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'Poor rich fen mosses': atmospheric N-deposition and P-eutrophication in base-rich fens

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Base-rich fens in the Netherlands are threatened by acidification and replacement of rich-fen bryophytes by *Sphagnum* spp. Acidification is a natural process when input of base-rich water is reduced, and is probably accelerated by high atmospheric deposition, leading to lower pH at similar calcium levels, and increased acidification capacity of *Sphagnum*. However, acidification may also be due to eutrophication, especially with P, which leads to a shift in stable states from base-rich to *Sphagnum*-dominated fen. Under nutrient-poor conditions, *Scorpidium scorpioides* fen is stabilized as long as sufficient base-rich water is supplied. The species is tolerant to rainwater and may even counteract acidification. Its successor *Sphagnum subnitens*, however, is intolerant to groundwater and has low acidification capacity, and can only become dominant after changes in hydrology and (local) accumulation of rain water. Under nutrient-rich conditions, however, *Scorpidium scorpioides* is replaced by *Calliergonella cuspidata*. In contrast to *Scorpidium scorpioides*, *Calliergonella cuspidata* is intolerant to rainwater. Moreover, its successor *Sphagnum squarrosum* grows well under base-rich conditions. High growth rates and high acidification capacity of *S. squarrosum* further lead to rapid expansion of this species, acidification of the fen, and loss of characteristic rich-fen species. For conservation of rich fens it is thus very important to keep the habitat base-rich, but nutrient-poor.

Bryophytes are important components of base-rich fens, which contain many red list species and belong to the EU priority habitat H7140 (Habitat directive 1992). The bryophyte layer in base-rich fens is often extensive, and species diversity is generally high (Sjörs 1950, Succow and Jeschke 1986). In the Netherlands, species such as *Scorpidium scorpioides* (Hedw.) Limpr., *S. cossoni* (Schimp.) Hedenäs, *Campylium stellatum* (Hedw.) Lange & C.E.O. Jensen, *Fissidens adianthoides* Hedw. and *Bryum pseudotriquetrum* (Hedw.) P.Gaertn.et al. were common inhabitants of base-rich fens. Rich-fen bryophytes also often indicate specific environmental conditions, because they have no roots to take up solutes from deeper layers, and remain in direct contact with the surrounding water through one-cell-layer-thick leaves without a cuticula (Proctor 1982).

In the Netherlands, a densely populated and agricultural country, base-rich fens and their characteristic bryophytes have become very rare (Kooijman 1992, van Tooren and Sparrius 2007). A major threat to rich-fen bryophytes is acidification and replacement by *Sphagnum* spp. Some *Sphagnum* species, such as *S. contortum* Schultz, *S. teres* (Schimp.) Ångstr. and *S. warnstorfia* Russow, may actually belong to the base-rich fen stage, but most other species, such as *S. subnitens* Russow & Warnst., *S. squarrosum* Crome, *S. fallax* (H.Klinggr.) H.Klinggr., *S. palustre* L. and *S. magellanicum* Brid., indicate a shift towards more acid conditions and disappearance of rich-fen bryophytes and, after some time, characteristic phanerogams as well.

Acidification is partly a natural process, due to hydrological isolation from the base-rich groundwater or surface water, when rainwater becomes the main water source (Clapham 1940, Sjörs 1950, Gorham et al. 1987). This may happen when peat layers become too thick to allow contact with the groundwater, but also when rich fens develop in (artificial) ponds where access of base-rich surface water is reduced by impermeable peat dikes, like a bath tub (van Diggelen et al. 1996). In the post-glacial landscape of north and western Europe, most peatlands developed from base-rich fens, but became dominated by *Sphagnum* spp. However, in areas where input of calcium-and bicarbonate-rich water was sufficiently high, base-rich fens have remained through time (O'Connell 1981). Also, in the Netherlands, under particular hydrological conditions which allow sufficient influx of base-rich water, fens still remain in the base-rich stage after more than five decades, while in more isolated areas, *Sphagnum* took over (van Wirdum 1991, van Diggelen et al. 1996). Also, a groundwater discharge fen, where seepage was approximately 3 mm day^{-1}, and calcium- and iron-rich groundwater contributed 51% of the water input, remained longer in a base-rich state than a recharge fen, where rain water percolated through the peat layer (Koerselman et al. 1990a, b).

In the Netherlands, in the late 1980s, even fens with substantial groundwater input, such as the above mentioned, became dominated by *Sphagnum*, first by *S. squarrosum* and then by *S. fallax*. A likely cause was high atmospheric deposition (Gorham et al. 1987), which showed a peak in the 1980–1990s (van der Eerden et al. 1998, Kros et al. 2008). However, in the following years it became clear that other factors played a role as well, and were possibly even more important. The aim of this paper is to give an overview of the main processes threatening the existence of base-rich fens. The paper is in honour of Dr. Heinjo During, who has been a long-time editor of this journal, and was closely involved in the research presented, and who recently retired from Utrecht University. A large part of this overview may be retrospective, but the data will be put in a present-day perspective, to make clear how important older research can be to contemporary problems in management of base-rich fens.

Atmospheric deposition

During the last decades, increased atmospheric deposition of nitrogen (N) (and sulphur, S) has become a major ecological problem in the Netherlands and many other industrialized countries (van Dobben and van Hinsberg 2008, Kros et al. 2008). Since the early 20th century, N-deposition in the Netherlands has gradually increased from natural levels of a few kg N ha^{-1} year^{-1} to values around 50 kg N ha^{-1} year^{-1} in 1988. Total acid deposition had an all time high in the 1980s, with values of 6000 mol ha^{-1} year^{-1} (Kros et al. 2008). Over the last decades, atmospheric N-deposition has considerably decreased to values of 30 kg N ha^{-1} year^{-1}, and 3000 mol acid ha^{-1} year^{-1} (Haan et al. 2008, Kros et al. 2008), but this is still almost two times as high as the critical level for habitat type H7140A, to which the base-rich fens belong. The critical N-deposition, above which negative changes are expected to occur, is 16.8 kg N ha^{-1} year^{-1} (van Dobben and van Hinsberg 2008).

