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Long-term effects of drainage and hay-removal on nutrient dynamics and limitation in the Biebrza mires, Poland

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Abstract To provide a reference for wetlands elsewhere we analysed soil nutrients and the vegetation of floodplains and fens in the relatively undisturbed Biebrza-valley, Poland. Additionally, by studying sites along a water-table gradient, and by comparing pairs of mown and unmown sites, we aimed with exploring long-term effects of drainage and annual hay-removal on nutrient availabilities and vegetation response. In undrained fens and floodplains, N mineralization went slowly ($0\text{--}30\text{ kg N ha}^{-1}\text{ year}^{-1}$) but it increased strongly with decreasing water table (up to $120\text{ kg N ha}^{-1}\text{ year}^{-1}$). Soil N, P and K pools were small in the

undisturbed mires. Drainage had caused a shift from fen to meadow species and the disappearance of bryophytes. Biomass of vascular plants increased with increasing N mineralization and soil P. Annual hay-removal tended to have reduced N mineralization and soil K pools, but it had increased soil P. Moreover, N concentrations in vascular plants were not affected, but P and K concentrations and therefore N:P and N:K ratios tended to be changed. Annual hay-removal had induced a shift from P to K limitation in the severely drained fen, and from P to N limitation in the floodplain. The low nutrient availabilities and productivity of the undisturbed Biebrza mires illustrate the vulnerability of such mires to eutrophication in Poland and elsewhere. In nutrient-enriched areas, hay removal may prevent productivity increase of the vegetation, but also may severely alter N:P:K stoichiometry, induce K-limitation at drained sites, and alter vegetation structure and composition.

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Introduction

The surface area of valley mires—notably fens and floodplains in river valleys and river plains—is relatively small, but their contribution to regional

biodiversity is large (Naiman and Decamps 1997). Floodplain mires have become scarce in Europe because rivers are regulated and dikes prevent flooding (Nienhuis 2006). Moreover, many floodplain mires have been converted into agricultural grasslands by draining and fertilizing them. Also the area of fens has been largely reduced because they were drained and developed for agriculture in the past (Stanners and Bourdeau 1995). The remaining fens are often surrounded by agricultural land which affects their hydrology (Wassen et al. 1996). Also drinking water extractions have altered the hydrology in mires. Nowadays, many remaining valley mires in Europe are protected reserves, but they are often subjected to various degrees of drainage (Grootjans et al. 1985, 1986; Wassen et al. 1996). Drainage and alteration of the natural flooding regime influence mire plant communities directly through changed hydrological conditions causing a shift from mire to grassland species, or indirectly through altered nutrient availabilities and subsequent eutrophication (Grootjans et al. 1985, 1986; Laine et al. 1995a). The latter may ultimately result in vegetation dominated by a few tall species.

Drainage can increase soil nutrient availabilities considerably (Laiho and Laine 1994; Laine et al. 1995a; Bridgham et al. 1998; Olde Venterink et al. 2002a), but to what extent is rather unclear, partly because a good reference for nutrient availabilities at relatively undisturbed conditions is lacking. From a study in which annual N mineralization rates were measured in two wet meadows before and after a deep ditch was created, we know that drainage may largely increase mineralization and N availability for plants (Grootjans et al. 1985, 1986). However, field studies of annual mineralization rates in undrained mires are rare, and studying the effect of drainage experimentally is generally not allowed in these protected areas. Effects of drainage on other nutrients such as P and particularly K are even less understood, but may be different to those on N, since availabilities of N, P and K are largely regulated by different mechanisms (Sundström et al. 2000; Olde Venterink et al. 2002a).

Natural resource managers try to mitigate nutrient enrichment in mires by specific measures, such as annual mowing and hay-removal, grazing, or burning. Worldwide, mires have been mown by local farmers, but in North America and Europe it ceased

during the second half of the 20th century. In Western Europe it is currently applied mainly by nature conservation organizations; in protected wetlands it is common practice. According to nutrient budget calculations in Western European mires, annual hay-removal seems to cause a relatively larger net export of P and K from the ecosystem than of N, which would lead to P and/or K limitation in the long term (Koerselman et al. 1990; Olde Venterink et al. 2002b). Reduced K concentrations in plants after 9 years of hay-removal (Oomes et al. 1996) and reduced N-mineralization rates only after 26–45 years of hay-removal (Olff et al. 1994) in various Dutch fen meadows are consistent with this view. In regions with a lower atmospheric N deposition, such as the Biebrza valley in North-Eastern Poland, hay-making does not have to induce a shift from N towards P and/or K limitation according to budget calculations (Wassen and Olde Venterink 2006). The effects of mowing and hay-removal on soil nutrient availabilities, however, have not been investigated in the Biebrza mires.

The aim of this study was to analyze soil nutrient dynamics in an array of mires, and evaluate the long-term effects of drainage and hay-removal on nutrient availabilities and limitation. We selected the mires in an area where other human disturbances are relatively small for European standards: the Biebrza valley. For practical reasons we studied annual N mineralization and soil extractable pools of N, P and K. We hypothesized that:

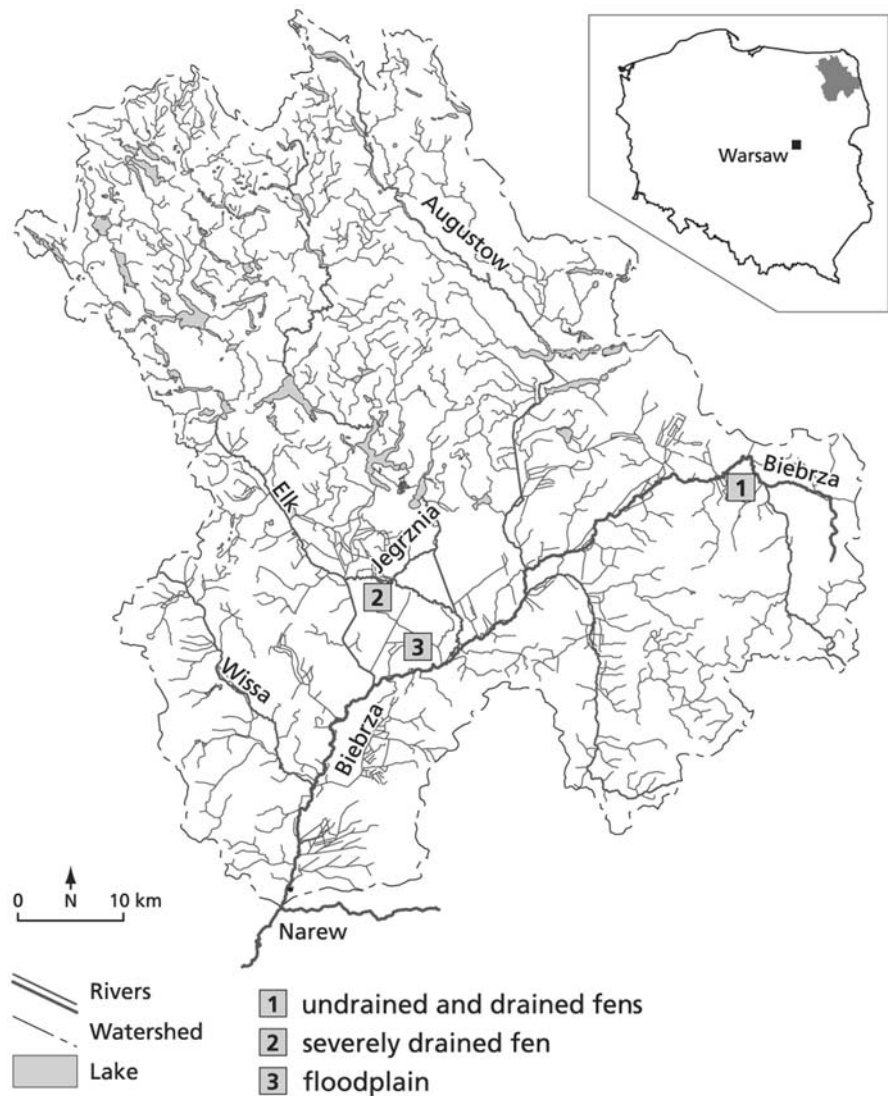
1. Mineralization rates are very slow and nutrient pools are small in undisturbed mires.
2. Drainage increases N mineralization rates and productivity of the vegetation.
3. Mowing and hay-removal reduces soil nutrient pools and productivity of the vegetation.

Methods

Study sites

This year-round study was carried out at eight field sites in the Biebrza National Park, NE Poland (Fig. 1). The Biebrza valley was very suitable for our study since it contains a wide variety of fens and floodplains in a relatively small area. The area is

Fig. 1 Location of the research sites in the valley of the river Biebrza, Poland



relatively undisturbed; large parts of the catchment are undrained and atmospheric N deposition is low compared to Western Europe (5–10 compared to 20–60 kg N ha⁻¹ year⁻¹; Wassen et al. 2005). Until World War II, mowing and hay-removal was common practice in the Biebrza valley and carried out almost annually in large parts of the valley. After that, the practice of hay-making was abandoned in most parts of the valley. We have been studying vegetation-soil-hydrology relationships in Biebrza fens and floodplains for the last 20 years.

