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# Nutrient limitation in the Biebrza fens and floodplain (Poland)

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## SUMMARY

Fertilization experiments were carried out at four stands of mire vegetation in the Biebrza valley, Poland. The stands included two rich fen communities, a moderate-rich/poor fen vegetation and a floodplain fen. In each stand five replicate sets of treatment plots (50 × 50 cm) were selected randomly. Each set consisted of five plots: a control plot, three plots which were fertilized with N, P, K, respectively and one plot with all three elements together. Fertilizer was applied in April. Groundwater and soil were sampled and analysed twice (April, July). In July aboveground biomass was harvested and nutrient concentrations in plant material were examined. Nutrient release from peat to pore water was measured by incubation experiments. Vascular plants were N-limited in the non-flooded fen communities. The vegetation in the floodplain was not limited by nutrients. The results compare well with the hypotheses of Wassen *et al.* (1995) on expected nutrient limitation of fens in the Biebrza valley, based on nutrient concentrations in (non-fertilized) mire vegetation. However, the critical nutrient concentration and the P/N-quotient in plant material should be regarded as rough indicators only. We expect N to be the controlling factor for the non-flooded fen communities as long as the fens are not drained and N-input by groundwater inflow and atmospheric deposition remains low.

*Key-words:* fertilization experiments, flooding, groundwater, moderate-rich fen, rich fen, site conditions.

## INTRODUCTION

Differences in water sources and in biogeochemical processes between rich fens and poorer fen types may cause differences in the availability of nutrients for their vegetation types. The input of nutrients into most poor fens comes mainly from the atmosphere, although some poor fens have developed under the influence of base-poor telluric water.

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*Nomenclature:* Phanerogams: Van der Meijden *et al.* (1983); Cryptogams: Margadant & During (1982); Syntaxa: Pałczynski (1984).

Rich fens have an extra input of nutrients from groundwater or surface water. Fens receiving water by surface floods from rivers usually have a higher biomass production than groundwater-fed fens (Wheeler 1980; Pałczynski 1984; Breen *et al.* 1988; Okruszko 1991; Mitsch & Gosselink 1993; Wassen 1995), suggesting a higher nutrient availability. The origin of the water feeding a fen also exerts an influence on physicochemical conditions which in turn play a role in nutrient availability. High concentrations of calcium or iron, for example, may cause phosphorus deficiency in rich fens since phosphorus may precipitate as Fe- or Ca-salts or may coprecipitate with calcite and become inaccessible to plants (Boyer & Wheeler 1989). The solubility of iron–phosphate complexes and the rates of nitrification and denitrification depend on the redox status of the soil (Brümmer 1974; Scheffer & Schachtschabel 1992; Faulkner & Patrick 1992), which is not only correlated with wetness but also with the origin of the water (De Mars 1996; Verhoeven *et al.* 1996a). Mineralization of organic matter is usually faster in subneutral to alkaline-rich fens than in acidic poor fens (Verhoeven *et al.* 1996a).

The most direct way to test limitation of nutrients is obtained by fertilization experiments, in which an excess of nutrients (N, P and K) is supplied and the growth and nutrient-uptake of the vegetation is measured. Overviews of fertilization experiments by Koerselman & Verhoeven (1995), Verhoeven *et al.* (1996b) and Wassen *et al.* (1995) showed that most rich fens fed by groundwater are N-limited, unless they have been mown for a long time. Mowing may lead to a shift from N-limitation to P- and/or K-limitation (Koerselman *et al.* 1990). Wet heaths, poor fens and bogs are sometimes found to be N-limited as well (Aerts *et al.* 1992), but in most cases they are colimited by N and P or only limited by P (Wassen *et al.* 1995). Drained fen meadows were found to be limited by K (Kajak & Okruszko 1990; De Mars *et al.* 1996; Van Duren *et al.* 1997).