Part of the negative effects of high N-deposition may be related to high levels of ammonium, which accounts for a major part of the total N-deposition. Rich-fen bryophytes have been shown to be very sensitive to ammonium toxicity (Paulissen et al. 2004, Verhoeven et al. 2010). As long as base-rich conditions in the fen can be maintained, part of the ammonium may be transformed to nitrate, because nitrification is stimulated at high pH. However, once the fen becomes acidified and pH levels drop, ammonium toxicity may become a major problem.

Apart from ammonium toxicity, high atmospheric deposition may lead to more acid conditions in the fen habitat. In central Sweden, pH values in rich fens slightly decreased over the past 50 years, possibly due to atmospheric deposition (Gunnarson et al. 2000). In the Netherlands, however, where atmospheric deposition is much higher (Remke et al. 2009), the situation may be worse. Compared to reference sites in areas with relatively low N-deposition in Ireland, western Denmark, Sweden and eastern Poland, the habitat of characteristic rich-fen species, such as *Scorpidium scorpioides* in the Netherlands, seems indeed more acidic (Fig. 1). The dataset with water samples from the bryophyte layer consists of 53 samples from the Netherlands, and 200 reference samples from areas with low N-deposition, where N-deposition is generally (far) below 10 kg ha^{-1} year^{-1} (Remke et al. 2009). Despite the range in sampling periods and countries, the correlation between pH and calcium or bicarbonate levels is very clear for both the Netherlands and the reference sites with low N-deposition, which is according to expectations, as both calcium and bicarbonate contribute to buffer capacity and thus pH. However, in the Netherlands, pH values lower than 5.8 were not found, in contrast to reference sites, and in contrast to the past (Kooijman and Westhoff 1995). Until the 1960s, weakly buffered sites with *S. scorpioides* still existed (Schoof-van Pelt 1973), but they have disappeared due to acid deposition (Roelofs 1983). Also, in Dutch fens with *S. scorpioides*, a similar calcium level, and to some extent alkalinity, is generally associated with a lower pH than in reference sites. A calcium level of 1000 µmol l^{-1} Ca (or 40 mg l^{-1}) may correlate with pH 6.4 in the Netherlands, but with pH 7.0 in the reference sites. This implies that, in the Netherlands, more calcium (and bicarbonate) is needed to maintain the pH at a certain level. In the Netherlands, pH 7.0 may require 1500 µmol l^{-1} Ca, while in reference sites, 1000 µmol l^{-1} may be sufficient. This means that the demand for calcium and bicarbonate-rich water in order to maintain the pH above 6.0 in the Netherlands, a country with high atmospheric deposition, is extra high.

Apart from direct acidification of the rich-fen habitat, increased atmospheric deposition may also promote more acid conditions via the acidification capacity of *Sphagnum* spp., by release of protons in exchange for other cations (Clymo 1963, 1973, Kooijman and Bakker 1994). *Sphagnum* species produce large amounts of polyuronic acids, which serve as cation exchange sites and proton donors. Rich-fen bryophytes may have high cation exchange capacity as well (Brown 1982, Soudz-

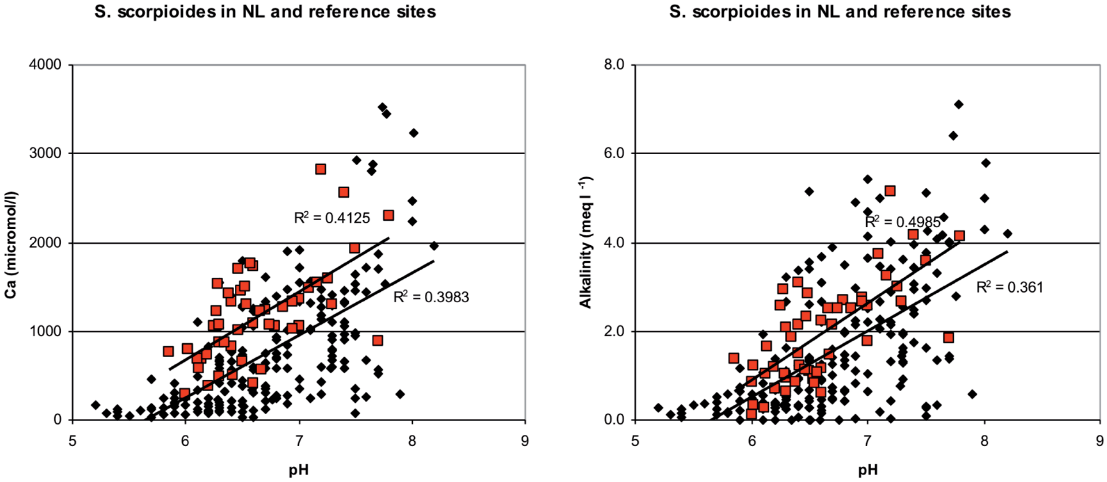


Figure 1. Calcium concentrations, alkalinity and pH in habitats of *Scorpidium scorpioides* in the Netherlands (red squares) and reference sites in parts of Europe (black diamonds) with lower atmospheric deposition. In the Netherlands, samples were collected in 1988–1990 (n = 21; Kooijman and Westhoff 1995) and 2008–2009 (n = 28; Cusell et al. 2011), but did not differ between sampling periods. Reference samples were collected in 1988–1990 in Ireland (n = 83) and Denmark (n = 8; Kooijman and Westhoff 1995), in 1990–1997 throughout Sweden (n = 106; Kooijman and Hedenäs unpubl.) and in 2010 in Poland (n = 3; Kooijman and Pawlikowski unpubl.).