For this study, we selected some sites in two undrained fens and one severely drained fen where we

carried out studies in the past (e.g., Wassen et al. 1990, 1995; Wassen and Joosten 1996; De Mars et al. 1996, 1997; Wassen and Olde Venterink 2006; Fig 1). We supplemented our intended drainage gradient with a drained fen located nearby the undrained fens. This fen had a summer water table in between the undrained and severely drained fen (Table 1). In the drained and the severely drained fens, we selected mown and unmown sites nearby each other. We also choose an undisturbed floodplain where we could select a mown and unmown site close to each other (Fig. 1). For the undrained fens we could only include unmown sites, since these types of fens are no longer

Table 1 Site descriptors, soil and vegetation characteristics of floodplains and fens in the Biebrza Valley

	Floodplain		Undrained fens		Drained fen		Severely drained fen	
	Unmown	Mown	Unmown-1	Unmown-2	Unmown	Mown	Unmown	Mown
Mowing and hay-removal since (years)	–	>65	–	–	–	>65	–	>65
Time not mown (years)	>25	–	>65	>65	>25	–	5–10	–
<i>Soil</i>								
Water table June 2002 (cm below surface)	10	50	10	5	70	70	200	200
Mean soil moisture content (%)	73 ± 0.7 b	55 ± 1.3 d	87 ± 0.2 a	86 ± 0.3 a	73 ± 0.5 b	77 ± 0.3 b	59 ± 0.9 c	63 ± 0.9 c
Soil moisture dynamics (% year ⁻¹)	11	10	3	4	6	4	12	9
N mineralization (kg N ha ⁻¹ year ⁻¹)	35 ± 23 bc	30 ± 14 b	0 ± 1 c	4 ± 3 bc	27 ± 6 b	8 ± 2 bc	119 ± 11 a	105 ± 12 a
Soil Extrable NO ₃ (kg N ha ⁻¹)	5.0 ± 1.2 b	1.8 ± 0.4 b c	0.1 ± 0.0 e	0.2 ± 0.0 de	1.0 ± 0.2 bc	0.4 ± 0.1 cd	26.7 ± 3.6 a	36.9 ± 6.2 a
Soil Extrable NH ₄ (kg N ha ⁻¹)	1.9 ± 0.2 b	2.9 ± 0.5 ab	2.3 ± 0.3 b	2.1 ± 0.3 b	2.3 ± 0.3 ab	1.7 ± 0.2 b	3.7 ± 0.7 a	2.3 ± 0.2 ab
Soil Extrable P (kg P ha ⁻¹)	8 ± 0 d	12 ± 1 c	7 ± 0 d	7 ± 0 d	65 ± 6 b	105 ± 3 a	9 ± 1 cd	13 ± 1 c
Soil Extrable K (ALA; kg K ha ⁻¹)	38 ± 3 bd	43 ± 4 bc	32 ± 3 cd	31 ± 2 cd	45 ± 4 bc	44 ± 1 b	73 ± 4 a	29 ± 2 d
Soil Extrable K (HCl; kg K ha ⁻¹)	88 ± 1 b	119 ± 6 a	57 ± 4 c	60 ± 4 c	87 ± 3 b	81 ± 3 b	116 ± 7 a	72 ± 3 b
Bulk density (g cm ⁻³)	0.28 ± 0.01 cd	0.55 ± 0.02 a	0.14 ± 0.00 e	0.14 ± 0.00 e	0.31 ± 0.01 bc	0.26 ± 0.00 d	0.32 ± 0.00 b	0.32 ± 0.01 b
pH-KCl	5.4 ± 0.0 de	5.3 ± 0.0 de	5.6 ± 0.1 cd	6.1 ± 0.0 b	5.6 ± 0.1 c	7.1 ± 0.1 a	5.2 ± 0.0 e	5.5 ± 0.0 cd
<i>Vegetation</i>								
Biomass living vasc. plants (tonne ha ⁻¹)	4.8 ± 1.2 a	4.3 ± 0.5 a	1.3 ± 0.2 c	1.7 ± 0.0 bc	3.2 ± 0.4 ab	3.0 ± 0.2 ab	4.0 ± 0.4 a	2.5 ± 0.3 ac
Biomass dead vasc. plants (tonne ha ⁻¹)	7.7 ± 1.2 a	2.2 ± 0.1 bc	0.5 ± 0.3 c	1.8 ± 0.3 bc	1.9 ± 0.2 bc	0.1 ± 0.1 c	3.3 ± 0.5 b	0.0 ± 0.0 c
Biomass bryophytes (tonne ha ⁻¹)	0 ± 0 c	0 ± 0 c	2.2 ± 0.2 b	2.8 ± 0.2 a	0 ± 0 c	0 ± 0 c	0 ± 0 c	0 ± 0 c
N conc. living vasc. plants (mg g ⁻¹)	14 ± 1.3 b	13 ± 0.1 b	14 ± 0.3 ab	14 ± 0.7 b	15 ± 0.8 ab	13 ± 0.4 b	18 ± 2.1 ab	19 ± 1.4 a
P conc. living vasc. plants (mg g ⁻¹)	0.9 ± 0.1 b	1.3 ± 0.0 b	1.2 ± 0.1 b	0.9 ± 0.1 b	2.6 ± 0.1 a	2.3 ± 0.2 a	1.2 ± 0.1 b	2.1 ± 0.2 a
K conc. living vasc. plants (mg g ⁻¹)	12 ± 1.3 a	12 ± 0.5 a	11 ± 0.7 a	10 ± 0.1 a	14 ± 0.1 a	11 ± 1.1 a	12 ± 1.4 a	3.3 ± 0.1 b
N:P ratio living vasc. plants	15.7 ± 0.8 a	10.6 ± 0.4 c	12.1 ± 0.6 bc	15.0 ± 0.4 ab	5.9 ± 0.3 d	5.8 ± 0.4 d	15.2 ± 0.4 a	9.4 ± 1.1 c
N:K ratio living vasc. plants	1.2 ± 0.2 b	1.1 ± 0.1 b	1.3 ± 0.1 b	1.3 ± 0.1 b	1.1 ± 0.2 b	1.2 ± 0.1 b	1.6 ± 0.4 b	5.9 ± 0.3 a
K:P ratio living vasc. plants	14.0 ± 2.4 a	9.4 ± 0.6 ab	9.4 ± 1.3 ab	11.3 ± 0.7 a	5.3 ± 0.4 bc	4.7 ± 0.2 c	10.8 ± 2.3 a	1.6 ± 0.1 d
N conc. bryophytes (mg g ⁻¹)	–	–	12 ± 0.6 b	15 ± 0.7 a	–	–	–	–
P conc. bryophytes (mg g ⁻¹)	–	–	1.0 ± 0.0 a	0.8 ± 0.1 a	–	–	–	–
K conc. bryophytes (mg g ⁻¹)	–	–	3.9 ± 0.3 a	2.3 ± 0.0 b	–	–	–	–
N stock in living vasc. plants (kg N ha ⁻¹)	62 ± 11 a	58 ± 7 a	18 ± 2 c	23 ± 1 bc	48 ± 4 a	40 ± 3 ab	73 ± 12 a	49 ± 5 a
P stock in living vasc. plants (kg P ha ⁻¹)	4.0 ± 0.9 a	5.5 ± 0.8 a	1.5 ± 0.3 b	1.6 ± 0.1 b	8.3 ± 1.1 a	7.0 ± 0.8 a	4.8 ± 0.7 a	5.2 ± 0.1 a
K stock in living vasc. plants (kg K ha ⁻¹)	58 ± 16 a	51 ± 7 a	14 ± 1 cd	18 ± 0 bcd	45 ± 8 ab	33 ± 4 ac	49 ± 9 a	8 ± 1 d
N stock in living biomass (kg N ha ⁻¹)	62 ± 11 a	58 ± 7 a	46 ± 4 a	65 ± 3 a	48 ± 4 a	40 ± 3 a	73 ± 12 a	49 ± 5 a

Table 1 continued

	Floodplain		Undrained fens		Drained fen		Severely drained fen	
	Unmown	Mown	Unmown-1	Unmown-2	Unmown	Mown	Unmown	Mown

P stock in living biomass (kg P ha⁻¹) 4.0 ± 0.9 b 5.5 ± 0.8 ab 3.8 ± 0.4 b 3.8 ± 0.3 b 8.3 ± 1.1 a 7.0 ± 0.8 ab 4.8 ± 0.7 ab 5.2 ± 0.1 ab

K stock in living biomass (kg K ha⁻¹) 58 ± 16 a 51 ± 7 a 23 ± 2 a 24 ± 0 a 45 ± 8 a 33 ± 4 a 49 ± 9 a 8 ± 1 b

Information about mowing was derived from local farmers. The water table was measured from peat profile observations or water levels in nearby piezometers, well or ditches. Soil variables are means of the samples from all periods ($n = 25$ – 30), except N mineralization ($n = 5$). Vegetation variables $n = 3$. Moisture dynamics is mean soil moisture of the wettest month minus that of the driest. Different letters indicate significant differences among the eight sites (ANOVA, Tukey, $P < 0.05$)

mown in the Biebrza, probably because hay-making in these low-productive fens is not profitable for the local farmers. All sites were on peat with a depth of minimally 1.5 m (Oswit 1973; Zurek 1984; Palczynski 1984; Okruszko 1990, 1993). Number of years that our sites have been mown, or not been mown, as well as other habitat descriptors are presented in Table 1. As far as we could trace back, none of the sites had ever been fertilized. Further details about our floodplain and fens are:

1. The mown and unmown floodplain sites were located about 450 m from each other in the middle course of the river, near the village of Goniadz (Fig. 1). Floodplains in the middle course of the Biebrza, including our sites, are flooded every spring, but in summer water levels drop below the surface (Wassen et al. 2003). Mowing and hay-removal was carried out with tractors and other heavy machines in the floodplain.
2. The undrained fens are located in 'Transect A' of our previous studies (e.g., Wassen et al. 1990, 1995; Wassen and Joosten 1996; De Mars et al. 1997), along the upper course of the river Biebrza (Fig. 1). Both fens are located in an undrained area north of the settlement Szusalewo, where the groundwater level is near soil surface during large parts of the year (De Mars et al. 1997), as it was also at the start of our experiment in June 2002 (Table 1), and were flooding with river water never occurs (Okruszko 1990; Wassen et al. 1990). Both fens can be classified as moderately rich-fens (sensu Vitt and Chee 1990), but differ in presence and abundance of fen species as well as in site factors such as pH and calcium saturation due to differences in fluxes of groundwater (Wassen and Joosten 1996).
3. The fen south of Szusalewo is principally the same fen type as the undrained one (Okruszko 1990; Palczynski 1984), but it has been marginally drained by the local farmers by means of shallow ditches, for at least 25 years. Here we selected the two (mown and unmown) drained rich sites about 300 m from each other (Fig. 1). Mowing and hay-removal was done with a tractor. The unmown site has not been mown for at least 25 years. Water table and soil moisture conditions indicate dryer conditions than the undrained fens (Table 1).