Most fertilization experiments in fens were carried out in areas influenced by man (e.g. Egloff 1983; Vermeer 1985; Boyer & Wheeler 1989; Verhoeven & Schmitz 1991; Boeye *et al.* 1997) with extra nutrient input by inflow of enriched water and increased atmospheric deposition. For fertilization experiments in undisturbed fens the Biebrza valley in northeast Poland was chosen. Four fen sites differing in species composition were fertilized experimentally. Much is known about vegetation, water flow and water and peat chemistry in this area (see Pałczynski 1984; Byczkowski & Kicinski 1984; Pajnowska *et al.* 1984; Dembek 1992; Wassen *et al.* 1990, 1995), but less about nutrient availability. Wassen *et al.* (1995) postulated N-limitation for several rich fens and a moderate-rich/poor fen in the Biebrza valley, based on nutrient concentrations in harvested aboveground biomass. Biomass production in the floodplain did not appear to be limited by nutrients.

In this paper two questions will be examined: (i) are fen vegetation types in the Biebrza valley limited in their growth by nutrients and, if so, by which nutrient(s)?; and (ii) can differences in nutrient availability between fen vegetation types be related to differences in site conditions?

## MATERIALS AND METHODS

### *Study area*

The valley of the river Biebrza is located in a post-glacial landscape in N.E. Poland (22°30′–23°60′E and 53°30′–53°75′N). There is no bedrock within 200 m depth and the permeability of the soils is relatively high. Moraines and sandrs surround the peaty valley, which is underlain by fluvial and eolian sands interbedded by gravel and silt series (Zurek 1984). Mean rainfall is 583 mm. The altitude of the *c.* 1000 $km^2$ valley ranges from *c.* 100 to 130 m above mean sea level. The catchment area of *c.* 7000 $km^2$ is covered by agricultural land, forests and lakes. Agriculture is inextensive and population density is low. The valley is one of the last vast undrained valley mires in Central Europe (Okruszko 1990). Atmospheric deposition of nitrogen is low (*c.* 10 kg $ha^{-1}$ $year^{-1}$; Bleuten, unpublished).

The peat deposits are up to 7 m deep. The river is not regulated and it has many oxbow lakes, which are again filling with vegetation. Extensive areas are flooded by the river in spring. Further away from the river, non-flooded groundwater- and rainwater-fed fens cover vast areas. The natural and pristine character of the peatlands is reflected in an intact regular pattern of peat-forming plant communities along the length and across the breadth of the valley (Oswit 1968; Pałczynski 1984).

The floodplain contains highly productive rich fen types *Glycerietum maximae, Caricetum gracilis* and *C. elatae* (Pałczynski 1984). These are tall sedge, grass and herb vegetation types, relatively poor in species. Typical associations of the zone that is only occasionally flooded are the *C. caespitosae* and *Peucedano-C. appropinquatae.*

Low-growing sedge vegetation is abundant not only along the moraines but also further away from the moraines, provided that the calcareous groundwater reaches the fen surface (Wassen *et al.* 1992). In the Biebrza valley several species-rich associations of this fen type (*Caricion diandrae*) are present (Pałczynski 1984). These are low-productivity sedge and herb stands with a moss layer of *Hypnaceae.*

Moderate-rich fen is found outside the reach of seasonal river flooding and where the influx of calcareous groundwater to the fen is small. This fen type is fed to a larger extent by rainwater (Wassen *et al.* 1990) and belongs syntaxonomically to *Betuletum humilis* with affinity to the *C. rostrato-diandrae*. It is a low sedge vegetation with sparse dwarf-shrubs and a thick moss layer of mainly *Aulacomnium palustre* and occasionally some *Sphagnum* hummocks (*S. recurvum, S. squarrosum, S. palustre*).

### *Experiments*

Fertilization and nutrient release experiments and sampling of soil and soil water were carried out at four sites in transects studied previously (Wassen *et al.* 1990, 1992). One of the sites is in the floodplain, the 'floodplain-rich fen'. This site has *C. elatae* vegetation (see Wassen *et al.* 1992, fig 3, site 11). Two other sites with different types of non-flooded rich fen will be referred to as 'rich fens 1 and 2'. They have *C. limoso-diandrae* vegetation (see Wassen *et al.* 1992, fig. 4, site 10 and fig. 2, site 5, respectively). The fourth site is an intermediate fen type referred to as 'moderate-rich fen". It has *B. humilis/C. rostrato-diandrae* vegetation (see Wassen *et al.* 1992, fig. 2, site 16).