ilovskaia et al. 2010), but this is generally loaded with base cations such as calcium (Hájek and Adamec 2009), which increases acid neutralization capacity rather than acidification capacity. The rate of cation exchange and acidification by bryophytes can be increased by atmospheric deposition, which for a large part consists of ammonium. In an artificial rain experiment in which clean rain was applied, bryophyte species indeed appeared to have different acidification capacity (Fig. 2). In the relatively small *Sphagnum subnitens*, which also showed lower growth rates, acidification capacity was lower than in the larger species *S. squarrosum* and *S. fallax*. In accordance with Soudzilovskaia et al. (2010), the rich-fen bryophyte *Scorpidium scorpioides*, however, did not show acidification at all. The species was able to counteract acidification, despite careful rinsing of the species in advance. Counteraction rather than increase of acidification by *S. scorpioides* had also been shown by Boryslawski (1978). When polluted rain was applied, differences between bryophyte species persisted. However, acidification capacity of the three *Sphagnum* species at least doubled, which further supports the hypothesis that acidification may increase when atmospheric deposition is high. *Scorpidium scorpioides* also showed higher cation exchange, but again

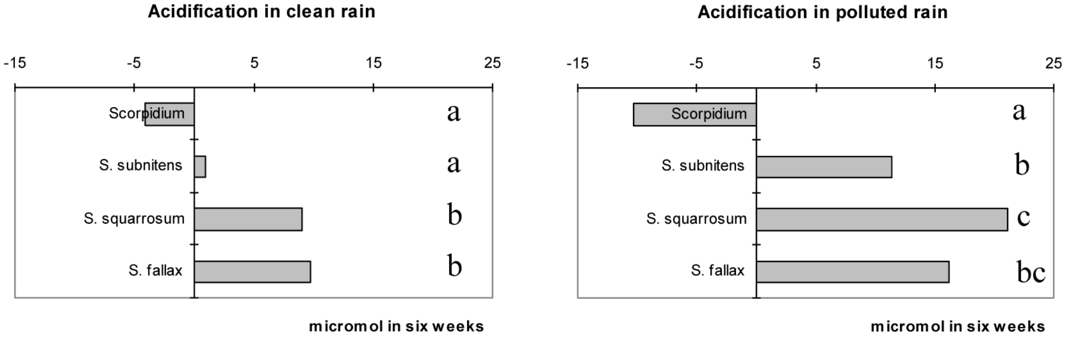


Figure 2. Acidification capacity of four wetland bryophyte species: *Scorpidium scorpioides*, *Sphagnum subnitens*, *S. squarrosum* and *S. fallax* in an artificial rain experiment with clean and polluted rain. Data are derived from Kooijman and Bakker (1994). Rain was applied weekly, with a total of 450 mm for each cup containing 30 (*Scorpidium. scorpioides, Sphagnum squarrosum* and *S. fallax*) or 40 (*S. subnitens*) bryophyte plants at field density. Values are mean amounts (n = 4) of protons released (positive) or consumed (negative) during the six weeks of the experiment. Different letters indicate significant differences between species ($p < 0.05$) within a particular rain treatment. Differences between clean and polluted rain are significant for all species.

counteracting acidification rather than increasing this. Under high N-deposition, counteracting acidification requires more base cations than in clean rain, which supports that, in the Netherlands, higher calcium levels are needed to maintain a neutral pH in *S. scorpioides* habitats. However, as long as calcium-rich water is supplied from time to time, the species can increase the base-saturation of its exchange complex, and thus counteract acidification even under high atmospheric deposition.

Eutrophication: differences between the Vechtplassen and NW-Overijssel

The above suggests that input of calcium- and bicarbonate-rich water is very important to counteract the effects of atmospheric deposition. Yet, this may not be the only factor. In the Netherlands, both the Vechtplassen area between Amsterdam and Utrecht, and NW-Overijssel, located in the northeastern part of the country, have been renowned for base-rich fens in the past. In both areas, fens with *Scorpidium scorpioides* were common (Kooijman 1992). At present, however, NW-Overijssel is still a hotspot for characteristic rich-fen bryophytes, but the Vechtplassen area is no longer so (Fig. 3). In NW-Overijssel, rich fens with characteristic species such as *S. scorpioides, S. cossoni* and *Hamatocaulis vernicosus* (Mitt.) Hedenäs still occur (van Wirdum 1991, Cusell et al. 2011), although they have decreased in surface area since the 1960s (van Diggelen et al. 1996). Within *Scorpidium*-fens, local mounds of *Sphagnum* can be found, but they are mainly occupied by *S. subnitens*, remain restricted in size and do not seem to expand. In the Vechtplassen area, base-rich fens were also common (Vermeer 1985, Verhoeven and Arts 1987, van Baaren et al. 1988, Koerselman et al. 1990a), but after 1990 they rapidly became dominated by *Sphagnum* spp., notably by *S. squarrosum*, and followed by *S. fallax* and *S. palustre* (Kooijman 1993a). At present, base-rich fens are very rare there, and restricted to local spots where upwelling groundwater is able to counteract acidification. The population of *Scorpidium scorpioides* has been reduced to a few square decimetres at 1–2 localities.