4. The two sites in the severely drained fen were located about 100 m from each other in the middle course of the Biebrza valley, along the Dead Elk River (Fig. 1). This area has been severely drained for about 150 years because of the digging of a deep canal, and since then the area has been mown and hay is removed, the last decades using machines. Besides a mown site, we selected a site that has not been mown for at least 5–10 years. The summer groundwater level is at about 2 m below soil surface. The peat in the top soil is strongly aerated and decomposed. For further information about this area we refer to Kajak and Okruszko (1990) and De Mars et al. (1996).

Although we carefully selected our sites to avoid bias from inherent different soil conditions—e.g., mown and unmown sites in nearby located pairs—we note that we explicitly assumed that the initial soil conditions of the undrained, drained, and severely drained fens were comparable, as well as those of the unmown and mown pairs of sites. In every site, one measuring plot was selected at random (the central subplot C), and four other subplots were selected 10-m. in N, E, S, and W direction.

Vegetation

In the third week of June 2002, we cut the above-ground standing biomass of vascular plants just above the soil in 50 cm × 50 cm frames, and bryophytes if present, in three subplots ($n = 3$ per site). Biomass of vascular plants was divided into living and dead. The plant material was dried for 48 h at 70°C, weighed, and Kjeldahl digested. N concentrations in the digests were analyzed colorimetrically, P and K concentrations by means of an ICP (cf. Olde Venterink et al. 2002b). N:P, N:K and K:P ratios in the living above-ground biomass of vascular plants were used as indicators for the type of nutrient limitation, following class borders of Olde Venterink et al. (2003); i.e., N limitation at $N:P < 14.5$ and $N:K < 2.1$, P- (co)-limitation at $N:P > 14.5$ and $K:P > 3.4$, K- (co)-limitation at $N:K > 2.1$ and $K:P < 3.4$. In early July 2003, we recorded the species composition at one square 10 m² plot at every site, using the Braun-Blanquet method in which individual species cover is estimated according to a six point scale: + = 1–5%;

1 = 5–15%; 2 = 15–25%; 3 = 25–50%; 4 = 50–75%; 5 ≥ 75% and in which mean height and total cover of different vegetation layers is estimated as well.

Soil nutrients and related properties

We measured annual net N mineralization at every site by in situ soil incubation, following the technique described by Olff et al. (1994) and Olde Venterink et al. (2002b). We measured net N mineralization between June 2002 and July 2003, during four periods of 6–8 weeks and one winter period of 6 months. The winter period had to be this long because the floodplains were inaccessible because of flooding. At the start of every period, we took one pair of soil cores (10 cm depth, 4.8 cm diameter) at every subplot ($n = 5$ per site). We took the soil cores in pairs (1–5 cm from each other) with sharpened PVC tubes. One of the paired tubes was incubated, the other transported to the laboratory in Warsaw and extracted after a night at 2°C. Soil extractable N (NO₃ and NH₄) was determined by extraction with 1 M KCl. We calculated net mineralization rates by subtracting values in initial soil cores from that in the incubated cores for each of the five periods.

Soil extractable P and ammonium-exchangeable K in the top 10 cm soil was assessed at every subplot by soil extraction with ALA (0.1 M NH₃ + 0.4 M acetic acid + 0.1 M lactic acid solution; Koerselman et al. (1993) and Olde Venterink et al. (2002b). Additionally, HCl extractable K was determined for every subplot (cf. Olde Venterink et al. 2002b). The HCl extractable K pool includes both ammonium-exchangeable K as well as an additional K fraction in the soil which is available for plants by soil acidification (Jungk and Claassen 1986). The ALA and HCl extractions were carried out with every initial soil core of the mineralization experiment (25 samples per site).

Bulk density, soil moisture content and pH_{KCl} were measured in the initial soil cores. All nutrient values were calculated per unit area using values per unit dry soil and the average bulk density of the top 10-cm soil per site. In addition to the average moisture content, we calculated the difference in soil moisture between the wettest and the driest measurement as an assessment of the annual soil moisture dynamics.

Data analysis

We tested whether the soil nutrient rates and pools, vegetation characteristics, and site conditions were significantly different among the eight sites by means of Tukey tests after one-way ANOVA. The data were log or square-root transformed to meet the assumptions of ANOVA. To evaluate general effects of drainage, we calculated regressions between soil and vegetation variables versus the water table in June 2002, as well as versus the annual soil moisture dynamics. To visualize these general effects of mowing we calculated the average soil and vegetation variables in the mown sites as percentage of those variables in the paired unmown sites (e.g., mown and unmown floodplain). To test for general effects of hay-making we calculated ANOVAs with mown as a fixed factor and site as a random factor, using the mean values of soil and vegetation variables

per site to avoid pseudoreplication. Statistics were carried with SPSS 16.0.

Results

Floodplains and undrained fens

N mineralization rates were close to zero in the undrained fens, and soil N, P and K pools were very low (Fig. 2). In the floodplain, N mineralization rates and soil N and P pools were still rather low, but soil K pools, in particular HCl-extractable-K, were higher than in the undrained fens (Fig. 2, Table 1).

The floodplain vegetation was characterized by tall sedges (Appendix 1) and had a high biomass of vascular plants (Fig. 3). The undrained fens had a low biomass of vascular plants, but a high biomass of bryophytes (Fig. 3; Table 1). Besides low-productive

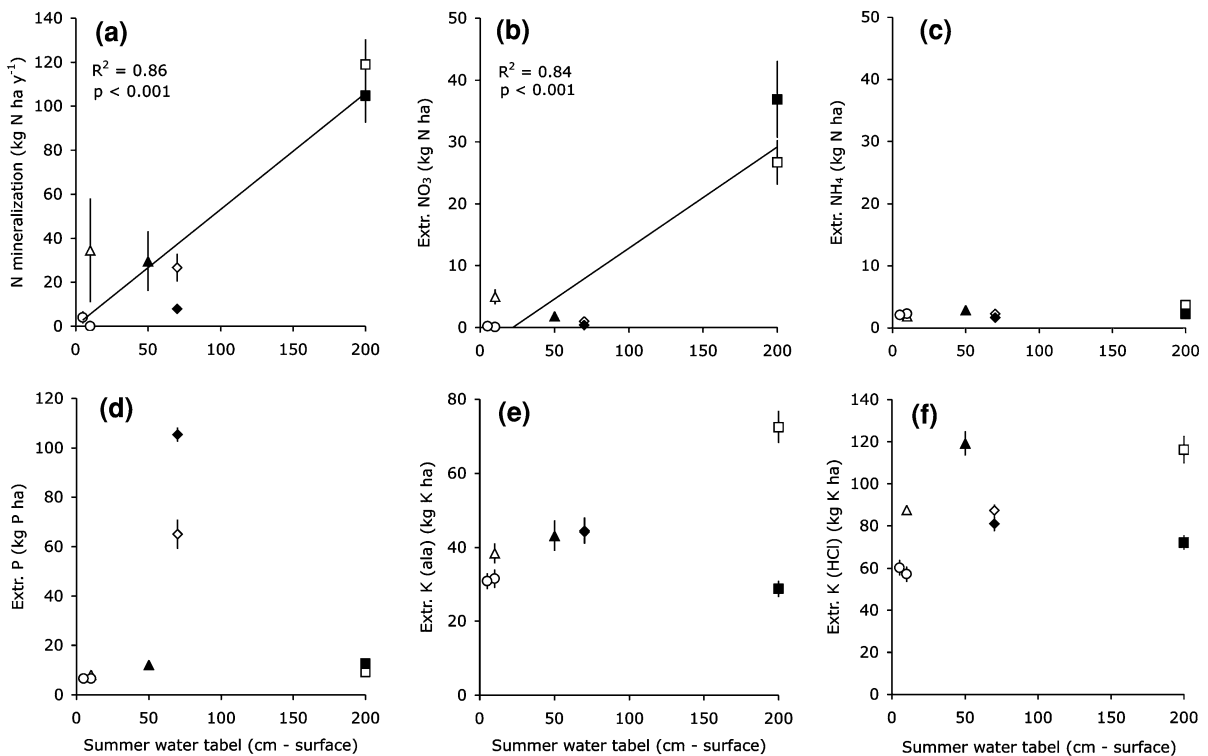


Fig. 2 Net annual N mineralization rates and mean extractable pools of nitrate, ammonium, phosphorus and potassium in the soils of various types of fens and floodplains in the Biebrza valley in relation to the water table of the sites June 2002. Δ unmown floodplain, \blacktriangle mown floodplain, \circ unmown undrained

fens, \diamond unmown drained fen, \blacklozenge mown drained fen, \square unmown severely drained fen, \blacksquare mown severely drained fen. Symbols are means of 5 (a) or 25 (b–f) replicates in the Y-direction; error bars are SE. Results of ANOVA-Tukey test comparisons among the sites are shown in Table 1