*Fertilization experiments.* For each fertilization experiment five replicate sets of treatment plots were selected randomly. Each set consisted of five 50 × 50 cm plots for fertilization with N, P, K and all three elements together, and a control plot, respectively. Three times in the third and fourth week of April 1992 the plots in three of the four fen sites (rich fens 1 and 2 and moderate-rich fen) were fertilized with solutions of $NH_4NO_3$ (N-treatment), $Na_2HPO_4$ (P-treatment) and KCl (K-treatment), and a combination of these solutions (NPK-treatment). Concentrated solutions were taken into the field and were diluted 10 times with water from the surface of the mire. The control plots only received surface mire water. In the fourth week of April 1993, only the floodplain plots were fertilized with so-called 'osmo-grains'. The nutrients that are stored inside these grains are released slowly (within 2 months). The mineral composition of the grains, of *c.* 2 mm diameter, was comparable with that of the solutions ($NH_4NO_3$ (N-treatment), $Na_2HPO_4$ (P-treatment) and KCl (K-treatment), respectively). Analysis of the grain remnants collected in July showed that they had lost all nutrients. A total of *c.* 200 kg N $ha^{-1}$, *c.* 50 kg P $ha^{-1}$, *c.* 160 kg K $ha^{-1}$, and these amounts combined, was supplied to the fertilized plots of each experiment. After *c.* 3 months (in July 1992 for rich fens 1 and 2 and the moderate-rich fen, and in July 1993 for the floodplain-rich fen), at the height of the growing season, the aboveground plant material (including mosses) was harvested in 40 × 40 cm plots. Dead plant material was removed. The rest was sorted into several plant groups: bryophytes, herbs (including *Equisetum* and *Thelypteris palustris* if present), grasses, sedges and woody species (only present in the moderate-rich fen). The separated plant material was weighed (g dry weight $m^{-2}$) and nutrient concentrations (mg $g^{-1}$ dry weight) were determined, after acid digestion of ground plant material with a mixture of sulphuric and salicylic acid (Kjeldahl-destruction), with a Skalar continuous flow analyser with colorimetrical detection (N and P) or flame emission spectroscopy (K).

The results of the experiments were analysed with a one-way ANOVA (Anonymous 1985) and tested for significance with respect to the control with Dunnet's test ($P = 0{\cdot}05$) (Sokal & Rohlf 1981; Zar 1984).

*Groundwater and peat.* Groundwater piezometers were placed in the plots of the fertilization experiments. In the field groundwater level and pH (WTW-pH96 with Ag/AgCl electrode) was measured in the piezometers. Water samples were taken in April and July as close to the surface as possible. Within 8 hours after collection they were centrifuged, acidified to pH = 1 and stored in polyethylene tubes. After a maximum of 2 weeks they were analysed for Ca, K and P using an inductively coupled plasma technique (Boumans 1987). $NH_4$ and $NO_3$ were analysed with a Skalar continuous flow analyser using the indophenol-blue method.

The redox potential (Eh) was measured in the peat at 15 cm depth threefold around the plot with the WTW-pH96 using a Pt-Ag electrode. Readings were taken when the value had stabilized. Values were corrected for temperature, adjusted to standard hydrogen potential (Eh) and standardized to pH = 7 (E7 in mV; Bohn 1971; Urquhart & Gore 1973).

In July *c.* 1 $dm^3$ of peat was cut at 5–15 cm below the surface from the middle of the control plots. These samples were stored in sealed polyethylene bags at 4–10°C. Water content of the peat was determined by drying a subsample at 105°C for 16 hours. Organic matter content was determined by weight loss on ignition at 550°C for 5 hours. Total N, P and K were determined with Kjeldahl-destruction (see above). pH of the peat was determined after shaking a subsample with 0·01 M $CaCl_2$ and measuring the pH of the suspension. Lime potential ($p_{lime}$) was calculated from: pH(peat) $-1{\cdot}15$. Easily extractable $PO_4$-P was determined by extraction with 0·1 M sulphuric acid and concentration measurement on a Skalar continuous flow analyser using the molybdenum-blue method.