These differences in bryophyte composition, and quality of base-rich fens in general, between the Vechtplassen area and NW-Overijssel are probably related to differences in nutrient availability. This may be illustrated by the species composition in the bryophyte layer in 1988 of the best rich-fens in Westbroek, located in the southern part of the Vechtplassen, and the Weerribben, located in NW-Overijssel (Table 1). In the Weerribben-fen, in which *S. scorpioides* still prevails, *S. scorpioides* was a very common species in 1988, present in 73% of the 5 × 5 m grid cells. In the Westbroek-fen, which has become dominated by *Sphagnum* in the early 1990s (Kooijman and Paulissen 2006), *S. scorpioides* was found in 1988 in only one grid cell. Also, *Campylium stellatum* occurred in 73% of the grid cells in the Weerribben-fen, but not

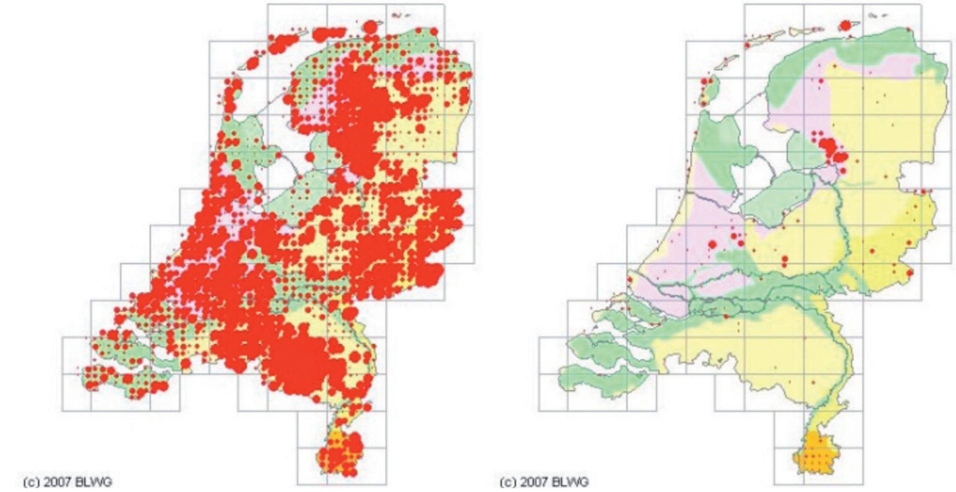


Figure 3. Hotspots of common (left) and rare (right) rich-fen bryophytes in the Netherlands, based on the combined distribution of ten characteristic species. Data are derived from the Dutch Bryological and Lichenological Society. Common species include: *Bryum pseudotriquetrum* (Hedw.) P.Gaertn.et al., *Calliergon cordifolium* (Hedw.) Kindb., *Calliergonella cuspidata* (Hedw.) Loeske, *Calypogeia fissa* (L.) Raddi, *Drepanocladus aduncus* (Hedw.) Warnst. , *Marchantia polymorpha* L., *Pellia neesiana* (Gottsche) Limpr., *Plagiomnium affine* (Blandow) T.J.Kop., *Aneura pinguis* (L.) Dumort and *Sphagnum squarrosum* Crome. Rare (and red-list) species include: *Calliergon giganteum* (Schimp.) Kindb., *Campylium stellatum* (Hedw.) Lange & C.E.O. Jensen, *Campyliadelphus elodes* (Lindb.) Kanda, *Drepanocladus sendtneri* (H.Müll.) Warnst., *Hamatocaulis vernicosus* (Mitt.) Hedenäs, *Preissia quadrata* (Scop.) Nees, *Pseudocalliergon trifarium* (F.Weber & D.Mohr) Loeske, *Scorpidium scorpioides* (Hedw.) Limpr., *S. cossoni* (Schimp.) Hedenäs and *Sphagnum contortum* Schultz.

Table 1. Species composition of rich-fen bryophytes in a floating rich fen in the Weerribben (Stobberibben; located in NW-Overijssel) and Westbroek (Grote van Garderen; located in the Vechtplassen), based on occurrence (%) in the total numer of 5 × 5 m grid cells. Data are derived from Kooijman 1988 (unpubl.).

	Weerribben (n = 194)	Westbroek (n = 123)
Scorpidium scorpioides (Hedw.) Limpr.,	73	1
Campylium stellatum (Hedw.) Lange & C.E.O. Jensen	73	–
Fissidens adianthoides Hedw.	40	–
Bryum neodamense Müll. Hal.	28	–
Sphagnum contortum Schultz	65	22
Calliergonella cuspidata (Hedw.) Loeske	77	99
Bryum pseudotriquetrum (Hedw.) P.Gaertn.et al.	44	85
Calliergon giganteum (Schimp.) Kindb.	23	71
Calliergon cordifolium (Hedw.) Kindb.	12	89
Plagiomnium affine (Blandow) T.J.Kop.	1	73
Drepanocladus polygamus (Schimp.) Hedenäs	1	68
Marchantia polymorpha L.	–	28
Kindbergia praelongum (Hedw.) Ochyra	2	25

at all in Westbroek. *Sphagnum contortum* and *Calliergon giganteum* (Schimp.) Kindb. were the only rich-fen species common in both fens. In the Westbroek-fen, more eutraphent species, such as *Calliergon cordifolium* (Hedw.) Kindb. and *Drepanocladus polygamus* (Schimp.) Hedenäs, predominated. *Calliergonella cuspidata* (Hedw.) Loeske was common in the Weerribben-fen as well, but except for a eutrophic border zone adjacent to the ditch, only in low densities. In Westbroek, however, the species generally reached high densities throughout the fen.