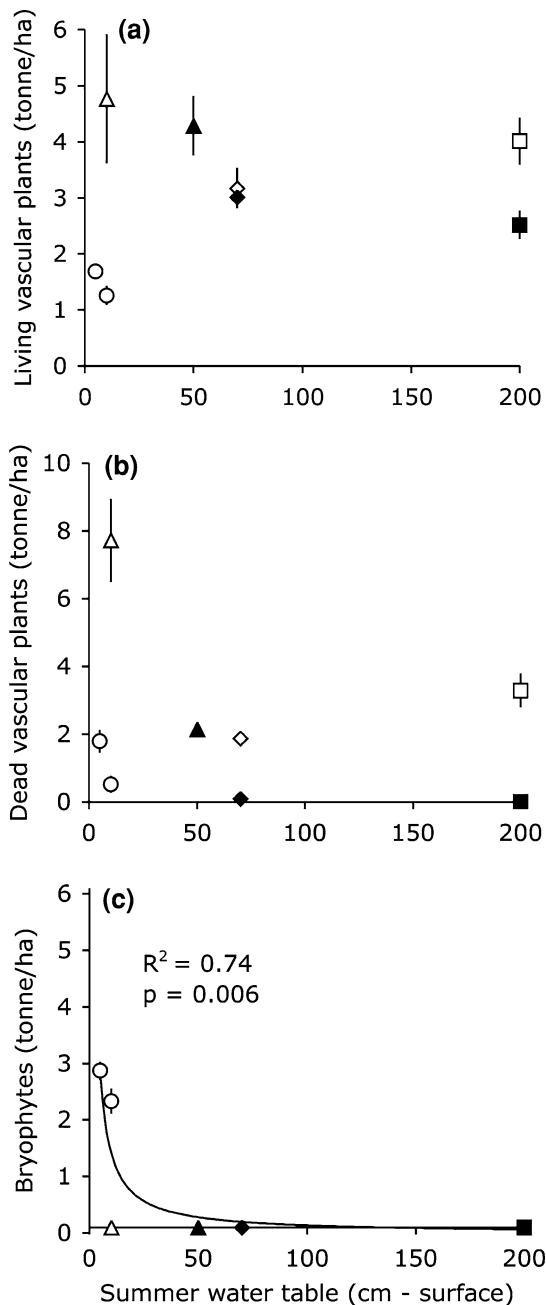


Fig. 3 Above ground biomass in of living (a) and dead (b) vascular plants and bryophytes (c) in various fens and floodplain types in the Biebrza valley in relation to the water table of the sites June 2002. \triangle unmown floodplain, \blacktriangle mown floodplain, \circ unmown undrained fens, \diamond unmown drained fen, \blacklozenge mown drained fen, \square unmown severely drained fen, \blacksquare mown severely drained fen. Symbols are means of three replicates in the Y-direction; error bars are SE. Results of ANOVA-Tukey test comparisons among the sites are shown in Table 1

fen species, one of the undrained fens (fen 1) contained 'poor fen' species as *Vaccinium oxycoccus* and *Andromeda polifolia*, whereas, the other undrained fen contained more calciphilous species such as *Carex flava*.

N, P and K concentrations in living biomass were rather similar in the floodplain and undrained fens (Fig. 4). The nutrient ratios indicated P (co)-limitation in the floodplain and in undrained fen 2, and N limitation in undrained fen 1 (Fig. 4; Table 1). The stock of N, P and K in aboveground vascular plants was higher in the floodplain than in the undrained fens, but for N and P this difference was not found if nutrient in bryophytes were taken into account; i.e., stock in total living biomass (Table 1).

Effects of drainage

N-mineralization rates and soil nitrate pools increased significantly with decreasing summer water table (Fig. 2a, b), and N mineralization also with annual soil moisture dynamics ($P < 0.05$; data not shown). ALA extractable K-pools increased with decreasing water table in seven of the eight sites; the mown severely drained fen strongly deviated from this pattern (Fig. 2e). A similar pattern, but with a larger variation, was observed for the HCL-extractable K-pools (Fig. 2f). Soil P-pools were much higher in the drained fen compared to the undrained fens, but not in the severely-drained fen (Fig. 2d; Table 1).

The vegetation composition changed strongly along the drainage gradient: from a fen vegetation with species such as *Menyanthes trifoliata* and *Carex diandra* to a meadow vegetation with species as *Holcus lanatus* and *Luzula campestris*. The drained fen contained both fen and meadow species (Appendix 1). In summer 2002, bryophyte biomass completely disappeared along the drainage gradient in fens (Fig. 3b), and biomass of living vascular plants increased ($P < 0.05$; Fig. 3a; not taking the high biomass in floodplains into account). Vegetation recordings in summer 2003 showed a strong decrease in cover by bryophytes along the drainage gradient, but also showed that bryophytes did not completely disappear in the drier sites (Appendix 1).

N concentrations in vascular plants were rather high in the severely drained fen although not significantly higher than in the other unmown fens,

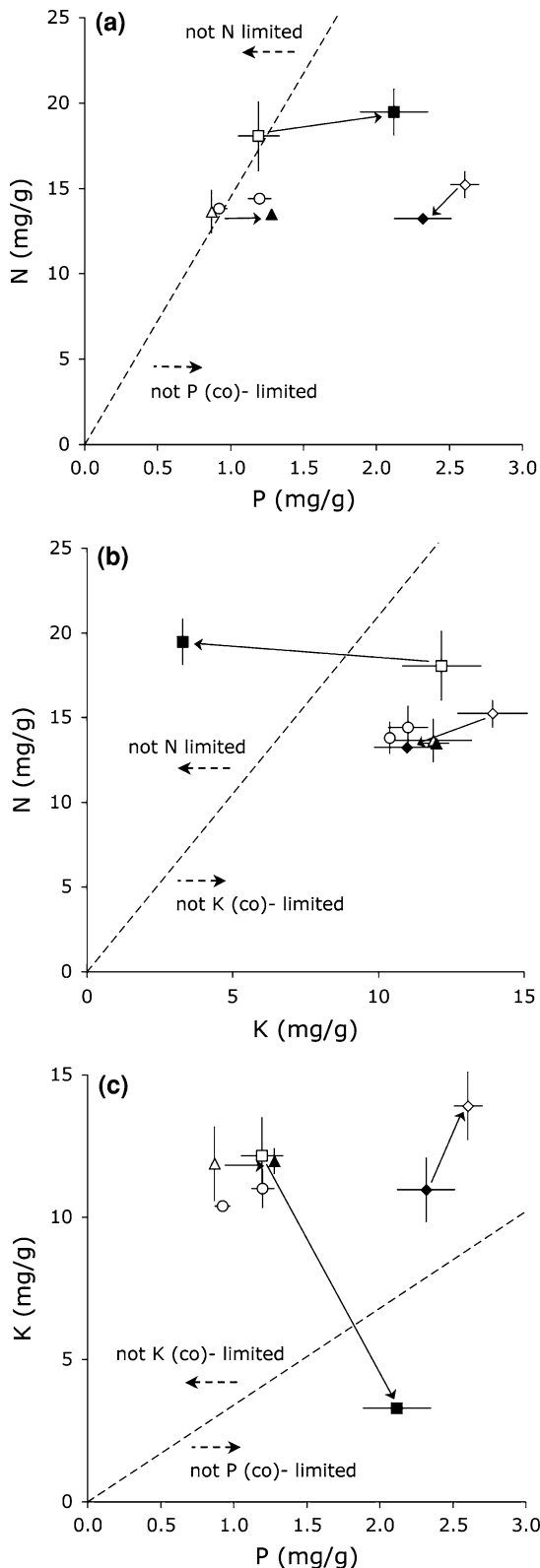


Fig. 4 Concentrations of N and P (a), N and K (b), or K and P (c) in the living above-ground biomass of vascular plants in various fens and floodplains in the Biebrza valley. Δ unowned floodplain, \blacktriangle mown floodplain, \circ unowned undrained fens, \diamond unowned drained fen, \blacklozenge mown drained fen, \square unowned severely drained fen, \blacksquare mown severely drained fen. Symbols are means of three replicates both directions; error bars are SE. The dashed line in (a) represents N:P = 14.5, in (b) N:K = 2.1, and in (c) K:P = 3.4. N limitation is indicated at N:P < 14.5 and N:K > 2.1; P-limitation or NP co-limitation at N:P > 14.5 and K:P > 3.4; K-limitation or NK co-limitation at N:K > 2.1 and K:P < 3.4 (Olde Venterink et al. 2003). Solid arrows connect mown-unmown pairs of sites, and indicate the shift mowing had on nutrient ratios. Results of ANOVA-Tukey test comparisons among the sites are shown in Table 1

and P concentrations were high in the drained fen (Fig. 4). The nutrient ratios indicated N-limitation in the unowned drained fen, and P (co)-limitation in the unowned severely drained fen. The stock of N in vascular biomass increased along the drainage gradient in fens ($P < 0.05$), but N in total biomass did not because of large N stocks in bryophytes in the undrained fens (living biomass in Table 1).

Effects of mowing and hay-removal

Average N-mineralization rates tended to be lower in mown compared to unowned sites, but the general effect of mowing was only significant at the $P < 0.1$ level (Fig. 5; Table 1). In general, soil P pools were higher in mown than in unowned sites (Fig. 5), this difference was very obvious in the drained fen (Table 1). In the severely drained fen mowing had lead to smaller soil K pools, whereas, in the floodplain higher K pools were found in the mown site (Table 1), hence the general trend was not significant (Fig. 5).

Generally, there was a large reduction in standing dead biomass of vascular plants in mown sites, which also lead to a significantly lower total aboveground biomass (Fig. 5). We did not observe a marked effect of mowing on species composition, but there was a strong effect on vegetation structure in the floodplains, where mowing caused sedges to no longer grow in tussocks.

Mowing and hay-removal did not alter N concentrations, but tended to increase P and decrease K concentrations in vascular plants, and hence affect N:P and N:K ratios (but all not significant due to only $n = 3$; Fig. 5). In the severely drained fen, mowing

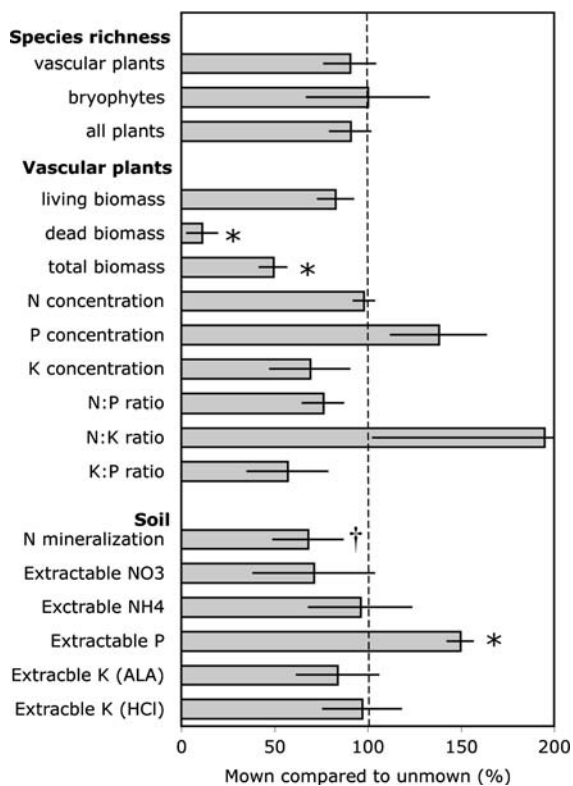


Fig. 5 General effects of long-term mowing on vegetation and soil nutrient characteristics. Bars show values of variables measured at mown sites divided by values of those variables measured at a paired unmown site, expressed in % of the unmown value. Error bars show SE of three replicated mown/unmown pairs (floodplain, drained fen severely drained fen). Significant differences: * $P < 0.05$, † $P < 0.1$ ANOVA with mowing as fixed factor and site as random factor

and hay-removal induced a shift from P (co)-limitation to K (co)-limitation, and in the floodplain from P (co)-limitation to N limitation (Fig. 4; Table 1). The hay-removal had significantly reduced K-stocks in vascular plants in the severely drained fen (Table 1).

