: 277–286.
- Güsewell, S. 2004. N: P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164: 243–266.
- Hajek, T. & Adamec, L. 2009. Mineral nutrient economy in competing species of *Sphagnum* mosses. *Ecological Restoration* 24: 291–302.
- Hallingbäck, T. & Hodgetts, N. 2000. *Mosses, liverworts and hornworts. Status survey and conservation action plan for bryophytes*. IUCN/SSC Bryophytes Species Group, IUCN, Gland, CH.
- Heino, J., Virtanen, R. & Vuori, K.M. 2005. Spring bryophytes in forested landscapes: land use effects on bryophyte species richness, community structure and persistence. *Biological Conservation* 124: 539–545.
- Juutinen, R. 2011. The decrease of rich fen bryophytes in springs as a consequence of large-scale environmental loss. A 50-year re-sampling study. *Lindbergia* 34: 2–8.
- Koerselman, W. & Meuleman, A.F.M. 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33: 1441–1450.
- Koerselman, W., Bakker, S.A. & Blom, M. 1990. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *Journal of Ecology* 78: 428–442.
- Kooijman, A.M. 1992. The decrease of rich fen bryophytes in the Netherlands. *Biological Conservation* 59: 139–143.
- Kooijman, A.M. 1993. Causes of the replacement of *Scorpidium scorpioides* by *Calliergonella cuspidata* in eutrophicated rich fens I. Field studies. *Lindbergia* 18: 78–84.

- Kooijman, A.M. 2012. 'Poor rich fen mosses': atmospheric N-deposition and P-eutrophication in base-rich fens. *Lindbergia* 35: 42–52.
- Kooijman, A.M. & Paulissen, M.P.C.P. 2006. Acidification rates in wetlands with different types of nutrient limitation. *Applied Vegetation Science* 9: 205–212.
- Kuiper, P. & Kuiper, C. 1958. Verlandingsvegetaties in Noordwest-Overijssel. *Kruipnieuws* 20: 1–19.
- 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 fen in Europe and North America: from trial and error to an evidence-based approach. *Biological Reviews* 90: 182–203.
- Limpens, J., Tomassen, H.B. & Berendse, F. 2003. Expansion of *Sphagnum fallax* in bogs: striking the balance between N and P availability. *Journal of Bryology* 25: 83–90.
- Makarewics, J.C. & Bertram, P. 1991. Evidence of the Lake Erie ecosystem: water quality, oxygen levels and pelagic functions appear to be improving. *BioScience* 4: 216–221.
- Mason, R.D., Lind, D.A. & Marchal, W.G. 1994. *Statistics, an introduction*, 4th edn, 660 pp. Harcourt Brace, Orlando, FL, US.
- 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 Biology and Biochemistry* 68: 317–328.
- Naiman, R.J., Magnuson, J.J., McKnight, D.M., Stanford, J.A. & Karr, J.R. 1999. Freshwater ecosystems and their management: a national initiative. *Science* 270: 584–585.
- Nienhuis, P.H. & Gulati, R.D. 2002. *Ecological restoration of aquatic and semi-aquatic ecosystems in the Netherlands*. Kluwer Academic, Dordrecht, NL.
- Nienhuis, P.H., Buijse, A.D., Leuven, R.S.E.W., Smits, A.J.M., de Nooij, R.J.W. & Samborska, E.M. 2002. Ecological rehabilitation of the lowland basin of the River Rhine (NW-Europe). *Hydrobiologia* 478: 53–72.
- Proctor, M.C.F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A.J.E. (ed.) *Bryophyte ecology*, pp. 333–381. Chapman & Hall, London, UK.
- Rudnick, D.T., Chen, Z., Childers, D.L., Boyer, J.N. & Fontaine, T.D. III 1999. Phosphorus and nitrogen inputs to Florida Bay: the importance of the Everglades Watershed. *Estuaries* 22: 398–416.
- Schot, P.P. & Molenaar, A. 1992. Regional changes in groundwater flow patterns and effects on groundwater composition. *Journal of Hydrology* 130: 151–170.
- Schouwenberg, E.P.A.G. & Van Wirdum, G. 1997. *Basenverzadiging van natte schraallanden; Deterministisch onderzoek naar de relatie tussen hydrologie, bodem en vegetatie*, 103 pp. Nationaal onderzoeksprogramma verdroging. [NOV-rapport 108], Wageningen, NL.
- Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. *Oikos* 2: 241–258.
- Soudzilovskaia, N.A., Cornelissen, J.H.C., During, H.J., van Logtestijn, R.S.P., Lang, S.I. & Aerts, R. 2010. Similar cation exchange capacities among bryophyte species refute a presumed mechanism of peatland acidification. *Ecology* 91: 2716–2726.
- Succow, M. & Jeschke, L. 1986. *Mires in the Landscape: development, functioning, organisms and communities, extension, use and management of peatlands*. Urania, Leipzig, DE.
- Tansley, A.G. 1946. *Introduction to plant ecology*. Allen & Unwin, London, UK.
- Touber, L. 1973. *Hydrologisch onderzoek in enige verlande petgaten in het C.R.M. Reservaat "de Weerribben", N.W.-Overijssel*, 34 pp. MSc thesis, University of Amsterdam, Amsterdam, NL.
- Van Diggelen, R., Molenaar, W.J. & Kooijman, A.M. 1996. Vegetation succession in a floating mire in relation to management and hydrology. *Journal of Vegetation Science* 7: 809–820.
- Van Diggelen, J.M.H., Bense, I.H.M., Brouwer, E., Limpens, J., van Schie, M.J.M., Smolders, A.J.P. & Lamers, L.P.M. 2015. Restoration of acidified and eutrophied rich fens: long-term effects of traditional management and experimental liming. *Ecological Engineering* 75: 208–216.
- Van Loon, A. 2010. *Unravelling hydrological mechanisms behind fen deterioration in order to design restoration strategies*, 139 pp. PhD thesis, Utrecht University, Utrecht, NL.
- Van Tooren, B.F. & Sparrius, L.B. 2007. *Voorlopige verspreidingsatlas van de Nederlandse mossen*, 350 pp. Bryologische en Lichenologische Werkgroep van de KNNV, Zeist, NL.
- Van Wirdum, G. 1991. *Vegetation and hydrology of floating rich fens*. PhD thesis, University of Amsterdam, Maastricht, NL.
- Verhoeven, J.T.A., Kooijman, A.M. & Van Wirdum, G. 1988. Mineralization of N and P along a trophic gradient in a freshwater mire. *Biogeochemistry* 6: 31–43.
- Vitt, D.H. & Wieder, R. 2009. Structure and function of bryophyte-dominated peatlands. In: Goffinet, B. & Shaw, A.J. (eds), *Bryophyte biology*, 2nd edn, p. 377. Cambridge University Press, Cambridge, UK.
- Wassen, M.J., Olde Venterink, H., Lapshina, E.D. & Tanneberger, F. 2005. Endangered plants persist under phosphorus limitation. *Nature* 437: 547–550.
- Westerman, R.L. 1990. *Soil testing and plant analysis*, 3rd edn. Soil Science Society of America, Madison, WI, US.