Potentially more eutrophic conditions in the Vechtplassen than in NW-Overijssel are supported by higher phosphate, nitrate and ammonium concentrations in the Vechtplassen fens (Kooijman 1993c). Also, net mineralization of N and P was higher in the Vechtplassen than in NW-Overijssel (Verhoeven and Arts 1987, Verhoeven et al. 1988). In both areas, net N-mineralization was generally 4–6 times higher in *Sphagnum* stages than in rich-fen soils. However, for both fen types, values in the Vechtplassen were at least two times higher than in NW-Overijssel. For net P-mineralization, response patterns were the same, but differences between areas and fen types were even larger. In both areas, net P-mineralization was more than 15 times lower in base-rich fens than in *Sphagnum*-soils, probably due to input of calcium- and iron-rich groundwater (Vechtplassen) or calcium-rich surface water (NW-Overijssel). Both calcium and iron may chemically sorb part of the P (Richardson and Marshall 1986, Lamers et al. 1998, 2002, Kooijman and Hedenäs 2009, Cusell et al. 2011). In addition, while the Vechtplassen showed at least some net P-mineralization in the rich-fen stage, NW-Overijssel showed immobilization of P rather than net release.

More eutrophic conditions in the Vechtplassen than in NW-Overijssel are further illustrated by differences in N:P ratios of phanerogam species (Table 2), which indicate whether N or P may be a limiting factor (Koerselman and Meuleman 1996, Güsewell 2004). N:P ratios around 10 suggest that N is a limiting factor, and P in relatively high supply, while values around 20 clearly indicate limitation by P. Over the past decades, N:P ratios in *Scorpidium*-fens in NW-Overijssel were close to or higher than 20, which points to P-limitation. In fertilization experiments, P was indeed a limiting factor (Kooijman 1993b, Cusell et al. 2011). In the Vechtplassen, data are only available for the end of the 1980s, when rich fens were still common. Like in NW-Overijssel, a fen dominated by *Scorpidium scorpioides*, which was actually located in a more isolated part outside the main study area Westbroek, also showed N:P ratios higher than 20, and was clearly P-limited as shown in a fertilization experiment (Verhoeven and Schmitz 1991). This particular fen has remained in a rich-fen stage for a long time, and has only recently become dominated by *Sphagnum*. In contrast, in the more agricultural part of the Westbroek area, rich fens were dominated by *C. cuspidata*. These fens had much lower N:P ratios, which suggests that N had become a limiting factor. However, high nitrate and ammonium concentrations in the fen water (Kooijman 1993c), high N-mineralization (Verhoeven and Arts 1987), high atmospheric N-deposition and high N-input via groundwater seepage (Koerselman et al. 1990a, b), suggest that N was not really in low supply, but

Table 2. Foliar N:P ratios of phanerogamous species in rich fens in NW-Overijssel and the Vechtplassen. Except the one with *Sphagnum squarrosum*, plant communities generally belong to the *Scorpidio-Caricetum diandrae*. In NW-Overijssel, the *Scorpidium scorpioides*- and *Sphagnum subnitens*-fens are located in the Weerribben and the *Scorpidium cossoni*-fen in the Wieden; in the Vechtplassen the *S. scorpioides*-fen is located in het Hol, and the *Calliergonella cuspidata*- and *Sphagnum squarrosum*-fens in Westbroek.

Habitat of bryophyte species	Foliar N:P ratio phanerogams	References
NW-Overijssel		
Scorpidium scorpioides	16.1	Verhoeven et al. 1988
	19.1	Kooijman 1993b
	26.3	Kooijman and Hedenäs 2005 unpubl.
	22.4	Cusell et al. 2011
Scorpidium cossoni	19.5	Cusell et al. 2011
Sphagnum subnitens	23.8	Verhoeven et al. 1988
	19.8	Kooijman and Hedenäs 2005 unpubl.
Vechtplassen		
Scorpidium scorpioides	23.9	Verhoeven et al. 1991
Calliergonella cuspidata	13.5	Verhoeven et al. 1983
	9.1	Vermeer 1985
	14.5	Verhoeven and Arts 1987
	11.8	Koerselman et al. 1990
	12.2	Verhoeven et al. 1991

rather that P-availability had increased to a large extent. The fens dominated by *Calliergonella cuspidata* at the end of the 1980s have all become acidified and dominated by *Sphagnum squarrosum* in the early 1990s (Kooijman and Paulissen 2006). In the best Westbroek-fen presented in Table 1, the vegetation now consists of a monospecific layer of *S. palustre*, with a thickness of 25 cm in the former area with *Scorpidium scorpioides* (Kooijman unpubl.).

It is not entirely clear why the Westbroek area has become more eutrophied than NW-Overijssel. Part of the explanation may be that the Westbroek fens are located within an agricultural landscape, surrounded by fertilized meadows (Verhoeven et al. 1983, Verhoeven and Arts 1987), while the fens of NW-Overijssel are part of a larger nature reserve. The latter area is also surrounded by agricultural polders, but high P-levels may be restricted to inlet points and major water ways (Cusell et al. 2011). Also, differences in hydrology may play a role. The Westbroek fens receive groundwater, which is not only rich in calcium, but also in iron (Koerselman et al. 1990a, b). Both substances may reduce P-availability by formation of iron and calcium phosphates (Boyer and Wheeler 1989, Geurts et al. 2008). However, iron phosphates may dissolve under anaerobic conditions, especially when polluted sulphate-rich water is introduced in the area (Lamers et al. 1998, 2002). The Weerribben fens, in contrast, are mainly fed by calcium-rich surface water (van Wirdum 1991, Schouwenberg 2000). Calcium phosphates may ultimately dissolve during acidification (Lindsay and Moreno 1966), but remain more or less insoluble as long as calcium concentrations are high.