Discussion

This study aimed at studying long-term effects of drainage on nutrient availability and vegetation productivity in mires, and analyzing if hay-removal would compensate for these effects. We compared sites that differed with respect to drainage or mowing, and assumed that the initial conditions had been the same; i.e., a similar approach used by others (e.g., Laiho and Laine 1994). The undisturbed fens and

floodplains were relatively poor in nutrients if compared to other river valley mires and floodplains (see below). Along the drainage gradient in fens we observed increases in N-mineralization, soil extractable NO₃, as well as ALA-extractable P and K in some sites (Fig. 2). In the unmown fens this corresponded to an increase in above-ground living biomass of vascular plants, but in the severely drained fen biomass of these plants was not significantly increased if the fen was mown and hay was removed (Fig. 3). Hay-removal had resulted in a strong K-depletion and a shift from P (co)-limitation to K (co)-limitation in this mown and severely drained fen (Fig. 4). Overall, mowing increased soil extractable P and showed a tendency towards a reduction in N mineralization (Fig. 5). A combination of the two factors may have lead to a shift from P (co)-limitation to N limitation in the floodplain (Fig. 4). Mowing also altered vegetation structure and species composition. Although our study was without true replication (we only could ‘pseudo-replicate’ within the sites), our observations demonstrated that soil nutrient dynamics and vegetation response in relation to drainage and haymaking were more complex than a priori expected, although all our hypotheses were supported. For understanding the vegetation response we needed to take the dynamics of N, P and K into account.

Variation among undrained mire types

Undrained fens and floodplains in the Biebrza valley were relatively poor in all nutrients (N, P and K). N mineralization in the undrained fens was very low compared to fens in Western Europe where annual rates are often higher than c. 50 kg N ha⁻¹ year⁻¹ and rates higher than 100 kg ha⁻¹ year⁻¹ are not an exception (Verhoeven and Arts 1987; Olde Venterink et al. 2002b; Fig. 6a). The extractable P and K pools in the Biebrza valley are smaller than those in Dutch and Belgian fens of Olde Venterink et al. (2002b; for P see Fig. 6b), but larger than those reported by Koerselman et al. (1993) for two other Dutch fens (for a review see Olde Venterink et al. 2002b). The indication of N limitation in our undrained fen 1 and P (co)-limitation in undrained fen 2 is consistent with vegetation samples taken 13 years earlier at the same sites (Wassen et al. 1995), although the differences in the N:P ratios between the two sites got smaller,

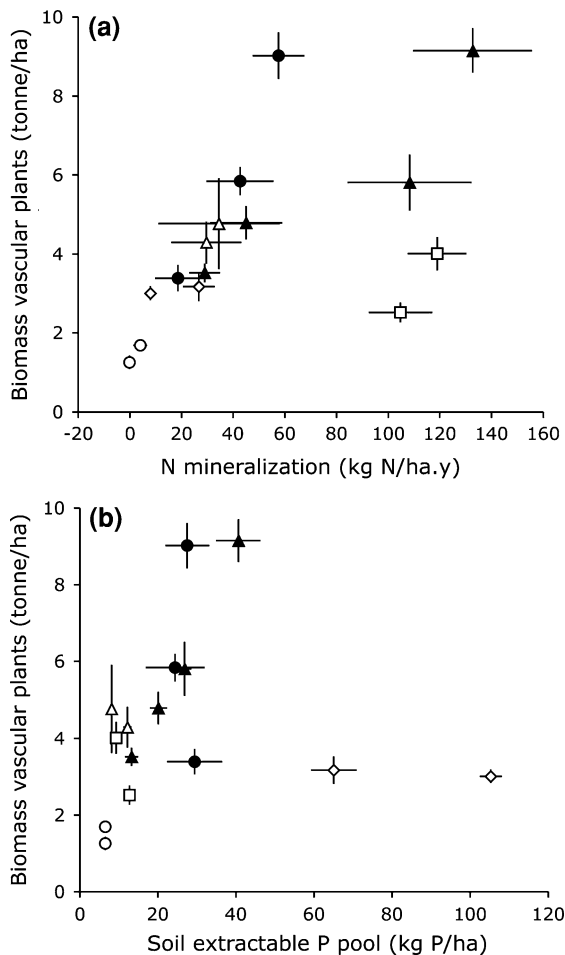


Fig. 6 Above-ground biomass of living vascular plants in relation to the net N mineralization rate (a) or the ALA-extractable soil P pool (b) of various fen and floodplain types. \triangle floodplains Biebrza, \circ undrained fens Biebrza; \diamond drained fens Biebrza; \square severely drained fens Biebrza; \bullet fens Dommel/Zwarte Beek; \blacktriangle meadows Dommel/Zwarte Beek. Data from the Biebrza are from this study, data from the Dommel (The Netherlands) or Zwarte Beek (Belgium) are from Olde Venterink et al. (2002b). Mean values (± 1 SE) per fen or floodplain type are shown. Graph (a) without the two severely drained fens: $R^2 = 0.67$, $P < 0.001$. Graph (b) without the two drained fens: $R^2 = 0.62$, $P = 0.002$, and not significant for the Biebrza types only

which also was observed by El-Kahloun et al. (2005). Fertilisation experiments performed in 1992 demonstrated N-limitation in both fens 1 and 2 (Wassen et al. 1998); in fen 2 the N:P ratio (13.5) of the control plot was close to the 15.0 in the present study. An N:P ratio of 15 is almost equal to the critical N:P value of 14.5 (for herbaceous wetland vegetation in

the temperate zones, Olde Venterink et al. 2003), and hence does not indicate a strong solo-limitation by N or P. Both N limitation and P limitation occur in undrained fens in Europe and North America (Bridgham et al. 1996; Verhoeven et al. 1996; Bedford et al. 1999; Olde Venterink et al. 2003; Walbridge and Navaratnam 2006).

Although annual N mineralization rates were somewhat higher in the floodplains than in the undrained fens in the Biebrza Valley, they were still very low compared to floodplains of other European rivers. Annual N mineralization rates of about 100–260 kg N ha⁻¹ year⁻¹ were reported for floodplains along the rivers Torridge (UK; Van Oorschot et al. 1997) and Garonne (F; Pinay et al. 1995). Spink et al. (1998) reported a large variation in N mineralization rates (–1 to 40 kg N ha⁻¹) during 4-week summer periods in some European and N-American floodplains, as well as highly variable soil extractable P pools (0–1500 kg P ha⁻¹). In our floodplains N mineralization was on average 20–25 kg N ha⁻¹ for the summer period (data not shown), which was consistent with rates of 9–42 kg N ha⁻¹ for a similar period in the Biebrza floodplain 30 km downstream in 1990 (Wassen et al. 2003). Soil extractable K pools in the Biebrza floodplains were comparable to those in flooded meadows along the river Dommel (NL), whereas, extractable P pools were clearly smaller in the Biebrza floodplains (cf. Olde Venterink et al. 2002b). Unlike most other European rivers which generally have catchments in which the main land use is agriculture and urban area, the Biebrza catchment is covered with forests, lakes and non-intensively used agricultural land. The smaller soil extractable nutrient pools in the Biebrza floodplains is not because of low overbank flooding frequency, but because the river water of the Biebrza has low P-concentrations (Wassen et al. 2003). Nutrient inputs from flooding were assessed at 31 kg N, 7 kg P and 2 kg K ha⁻¹ year⁻¹ in the Biebrza floodplain (Wassen and Olde Venterink 2006, and unpublished data), compared to 42–240 kg N and 15–102 kg P ha⁻¹ year⁻¹ for floodplains along the Rhine (Olde Venterink et al. 2006), and >500 kg N in riparian forests along the Garonne (Pinay et al. 1995). Nutrient ratios in the studied floodplain vegetation indicated slight P (co)-limitation. A previous fertilization in a floodplain site 30 km downstream, which had a higher productivity, showed no biomass

response to N, P or K addition (Wassen et al. 1998, 2003). Floodplain vegetation in Western Europe, but also of other Polish rivers, is generally N-limited or limited by other factors such as light (Van Oorschot et al. 1997; Spink et al. 1998; Anthéunisse et al. 2006). The local difference between Biebrza floodplain sites might be related to local variation in soil texture (loam, sand, organic matter), or it may reflect differences among years and climatic conditions (cf. Olde Venterink et al. 2001).

Effects of drainage

Nitrogen mineralization and extractable NO_3 clearly increased along the drainage gradient in our fens (Fig. 2). This is consistent with laboratory studies where soil cores were subjected to drainage and aeration (Heathwaite 1990; Updegraff et al. 1995; Bridgham et al. 1998; Olde Venterink et al. 2002a). The N mineralization rate was not dramatically increased in the drained fens, and still rather slow compared to for instance rates in Western European meadows (cf. Fig. 6a, and review in Olde Venterink et al. (2002b)). In the severely drained sites, N mineralization rates were strongly increased ($>100 \text{ kg N ha}^{-1} \text{ year}^{-1}$), just as in other fen meadows where the water levels have been severely lowered in summer (Grootjans et al. 1985, 1986).