*Nutrient release experiments.* The net release of nutrients from peat to the pore water was measured by peat incubation experiments carried out in triplicate at each location outside the fertilized plots. Peat columns (0–15 cm below ground surface) were cut by inserting a tube following removal of the sod. The tube was closed at both ends with lids. The top lid contained an opening to allow gas-exchange with the air. A hole was drilled into the pipe wall at 7·5 cm from the top. Before the tube was replaced a water sample (10 ml) was taken with an injection needle and the hole was sealed. The tube was replaced in the borehole with the top lid above the groundwater level and covered with the sod. After 4 weeks of *in situ* incubation a second water sample of 10 ml was taken. Water samples were centrifuged, acidified to pH 1 and stored in polyethylene tubes within 8 hours after collection. Storage time was never longer than 3 weeks. Samples were analysed for major ions and nutrients, as described above. The release rates were calculated by subtracting the initial value from the value after 4 weeks of incubation (mg N, P and K $dm^{-3}{}_{peat\ water}$ (4 weeks)$^{-1}$).

A Tukey's Studentized range test (Anonymous 1985) was applied to test differences between fen types in groundwater and peat variables and in nutrient release rates.

## RESULTS

### *Growth response*

The growth response of the distinguished plant groups (herbs, grasses, etc.) on fertilization did not differ from each other in most cases. Therefore groups were joined together to 'phanerogams' and bryophytes.

In all non-flooded fen sites N- and NPK-treatments resulted in a significantly higher biomass production of the phanerogams (Fig. 1). In rich fen 1 the total aboveground biomass was significantly higher after both P- and NPK-treatment. For the floodplain-rich fen none of the treatments led to a significant growth response compared to the control (vegetation was patchy leading to large standard deviations). Bryophytes did not show a significant increase in biomass production after fertilization at any site.

### *Nutrient concentrations in aboveground biomass*

*Phanerogams.* N-concentrations in the biomass did not differ among the treatments in rich fens 1 and 2 (Table 1). In both fens significantly higher P-concentrations were found after P- and NPK-treatment for the total biomass and for phanerogams separately (Table 2). In rich fen 1 significantly higher K-concentrations, after both K- and NPK-treatment, were found for the total biomass and for phanerogams (Table 3). In rich fen 2 no differences in K-concentrations were found among the treatments.

*Bryophytes.* N-concentrations in the biomass did not differ among the treatments in rich fens 1 and 2 (Table 1). In both fens significantly higher P-concentrations were found after P- and NPK-treatment (Table 2). In the moderate-rich fen a significantly higher N-concentration was found after both N- and NPK-treatment (Table 1). K-concentrations were significantly higher after K-treatment (Table 3). In the floodplain-rich fen the only significantly higher concentration (P) was found after both P- and NPK-treatment (Table 2).