Slow and rapid succession

The rich fens in NW-Overijssel and the Vechtplassen thus seem to differ in rates of acidification, but also in availability of nutrients. But how could eutrophication and acidification be related? A first step seems to be the replacement of *Scorpidium scorpioides* by *Calliergonella cuspidata* under more eutrophic conditions. The above mentioned differences between the Vechtplassen and NW-Overijssel already point in this direction, but habitats of *Scorpidium scorpioides* and *Calliergonella cuspidata* mainly differ in P-availability, while pH, calcium, nitrate and ammonium are generally the same (Table 3).

It is not exactly clear how and why *Scorpidium scorpioides* is replaced by *Calliergonella cuspidata* under more eutroph-

Table 3. Mean chemical composition (n = 3–6) of the water in the bryophyte layer in sites with *Scorpidium scorpioides* and *Calliergonella cuspidata*. 1 = Stobberibben, NL; 2 = Buitenmuy, NL; 3 = Lonborg Hede, DK; 4 = Scragh Bog, Irl; 5 = Brackloon lough, Irl. Values are in mg l^{1-}. Data are derived from Kooijman (1993). * Only PO$_4^{3-}$ showed significant differences between the two species ($p < 0.05$).

		1	2	3	4	5
pH	*S. scorpioides*	6.8 (0.3)	7.1 (0.4)	6.5 (0.4)	6.7 (0.1)	6.5 (0.5)
	C. cuspidata	7.5 (0.3)	7.1 (0.4)	6.2 (0.8)	6.8 (0.2)	7.2 (0.3)
Ca$^+$	*S. scorpioides*	62 (12)	128 (48)	13 (4)	36 (15)	17 (2)
	C. cuspidata	62 (9)	112 (52)	22 (13)	77 (20)	46 (8)
NO$_3^-$	*S. scorpioides*	0.02 (0.03)	0.19 (0.21)	1.51 (1.16)	0.07 (0.10)	0.10 (0.12)
	C. cuspidata	1.10 (0.79)	0.16 (0.18)	2.35 (1.56)	1.43 (3.30)	0.25 (0.34)
NH$_4^+$	*S. scorpioides*	0.02 (0.02)	0.04 (0.08)	0.06 (0.07)	0.11 (0.13)	0.13 (0.18)
	C. cuspidata	0.25 (0.20)	0.02 (0.03)	0.44 (0.47)	0.20 (0.26)	0.18 (0.29)
PO$_4^{3-}$	*S. scorpioides*	0.01 (0.01)	0.02 (0.02)	0.03 (0.03)	0.01 (0.01)	0.11 (0.04)
	C. cuspidata	0.24 (0.30)	0.03 (0.02)	0.22 (0.22)	0.14 (0.30)	0.26 (0.20) *

ic conditions. Photosynthetic capacity of *C. cuspidata* may be slightly higher, especially when light levels increase, and the species seems to grow better when support is provided as a 'climbing frame', but is not stimulated by nutrient supply per se (Kooijman and Bakker 1993). Nevertheless, the shift in rich-fen bryophytes under more eutrophic conditions is important because *C. cuspidata* seems to be more sensitive to changes in water chemistry and acidification than *Scorpidium scorpioides* (Fig. 4, 5). In nutrient-poor fens, the dominant species in the rich-fen stage, *Scorpidium scorpioides*, is usually replaced by *Sphagnum subnitens* in the course of succession (Clapham 1940, O'Connell 1981, van Wirdum 1991). In nutrient-rich fens, with *Calliergonella cuspidata* as rich-fen species, the successor is usually *Sphagnum squarrosum*, followed by *S. fallax*, and later by *S. palustre*. Succession from *Scorpidium scorpioides* to *Sphagnum squarrosum* directly has been observed, but only in nutrient-rich fens where *Calliergonella cuspidata* was the dominant species, and only a few patches with *Scorpidium scorpioides* remained. Also, *Sphagnum squarrosum* did not perform well when transplanted into a nutrient-poor fen with *Scorpidium scorpioides* as dominant species (Kooijman 1993c), and *S. scorpioides* appeared to be the better competitor when grown with *Sphagnum squarrosum* in nutrient-poor groundwater (Kooijman and Bakker 1995).

The two rich-fen species, *Scorpidium scorpioides* and *Calliergonella cuspidata*, show a different response to the habitat of their successor. *Scorpidium scorpioides* did grow in rainwater under laboratory conditions (Fig. 4) and in the habitat of its successor *Sphagnum subnitens* in the field

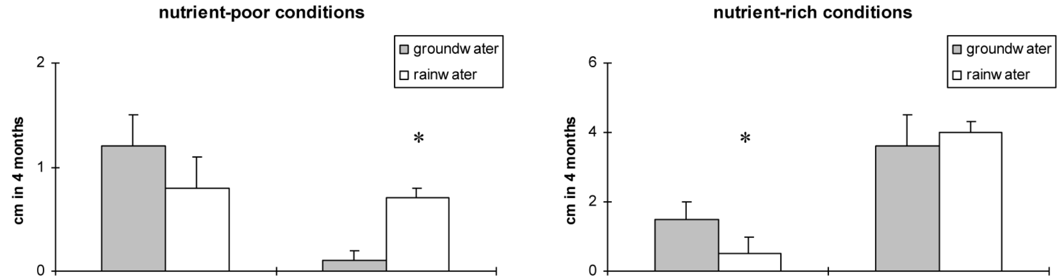


Figure 4. Growth in length of four bryophyte species in a 4 month-culture experiment under laboratory conditions in groundwater and rain water, without extra nutrients, or with N and P added (n = 4). Data are derived from Kooijman and Bakker (1995). * = significant differences within a particular species between water types ($p < 0.05$).