The relevance of increased N mineralization rates for above-ground biomass production becomes evident by plotting the biomass of vascular plants against N mineralization rates (Fig. 6a, open symbols). If we do not take the severely drained fens (open squares) into account, there is a strong significant correlation between the two variables. This pattern also fits remarkably well with similar data from a previous study in rich fens and meadows in The Netherlands and Belgium (Fig. 6a, closed symbols). Including these previous data in the comparison, it becomes even clearer that the severely drained sites are outliers; i.e., in these sites biomass production seems not to be controlled by N availability but by another limiting resource, e.g., water or potassium (see below). Plants may also have invested more biomass in roots under these dry conditions. Nevertheless, the clear relationship in Fig. 6a points to a rather general pattern between N mineralization and above-ground biomass production of vascular plants. This indicates that N has an important role as

limiting factor. The patterns from the sites in the Biebrza valley and those in The Netherlands and Belgium fit remarkably well, particularly if undrained fens (open en closed circles) and drained sites (diamonds, closed triangles) are analyzed separately, and if one realizes that another important N source as atmospheric N deposition differs considerably between the two regions ($10 \text{ vs. } 40 \text{ kg N ha}^{-1} \text{ year}^{-1}$; cf. Wassen and Olde Venterink 2006). The steeper pattern for undrained sites than for the drained sites may be explained by an underestimation of net N mineralization in the constantly wet sites through higher denitrification rates in the incubated soil (cf. Olde Venterink et al. 2002a; Wassen and Olde Venterink 2006), rather than higher N use efficiency in the fen species compared to the meadow species.

We have assessed also relationships between biomass versus extractable soil P and K pools for the sites in Fig 6. For the K pools this did yield significant patterns (data not shown). The pattern for the P pool was significant if the sites in the drained Biebrza fen were not included (Fig. 6b). This analysis illustrates the remarkably high extractable P pools in the drained fen. One reason for this might be that these sites are subjected to repeated drying-wetting cycles, which might be more important for P-release in wetlands than drainage as such (Olila et al. 1997; Olde Venterink et al. 2002a). However, considering that these P pools are very much higher than those in all other sites in Fig 6b, including the severely drained fens, we can not rule out that the difference was due to inherent differences in soil-P rather than an effect of drainage.

Many endangered wetland plants are short growing species and poor light competitors. Considering that endangered plant species only occur at sites with an above-ground biomass of vascular plants below 6 ton ha^{-1} (Moore et al. 1989; Wheeler and Shaw 1991; Wassen et al. 2005), it can be read from Fig 6a that the net N mineralization rates should not exceed 40 and $60\text{--}80 \text{ kg ha}^{-1} \text{ year}^{-1}$ for undrained fens and drained fens/meadows, respectively. Hence, N mineralization rates in many Western European fens and meadows seem to be high for the endangered species (cf. Olde Venterink et al. 2002b). Furthermore, the ALA extractable P pool should not exceed 25 kg P ha^{-1} (Fig. 6b). The loss of endangered species in Western Europe is often ascribed to high atmospheric N deposition rates (Bobbink et al. 1998; Stevens et al.

2004); high N mineralization rates and increased soil P pools provide alternative explanations. The latter would fit with our observation that many endangered wetland species in Western Europe persist at P-limited conditions (cf. Olde Venterink et al. 2003; Wassen et al. 2005).

The drained and severely drained fens in this study did not contain fewer plant species than the undrained fens (Appendix 1). However, fen species were replaced by meadow species. Drainage also resulted in a dramatic loss of bryophyte biomass and cover, similar to the pattern described in drained Finnish peatlands (Laiho et al. 2003). In summer 2002, bryophytes were almost completely absent in the drained fens or floodplains, but in 2003 they covered up to 40–50% of the soil in some sites (Appendix 1). The difference among years may be due to differences in (micro) climate and feedbacks with vascular plants (e.g., Limpens et al. 2004). The disappearance of bryophytes could be due to reduced soil wetness, or a result of eutrophication and competition for light (Berendse et al. 2001; Kotowski and Van Diggelen 2004; Van der Wal et al. 2005).

Effects of mowing and hay-removal

The annual mowing and hay-making resulted in a significantly lower aboveground biomass due to a lower amount of dead biomass (Fig. 5). In the severely drained fen, mowing could also prevent a large biomass increase of living vascular plants. In fen meadows and fens in the UK and The Netherlands, a clear reduction in biomass is found through long term hay-removal (Marrs 1985; Koerselman et al. 1990; Berendse et al. 1992; Bakker and Olff 1995).

Olff et al. (1994) also found a reduced N mineralization rate in meadows after long-term hay-removal. Our overall comparison of the three pairs of mown-unmown sites showed a tendency ($P < 0.1$) that supports these results (Fig. 5). We note, however, that the relatively small reduction in N mineralization through hay-making can by far not compensate for the largely increased N mineralization through severe drainage (Fig. 2).

Soil extractable P was higher in the mown sites. We can not explain this result from the use of heavy mowing machines and soil compaction, since bulk density was only higher in the floodplain and not in

the fens, and extractable N and K pools were not consistently increased (Table 1; Fig 2). In contrast, Olff et al. (1994) observed a four fold decrease in total P concentrations with increasing time of haymaking. The effect of haymaking on soil P availability requires further study.

Mowing and annual hay removal had a strong effect on potassium availability in the severely drained fen. A stronger effect of annual hay removal on K than on P or N also was found for some fens and wet meadows in The Netherlands, Belgium and Norway (Koerselman et al. 1990; Øien and Moen 2001; Olde Venterink et al. 2002b). In many wetland sites, the soil K pool is relatively small (Laine et al. 1995b; Olde Venterink et al. 2002b), and output by hay compared to the soil nutrient pool, is often much higher for K than for N or P (Koerselman et al. 1990; Olde Venterink et al. 2002b). In the present study, we did not analyse total nutrient pools in the soil. Extractable K pools were reduced in the mown plots, but only if they were also severely drained (Fig. 2e, f). In drained peat, K can easily leach to deeper soil layers since it is not biologically immobilized in contrast to N and P (cf. Braekke 1987; Sundström et al. 2000). Without K input from dead aboveground plant material, and with a large annual K output in hay, the vegetation can quickly mine the K pool in the top soil (Olde Venterink et al. 2002b). This interactive effect of drainage and mowing on K availability and K limitation agrees with previous studies (Kajak and Okruszko 1990; De Mars et al. 1996; Van Duren and Pegtel 2000). The large K-output by haymaking may cause a shift from N or P limitation towards K limitation particularly in drained mires (Olde Venterink et al. 2002b). Such a shift was indeed indicated for our severely drained and mown site by the nutrient ratios in the aboveground vegetation (Fig. 4). An acute shift to K limitation could lead to severe growth problems for plants and disappearance of most of the herbaceous species (Okruszko 1990). In the dataset of Wassen et al. (2005), we observed only nine K limited sites out of 276 sites; the K limited sites were all drained. These sites, however, were not particularly species poor, and some K-limited sites contained endangered species. Hence, it can not be concluded that K limitation will generally lead to poor species composition.

Some implications for conservation management

The Biebrza mires contain target plant communities and serve as reference ecosystems for nature conservation and restoration elsewhere in Europe. Results of our study show that low availabilities of particularly N and P seem crucial prerequisites for preserving fen plant communities. Nitrogen mineralization should be close to zero, and at least below 40 kg N ha⁻¹ year⁻¹, otherwise productivity of vascular plants may exceed the level above which endangered species no longer occur, unless another resource is growth-limiting (e.g., P or K). To avoid increased N mineralization rates, peatland drainage should be avoided and drained peatland should be rewetted. We note that rewetting may be successful (Van Bodegom et al. 2006), but also has the risk of initiating a strong P release which may stimulate eutrophication rather than prevent it (Lamers et al. 1998; Olde Venterink et al. 2002a).

Annual hay-making may strongly alter N:P:K stoichiometry, and particularly at drained conditions

it may induce K limitation. Kajak and Okruszko (1990) reported that previously species-rich meadow vegetation in severely drained and K-limited sites at Biebrza, could be restored only after K-fertilization. We do not recommend K fertilization as a general management measure at K limited sites because of the productivity increase that can be expected and the negative effects this might have on particularly endangered species. Some drained mires may only be restored by top soil removal and subsequent rewetting (Lamers et al. 2006).

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See Appendix 1.

Appendix 1 Vegetation composition and cover of species in floodplain (FL), undrained fens (UF), drained fen (DF) and severely drained fen (SDF) sites of the Biebrza Valley, Poland.