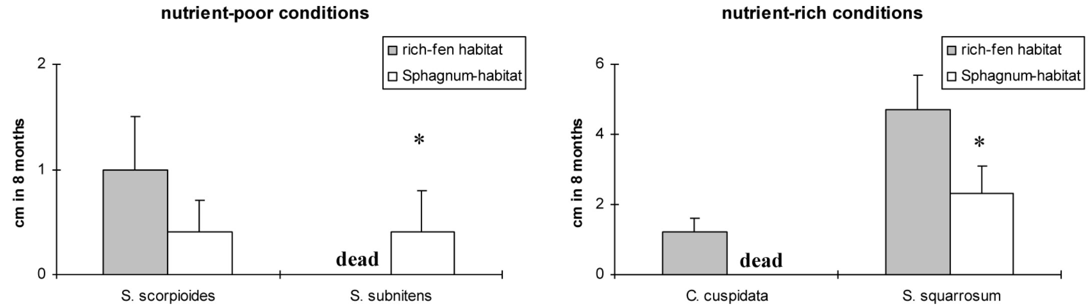


Figure 5. Growth in length of four bryophyte species in a 8 month-transplantation experiment under field conditions in rich-fen and *Sphagnum* habitats (n = 5). Data are derived from Kooijman (1993). Nutrient-poor conditions = the Weerribben fen; nutrient-rich conditions = the Westbroek fen. * = significant differences within a particular species between habitats ($p < 0.05$).

(Fig. 5). Growth rates were slightly lower than in groundwater or in its own habitat, but differences were not significant. In contrast, the rich-fen species *Calliergonella cuspidata* showed clearly reduced growth in rainwater under laboratory conditions, with growth rates only 30% of those in groundwater, and even died in the field in the *Sphagnum squarrosum* habitat.

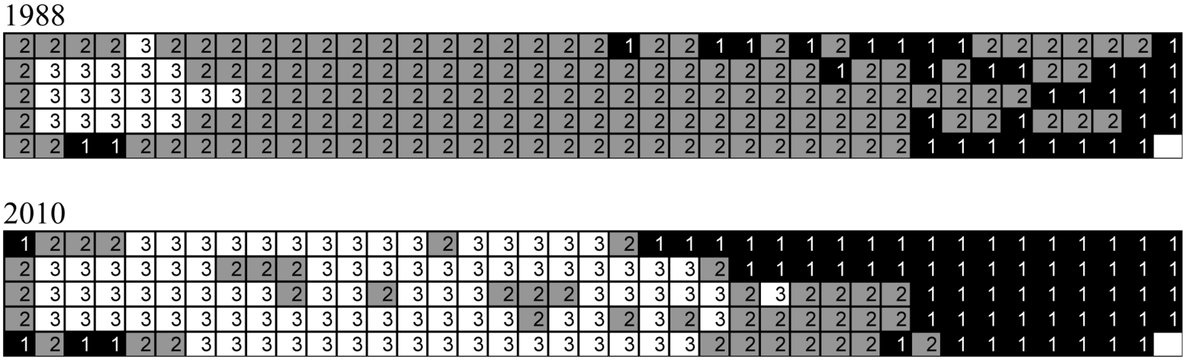
The two *Sphagnum* species also differed in response to the habitat of its predecessor. *Sphagnum subnitens*, the successor of *Scorpidium scorpioides* in nutrient-poor fens, showed strongly reduced growth in groundwater. Under laboratory conditions, growth rates in groundwater were only 14% of those in rainwater. In the field, *Sphagnum subnitens* even died in the habitat of its predecessor *Scorpidium scorpioides*. This implies that succession in nutrient-poor fens from *S. scorpioides* to *Sphagnum subnitens* may be prohibited without a clear change in hydrology and (local) accumulation of rainwater. In contrast, under laboratory conditions, the eutraphent *Sphagnum squarrosum* grew as well in groundwater as in rainwater. Growth rates were also considerably higher than for the nutrient-poor *S. subnitens*. In the field, growth rates of *S. squarrosum* in the habitat of *Calliergonella cuspidata* were even twice as high compared to its own habitat. Succession from *C. cuspidata* to *Sphagnum squarrosum* may thus be much easier than succession from *Scorpidium scorpioides* to *Sphagnum subnitens*: the rich-fen species is intolerant to the *Sphagnum* stage, rather than tolerant, while the successor can already grow well under base-rich conditions, rather than being inhibited.

Shift in stable states

These differences in sensitivity to water chemistry and other species' habitats suggest that in nutrient-poor and nutrient-rich fens not only different bryophyte species are involved in succession, but also that they may have different stable states, even when base-rich water is supplied to the fen.

Under nutrient-poor conditions, *Scorpidium scorpioides* is a strong and competitive species. It can stand a wide range in pH and calcium content (Fig. 1), can grow in rainwater and the more acid habitat of *Sphagnum subnitens* (Fig. 4, 5), is a stronger competitor than *S. subnitens* even in rainwater (Kooijman and Bakker 1995), and can counteract acidification as long as sufficient calcium- and bicarbonate-rich water is supplied to the fen (Fig. 2). *Sphagnum subnitens*, in contrast, is a small species with low acidification capacity, low growth rates, unable to grow in groundwater or in the *Scorpidium scorpioides* habitat, and a relatively weak competitor. This species has no chance of successful establishment without a clear shift in hydrology. This is in line with Soudzilovskaia et al. (2010), who argued that fen-bog succession is associated with blocking of upward alkaline soil water transport rather than high *Sphagnum* CEC. This means that, as long as sufficient calcium- and bicarbonate-rich water is supplied to the fen, conditions will stabilize around the rich-fen stage, with only local mounds of *S. subnitens* (O'Connell 1981). If present, *S. subnitens* may potentially be replaced by *S. fallax*, but this species is also inhibited by base-rich water (Kooijman and Kanne 1993). Stabilization of the rich-fen stage may be illustrated by the fen in NW-Overijssel presented earlier (Fig. 6). In the hydrologically more isolated part of the fen, *Sphagnum* communities have increased between 1988 and 2010. However, in the area closer to the ditch, from which base-rich and nutrient-poor water is supplied to the fen, *Scorpidium* communities still prevail and have even expanded.

Under nutrient-rich conditions, however, the fen will stabilize around the *Sphagnum* stage, even if base-rich water is still supplied. *Scorpidium scorpioides* will (have) be(en) replaced by *Calliergonella cuspidata*. The latter species seems unable to grow in rainwater or in the habitat of its successor *Sphagnum squarrosum,* in contrast to *Scorpidium scorpioides*, It is not exactly clear why *Calliergeonella cuspidata* is unable to grow in rain water, because many rich-fen bryophytes show high cation exchange capacities



1988

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

2010

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

Figure 6. Changes in bryophyte communities in 5 × 5 m grid cells the Stobberibben fen over the period 1988–2010, based on the presence of 15 moss species. 1 = base-rich fen dominated by *Scorpidium scorpioides*; 2 = transition stages with rich-fen hollows and *Sphagnum*-hummocks; 3 = *Sphagnum*-lawns. The ditch from which the fen is supplied with base-rich, nutrient-poor water is located at the right of the fen. Data are based on Kooijman et al. (unpubl.).

(Soudzilovskaia et al. 2010), and in bryophytes from more terrestrial habitats, CEC increased from acid to more neutral soil (Büscher et al. 1990). It is thus likely that *C. cuspidata* shows at least some acid neutralizing capacity. In any case, succession towards *Sphagnum* stages in nutrient-rich habitats is stimulated by the early arrival of *Sphagnum squarrosum*, which can already establish in base-rich water, especially under nutrient-rich conditions. The species has been found at calcium levels of 40 mg l^{-1} (Clymo 1973), grew well in groundwater, and performed best in the base-rich habitat of *Calliergonella cuspidata*, its predecessor. It is also very likely that the shift from base-rich to *Sphagnum* fen is not driven by changes in hydrology, but by increased acidification by *S. squarrosum,* in contrast to the findings of Soudzilovskaia et al. (2010) for fen-bog succession. Chloride concentrations, which can be used as inert tracer, remained the same in *Calliergonella cuspidata* and *Sphagnum squarrosum* habitats with values around 30 mg l^{-1}, while pH and calcium significantly decreased (Kooijman 1993c). Also, high growth rates of *Sphagnum squarrosum* may allow continuous production of polyuronic acids, which is suggested by the high release of protons compared to the much smaller *S. subnitens*, especially in polluted rain. High growth rates and active acidification thus allow *S. squarrosum* to expand rapidly and acidify the fen. *Sphagnum squarrosum* may soon be followed by *S. fallax*, but this species has equally high growth rates and acidification capacity (Kooijman and Bakker 1994). This mechanism has led to the rapid acidification of almost all base-rich fens in the Vechtplassen area (Kooijman and Paulissen 2006), even those supplied with base-rich water by groundwater discharge and surface water inflow.

Concluding remarks

Base-rich fens, one of the most threatened habitats in Europe, disappear through natural succession when influx of base-rich water is prohibited, and rich-fen bryophytes such as *Scorpidium scorpioides* are replaced by *Sphagnum* spp. In the Netherlands, acidification and replacement of rich-fen bryophytes is probably stimulated by high atmospheric deposition, which reached an all time high in the 1980s, and presently is still higher than the critical levels. Base-rich fens are also threatened by eutrophication, not only because rich-fen species are replaced by more eutraphent and possibly more productive ones, but especially because high nutrient levels allow establishment of fast-growing *Sphagnum* species under relatively base-rich conditions. *Sphagnum squarrosum*, followed by *S. fallax* and *S. palustre*, in turn rapidly acidify the fen, and within a short period take over the base-rich fen completely, even in areas where base-rich water is still supplied. However, even in a country with high anthropogenic pressure, such as the Netherlands, base-rich fens can persist, at least on a time scale of decades. As long as habitat conditions remain calcium-rich, but nutrient-poor, the rich-fen bryophytes will remain, along with associated phanerogamous species such as *Liparis loeselii* (L.) Rich., which is a European habitat directive species.

However, maintenance of base-rich and nutrient-poor conditions is not an easy task. First, the supply water should be calcium-rich, but nutrient-poor, which has become rare in a country as polluted as the Netherlands. Second, calcium-rich and nutrient-poor water should not only be available, but also really pass through the fen and reach the fen surface. This can be achieved by strong upward seepage of calcium-rich groundwater (Koerselman et al. 1990a, b), such as in the last remaining spot of *Scorpidium scorpioides* in the Vechtplassen, but also with strong downward seepage, in places close to deeply drained polders (van Wirdum 1991, Schouwenberg 2000). In the latter case, calcium-rich and nutrient-poor water comes from the ditch at one end of the fens, and is pulled through the floating fen by the downward movement of water. In areas with low rates of exfiltration or infiltration, however, water movement through the fen is much more difficult, and rich fens are probably more sensitive to acidification (van Diggelen et al. 1996), especially in areas with high atmospheric deposition. Increase of buffer capacity may also be achieved by incidental flooding with calcium-rich, but nutrient-poor water. With the artificial and strongly regulated water level regimes in the Netherlands, this is also not easy (Cusell et al. 2011), but worth a try.

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