Sites in FL, DF and SDF were selected in pairs: one site unmown, the other mown and hay removed

Mire type Unmown (U) or mown (M)	FL U	FL M	UF U-1 ^a	UF U-2 ^a	DF U	DF M	SDF U	SDF M
Cover shrub layer (%)	0	0	30	0	0	0	0	0
Cover herb layer (%)	100	100	70	50	100	90	80	90
Cover moss layer (%)	50	1	80	90	1	40	1	10
Total number of species	17	15	26	23	26	29	43	31
Total number of phanerogam species	14	14	20	18	23	25	37	23
Total number of moss species	3	1	6	5	3	4	6	8
Mean Ellenberg <i>F</i> value	8.9	9.0	8.4	8.2	7.6	7.8	6.1	6.4
Mean Ellenberg <i>N</i> value	3.5	4.8	3.0	3.9	4.2	4.3	4.9	4.4
Forbs								
<i>Lysimachia vulgaris</i>	3	2						
<i>Potentilla palustris</i>	3		2	+				
<i>Galium palustre</i>	+			+				
<i>Lythrum salicaria</i>	2				+		+	
<i>Stachys palustris</i>		+		+				
<i>Epilobium palustre</i>	+				+			
<i>Caltha palustris</i>		+				+		
<i>Menyanthes trifoliata</i>			3	2				
<i>Lysimachia thyrsoiflora</i>			+	+				
<i>Cirsium rivulare</i>				+	3			

Appendix 1 continued

Mire type Unmown (U) or mown (M)	FL U	FL M	UF U-1 ^a	UF U-2 ^a	DF U	DF M	SDF U	SDF M
<i>Galium uliginosum</i>			1	+	1	1		
<i>Lycopus europaeus</i>				r	+	+		
<i>Polygonum bistorta</i>					1	1		
<i>Valeriana officinalis</i>				+		+		+
<i>Filipendula ulmaria</i>					1		+	
<i>Cirsium palustre</i>						1		
<i>Potentilla anserina</i>					+	2	+	2
<i>Ranunculus acris</i>					+	1	+	1
<i>Lychnis flos-cuculi</i>					+	1	+	+
<i>Geum rivale</i>					4		3	3
<i>Rumex acetosa</i>					+	+		+
<i>Mentha pulegium</i>					+	+	r	
<i>Achillea millefolium</i>							1	
<i>Hypericum perforatum</i>							1	
<i>Sonchus asper</i>							1	
<i>Carduus crispus</i>							2	
<i>Galium mollugo</i>							1	2
<i>Veronica longifolia</i>							+	+
<i>Cardaminopsis arenosa</i>								3
Sedges								
<i>Carex vesicaria</i>	1	1						
<i>Carex elata ssp. elata</i>	2	+						
<i>Carex acutiformis</i>	1	+						
<i>Carex lasiocarpa</i>	3							
<i>Carex acuta</i>		3						
<i>Carex pseudocyperus</i>		2						
<i>Carex diandra</i>			+	+				
<i>Carex flava</i>				1	+			
<i>Carex appropinquata</i>				+	2	2		
<i>Carex rostrata</i>						1		
<i>Carex panicea</i>			2	3		2	1	+
<i>Carex nigra</i>			+		2	4	+	+
Grasses								
<i>Calamagrostis stricta</i>	1	1	1			1		
<i>Agrostis canina</i>			1	1		2		
<i>Festuca rubra</i>			2	1	2	2	2	4
<i>Poa pratensis</i>			1	+			3	+
<i>Deschampsia cespitosa</i>					1		+	
<i>Anthoxanthum odoratum</i>							1	3
<i>Holcus lanatus</i>							+	1
<i>Bromus inermis</i>							2	
Other graminoids								
<i>Luzula campestris</i>							+	1

Appendix 1 continued

Mire type	FL	FL	UF	UF	DF	DF	SDF	SDF
Unmown (U) or mown (M)	U	M	U-1 ^a	U-2 ^a	U	M	U	M
Shrubs								
<i>Betula humilis</i>			3					
<i>Betula pubescens</i>			2					
<i>Vaccinium oxycoccus</i>			2					
<i>Andromeda polifolia</i>			1					
<i>Salix rosmarinifolia</i>			1					
Other vascular plants								
<i>Equisetum fluviatile</i>	+	1	1	1	1	1		
<i>Equisetum palustre</i>					2			
<i>Ophioglossum vulgatum</i>							+	+
Bryophytes								
<i>Hamatocaulis vernicosus</i>	3		4	5				
<i>Drepanocladus aduncus</i>	1		1	+				
<i>Calliergon cordifolium</i>	+		+					
<i>Brachythecium mildeanum</i>	1	+					+	
<i>Aulacomnium palustre</i>			1					
<i>Calliergonella cuspidata</i>			2	1		3		
<i>Bryum pseudotriquetrum</i>			+	1				1
<i>Climacium dendroides</i>					+	+		1
<i>Plagiomnium affine</i>					+	+		
<i>Brachythecium salebrosum</i>					+		+	
<i>Plagiomnium rostratum</i>							+	+

Indication values for wetness and fertility and acidity are based on Ellenberg et al. (1991); higher *F* and *N* values indicate wetter and more nutrient-rich conditions, respectively. Species are sorted by functional group. Numbers for species cover: + = 1–5%; 1 = 5–15%; 2 = 15–25%; 3 = 25–50%; 4 = 50–75%; 5 ≥ 75%. Species occurring at one site with low cover are not shown

^a Refers to unmown fen 1 and 2 in Table 1

References

- Antheunis AM, Loeb R, Lamers LPM, Verhoeven JTA (2006) Regional differences in nutrient limitation in floodplains of selected European rivers: implications for rehabilitation of characteristic floodplain vegetation. *River Res Appl* 22:1039–1055. doi:[10.1002/rra.956](https://doi.org/10.1002/rra.956)
- Bakker JP, Olff H (1995) Nutrient dynamics during restoration of fen meadows by haymaking without fertiliser application. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) *Restoration of temperate wetlands*. Wiley, Chichester
- Bedford BL, Walbridge MR, Aldous A (1999) Patterns of nutrient availability and plant diversity of temperate North American wetlands. *Ecology* 80:2151–2169
- Berendse F, Oomes MJM, Altena HJ, Elberse WT (1992) Experiments on the restoration of species-rich meadows in The Netherlands. *Biol Cons* 62:59–65. doi:[10.1016/0006-3207\(92\)91152-1](https://doi.org/10.1016/0006-3207(92)91152-1)
- Berendse F, Van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B (2001) Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Glob Change Biol* 7:591–598. doi:[10.1046/j.1365-2486.2001.00433.x](https://doi.org/10.1046/j.1365-2486.2001.00433.x)
- Bobbink R, Hornung M, Roelofs JGM (1998) The effect of air-borne nitrogen pollutant on species diversity in natural and semi-natural European vegetation. *J Ecol* 86:717–738. doi:[10.1046/j.1365-2745.1998.8650717.x](https://doi.org/10.1046/j.1365-2745.1998.8650717.x)
- Braekke FH (1987) Nutrient relationships in forest stands: effects of drainage and fertilization on surface peat layers. *For Ecol Manag* 21:269–284
- Bridgman SD, Pastor J, Janssens JA, Chapin C, Malterer TJ (1996) Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands* 16:45–65
- Bridgman SD, Updegraff K, Pastor J (1998) Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79:1545–1561
- De Mars H, Wassen MJ, Peeters WHM (1996) The effect of drainage and management on peat chemistry and nutrient deficiency in the former Jęgrznia-floodplain (NE-Poland). *Vegetatio* 126:59–72

- De Mars H, Wassen MJ, Olde Venterink H (1997) Flooding and groundwater dynamics in fens in eastern Poland. *J Veg Sci* 8:319–328. doi:[10.2307/3237320](https://doi.org/10.2307/3237320)
- El-Kahloun M, Gerard M, Meire P (2005) Phosphorus and nitrogen cycling in fen vegetation along different trophic conditions in the Biebrza valley, Poland. *Ecophysiol Hydrobiol* 5:68–79
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot* 18:1–248
- Grootjans AP, Schipper PC, Van der Windt HJ (1985) Influence of drainage on N-mineralization and vegetation response in wet meadows: I *Calthion palustris* stands. *Acta Oecol* 6:403–417
- Grootjans AP, Schipper PC, Van der Windt HJ (1986) Influence of drainage on N-mineralization and vegetation response in wet meadows: II *Cirsio-Molinietum* stands. *Acta Oecol* 7:3–14
- Heathwaite AL (1990) The effect of drainage on nutrient release from fen peat and its implications for water quality, a laboratory simulation. *Water Air Soil Poll* 49:159–173. doi:[10.1007/BF00279518](https://doi.org/10.1007/BF00279518)
- Jungk A, Claassen N (1986) Availability of phosphate and potassium as the result of interactions between root and soil in the rhizosphere. *Z Pflanzen Boden* 149:411–427. doi:[10.1002/jpln.19861490406](https://doi.org/10.1002/jpln.19861490406)
- Kajak A, Okruszko H (1990) Grasslands on drained peats in Poland. In: Breymeyer AI (ed) *Ecosystems of the World vol 17A: managed grasslands*. Elsevier, Amsterdam, pp 213–253
- Koerselman W, Bakker SA, Blom M (1990) Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *J Ecol* 78:428–442. doi:[10.2307/2261122](https://doi.org/10.2307/2261122)
- Koerselman W, Van Kerkhoven MB, Verhoeven JTA (1993) Release of inorganic N, P and K in peat soils; effect of temperature, water chemistry and water level. *Biogeochem* 20:63–81. doi:[10.1007/BF00004135](https://doi.org/10.1007/BF00004135)
- Kotowski W, Van Diggelen R (2004) Fen vegetation composition in relation to light availability. *J Veg Sci* 15:583–594. doi:[10.1658/1100-9233\(2004\)015\[0583:LAAEFJ\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2004)015[0583:LAAEFJ]2.0.CO;2)
- Laiho R, Laine J (1994) Nitrogen and phosphorus stores in peatlands drained for forestry in Finland. *Scand J For Res* 9:251–260. doi:[10.1080/02827589409382838](https://doi.org/10.1080/02827589409382838)
- Laiho R, Vasander H, Penttilä T, Laine J (2003) Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. *Glob Biogeochem Cycles* 17:1053. doi:[10.1029/2002GB002015](https://doi.org/10.1029/2002GB002015)
- Laine J, Vasander H, Laiho R (1995a) Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *J Appl Ecol* 32:785–802. doi:[10.2307/2404818](https://doi.org/10.2307/2404818)
- Laine J, Vasander H, Sallantausta T (1995b) Ecological effects of peatland drainage for forestry. *Environ Rev* 3:286–303
- Lamers LPM, Tomassen HBM, Roelofs JGM (1998) Sulphate induced eutrophication and phytotoxicity in freshwater wetlands. *Environ Sci Technol* 32:199–205. doi:[10.1021/es970362f](https://doi.org/10.1021/es970362f)
- Lamers LPM, Loeb R, Antheunis AM, Miletto M, Lucassen ECHET, Boxman AW, Smolders AJP, Roelofs JGM (2006) Biogeochemical constraints on the ecological rehabilitation of wetland vegetation in river floodplains. *Hydrobiol* 565:165–186. doi:[10.1007/s10750-005-1912-8](https://doi.org/10.1007/s10750-005-1912-8)
- Limpens J, Berendse F, Klees H (2004) How phosphorus availability affects the impact of nitrogen deposition on Sphagnum and vascular plants in bogs. *Ecosystems* 7:793–804. doi:[10.1007/s10021-004-0274-9](https://doi.org/10.1007/s10021-004-0274-9)
- Marrs RH (1985) Techniques for reducing soil fertility for nature conservation purposes: a review in relation to research at Ropert's heath, Suffolk, England. *Biol Cons* 34:307–332. doi:[10.1016/0006-3207\(85\)90038-2](https://doi.org/10.1016/0006-3207(85)90038-2)
- Moore DRJ, Keddy PA, Gaudet CL, Wisheu IC (1989) Conservation of wetlands: do infertile wetlands deserve a higher priority? *Biol Cons* 47:203–217. doi:[10.1016/0006-3207\(89\)90065-7](https://doi.org/10.1016/0006-3207(89)90065-7)
- Naiman RJ, Decamps H (1997) The ecology of interfaces: riparian zones. *Ann Rev Ecol Syst* 28:621–658. doi:[10.1146/annurev.ecolsys.28.1.621](https://doi.org/10.1146/annurev.ecolsys.28.1.621)
- Nienhuis PH (2006) Water and values: ecological research as the basis for water management. *Hydrobiol* 565:261–275. doi:[10.1007/s10750-005-1918-2](https://doi.org/10.1007/s10750-005-1918-2)
- Øien DI, Moen A (2001) Nutrient limitation in boreal plant communities and species influenced by scything. *Appl Veg Sci* 4:197–206
- Okruszko H (1990) Wetlands of the Biebrza valley. Their value and future management. Polish Academy of Sciences, Warsaw
- Okruszko H (1993) Transformation of fen peat soil under the impact of draining. *Zeszyty Problemowe Postepow Nauk Rolniczych* 406:3–73
- Olde Venterink H, van der Vliet RE, Wassen MJ (2001) Nutrient limitation along a productivity gradient in wet meadows. *Plant Soil* 234:171–179. doi:[10.1023/A:1017922715903](https://doi.org/10.1023/A:1017922715903)
- Olde Venterink H, Davidsson TE, Kiehl K, Leonardson L (2002a) Impact of drying and re-wetting on N, P and K dynamics in a wetland soil. *Plant Soil* 243:119–130. doi:[10.1023/A:1019993510737](https://doi.org/10.1023/A:1019993510737)
- Olde Venterink H, Pieterse NM, Belgers JDM, Wassen MJ, De Ruiter PC (2002b) N, P and K budgets along nutrient availability and productivity gradients in wetlands. *Ecol Appl* 12:1010–1026. doi:[10.1890/1051-0761\(2002\)012\[1010:NPAKBA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1010:NPAKBA]2.0.CO;2)
- Olde Venterink H, Wassen MJ, Verkroost AWM, De Ruiter PC (2003) Species richness-productivity patterns differ between N-, P- and K-limited wetlands. *Ecology* 84:2191–2199. doi:[10.1890/01-0639](https://doi.org/10.1890/01-0639)
- Olde Venterink H, Vermaat JE, Pronk M, Wiegman F, Van der Lee GEM, Van den Hoorn MW, Higler LWG, Verhoeven JTA (2006) Importance of sediment deposition and denitrification for nutrient retention in floodplain wetlands. *Appl Veg Sci* 9:163–174. doi:[10.1658/1402-2001\(2006\)9\[163:IOSDAD\]2.0.CO;2](https://doi.org/10.1658/1402-2001(2006)9[163:IOSDAD]2.0.CO;2)
- Oloff H, Berendse F, De Visser W (1994) Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application. *J Ecol* 82:611–620. doi:[10.2307/2261268](https://doi.org/10.2307/2261268)
- Olila OG, Reddy KR, Stites DL (1997) Influence of draining on soil phosphorus forms and distribution in a constructed wetland. *Ecol Eng* 9:157–169. doi:[10.1016/S0925-8574\(97\)10006-4](https://doi.org/10.1016/S0925-8574(97)10006-4)
- Oomes MJM, Oloff H, Altena HJ (1996) Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *J Appl Ecol* 33:576–588. doi:[10.2307/2404986](https://doi.org/10.2307/2404986)

- Oswit J (1973) The development of peatlands in the lower Biebrza valley versus water conditions. *Roczn. Nauk Roln. Serie D*, pp 143 (in Polish)
- Palczynski A (1984) Natural differentiation of plant communities in relation to hydrological conditions of the Biebrza Valley. *Pol Ecol Stud* 10:347–385
- Pinay G, Ruffinoni C, Fabre A (1995) Nitrogen cycling in two riparian forest soils under different geomorphic conditions. *Biogeochem* 30:9–29. doi:[10.1007/BF02181038](https://doi.org/10.1007/BF02181038)
- Spink A, Sparks RE, Van Oorschot M, Verhoeven JTA (1998) Nutrient dynamics of large river floodplains. *Reg Riv* 14: 203–216. doi:[10.1002/\(SICI\)1099-1646\(199803/04\)14:2<203::AID-RRR498>3.0.CO;2-7](https://doi.org/10.1002/(SICI)1099-1646(199803/04)14:2<203::AID-RRR498>3.0.CO;2-7)
- Stanners D, Bourdeau P (1995) Europe's environment, the Dobbris assessment. European Environmental Agency, Copenhagen
- Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science* 303:1876–1879. doi:[10.1126/science.1094678](https://doi.org/10.1126/science.1094678)
- Sundström E, Magnusson T, Hånell B (2000) Nutrient conditions in drained peatlands along a north–south climatic gradient in Sweden. *For Ecol Manag* 126:149–161
- Updegraff K, Bridgman SD, Pastor J, Johnston CA (1995) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecol Appl* 5:151–163. doi:[10.2307/1942060](https://doi.org/10.2307/1942060)
- Van Bodegom PM, Oosthoek A, Broekman R, Bakker C, Aerts R (2006) Raising groundwater differentially affects mineralization and plant species abundance in dune slacks. *Ecol Appl* 16:1785–1795. doi:[10.1890/1051-0761\(2006\)016\[1785:RGDAMA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1785:RGDAMA]2.0.CO;2)
- Van der Wal R, Pearce ISK, Brooker RW (2005) Mosses and the struggle for light in a nitrogen-polluted world. *Oecologia* 142:159–168. doi:[10.1007/s00442-004-1706-0](https://doi.org/10.1007/s00442-004-1706-0)
- Van Duren IC, Pegtel DM (2000) Nutrient limitations in wet, drained and rewetted fen meadows: evaluation of methods and results. *Plant Soil* 220:35–47. doi:[10.1023/A:1004735618905](https://doi.org/10.1023/A:1004735618905)
- Van Oorschot M, Robbemont E, Boerstal M, Van Strien I, Van Kerkhoven-Smitsch M (1997) Effects of enhanced nutrient availability on plant and soil nutrient dynamics in two English riverine ecosystems. *J Ecol* 85:167–180. doi:[10.2307/2960649](https://doi.org/10.2307/2960649)
- Verhoeven JTA, Arts HHM (1987) Nutrient dynamics in small mesotrophic fens surrounded by cultivated land. II: N and P accumulation in plant biomass in relation to the release of inorganic N and P in the peat soil. *Oecologia* 72:557–561. doi:[10.1007/BF00378982](https://doi.org/10.1007/BF00378982)
- Verhoeven JTA, Koerselman W, Meuleman AFM (1996) Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends Ecol Evol* 11:494–497. doi:[10.1016/S0169-5347\(96\)10055-0](https://doi.org/10.1016/S0169-5347(96)10055-0)
- Vitt DH, Chee WL (1990) The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89:87–106. doi:[10.1007/BF00032163](https://doi.org/10.1007/BF00032163)
- Walbridge MR, Navaratnam JA (2006) Phosphorous in boreal peatlands. In: Wieder RK, Vitt DH (eds) *Boreal peatland ecosystems*. Springer, Berlin, pp 231–258
- Wassen MJ, Joosten JHJ (1996) In search of a hydrological explanation for vegetation changes along a fen gradient in the Biebrza upper basin (Poland). *Vegetatio* 124:191–209
- Wassen MJ, Olde Venterink H (2006) Comparison of nitrogen and phosphorus fluxes in some European fens and floodplains. *Appl Veg Sci* 9:213–222. doi:[10.1658/1402-2001\(2006\)9\[213:CONAPF\]2.0.CO;2](https://doi.org/10.1658/1402-2001(2006)9[213:CONAPF]2.0.CO;2)
- Wassen MJ, Barendregt A, Palczynski A, De Smidt JT, De Mars H (1990) The relationship between fen vegetation gradients, groundwater flow and flooding in an undrained valley mire at Biebrza, Poland. *J Ecol* 78:1106–1122
- Wassen MJ, Olde Venterink HGM, De Swart EOAM (1995) Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *J Veg Sci* 6:5–16. doi:[10.2307/3236250](https://doi.org/10.2307/3236250)
- Wassen MJ, van Diggelen R, Wolejko L, Verhoeven JTA (1996) A comparison of fens in natural and artificial landscapes. *Vegetatio* 126:5–26
- Wassen MJ, Van der Vliet R, Verhoeven JTA (1998) Nutrient limitation in the Biebrza valley fens and floodplain (Poland). *Acta Bot Neerl* 47:241–253
- Wassen MJ, Peeters WHM, Olde Venterink H (2003) Patterns in vegetation, hydrology, and nutrient availability in an undisturbed floodplain in Poland. *Plant Ecol* 165:27–43. doi:[10.1023/A:1021493327180](https://doi.org/10.1023/A:1021493327180)
- Wassen MJ, Olde Venterink H, Lapshina ED, Tanneberger F (2005) Endangered plants persist under phosphorus limitation. *Nature* 437:547–550. doi:[10.1038/nature03950](https://doi.org/10.1038/nature03950)
- Wheeler BD, Shaw SC (1991) Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *J Ecol* 79:285–301. doi:[10.2307/2260713](https://doi.org/10.2307/2260713)
- Zurek S (1984) Relief, geologic structure and hydrography of the Biebrza ice-marginal valley. *Pol Ecol Stud* 10: 239–252