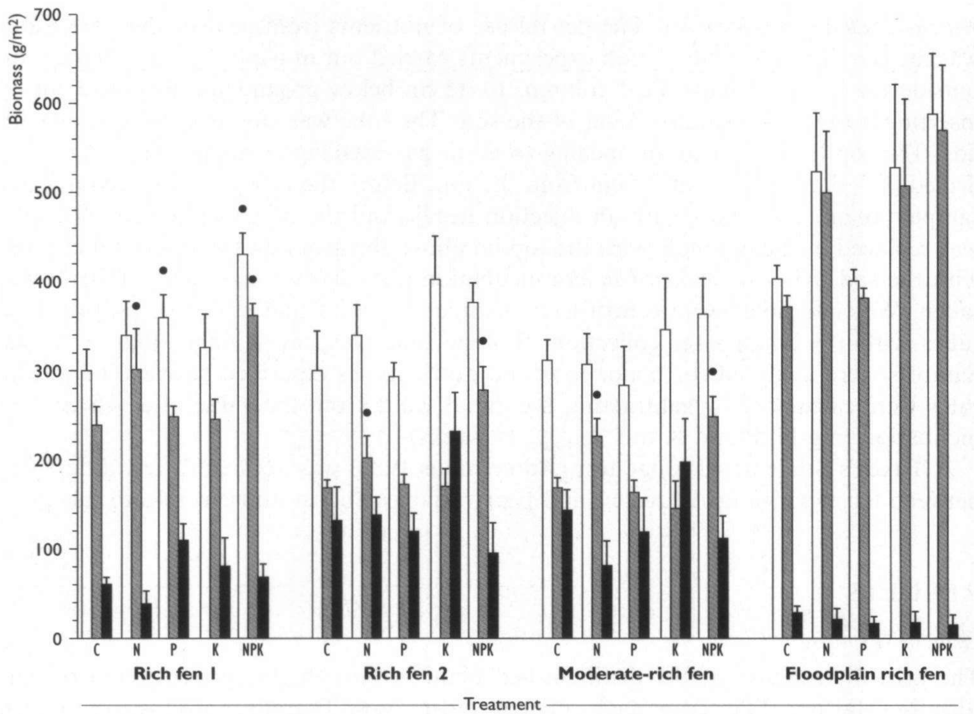


**Fig. 1** Mean growth response on fertilization treatments (C = control, N, P and K = single nutrient addition, NPK = combined nutrient addition). Values marked with a dot significantly differ from that in control treatment (one-way ANOVA and Dunnet's test, $P<0.05$). Vertical lines are SD. □, Total biomass; ▩, vascular plants; ■, bryophytes.

**Table 1.** Nitrogen concentrations in total living aboveground biomass and in phanerogam and bryophyte living aboveground material in the different fertilization treatments

| | Rich fen 1 | | | Rich fen 2 | | |
|---|---|---|---|---|---|---|
| Fen type | Total | Phan | Bryo | Total | Phan | Bryo |
| Control | 12·9±0·7 | 12·6±0·6 | 14·1±1·8 | 14·2±1·9 | 14·3±2·3 | 15·2±2·1 |
| N | 12·8±0·6 | 12·3±1·0 | 14·2±1·6 | 15·4±0·9 | 14·3±0·8 | 16·8±1·8 |
| P | 12·9±0·3 | 11·9±0·7 | 15·1±1·0 | 14·1±0·7 | 12·9±1·3 | 15·1±1·3 |
| K | 12·5±0·3 | 12·4±0·6 | 13·9±2·2 | 14·1±1·3 | 13·7±0·7 | 11·7±6·4 |
| NPK | 13·2±0·9 | 13·0±0·9 | 14·5±0·3 | 14·6±1·4 | 13·6±1·2 | 17·7±0·8 |
| | Moderate-rich fen | | | Floodplain rich fen | | |
| Fen type | Total | Phan | Bryo | Total | Phan | Bryo |
| Control | 14·8±0·6 | 16·7±1·0 | 12·5±0·7 | 11·2±1·6 | 13·1±1·4 | 18·5±5·0 |
| N | 17·4±2·3 | 16·8±2·7 | 19·6±2·0* | 13·5±3·5 | 13·2±2·3 | 16·1±10·7 |
| P | 15·7±1·5 | 17·3±1·3 | 13·5±0·8 | 11·2±2·0 | 11·4±1·8 | 16·0±2·2 |
| K | 14·8±2·4 | 16·4±1·4 | 12·6±3·0 | 13·0±3·9 | 11·6±1·0 | 15·2±1·4 |
| NPK | 16·1±1·1 | 15·1±1·4 | 19·1±1·0* | 14·8±2·7 | 12·4±1·3 | 15·3±7·3 |

Values in mg N/g dry weight ±SD ($n=5$). * = Value significantly different from that in control treatment (one-way ANOVA and Dunnet's test, $P<0.05$). Vertical lines are SD.

**Table 2.** Phosphorus concentrations in total living aboveground biomass and in living phanerogam and bryophyte aboveground material in the different fertilization treatments.

| | Rich fen 1 | | | Rich fen 2 | | |
|---|---|---|---|---|---|---|
| Fen type | Total | Phan | Bryo | Total | Phan | Bryo |
| Control | 0·81±0·07 | 0·87±0·07 | 0·62±0·14 | 1·01±0·16 | 1·06±0·23 | 0·94±0·13 |
| N | 0.72±0·15 | 0·73±0·14 | 0·55±0·08 | 0·89±0·22 | 0·89±0·11 | 0·91±0·16 |
| P | 1·29±0·25* | 1·21±0·29* | 1·49±0·21* | 1·91±0·17* | 1·47±0·14* | 2·41±0·19* |
| K | 0·76±0·08 | 0·82±0·08 | 0·60±0·14 | 0·70±0·17 | 0·93±0·16 | 0·80±0·68 |
| NPK | 1·28±0·19* | 1·29±0·22* | 1·02±0·04* | 1·79±0·22* | 1·55±0·07* | 2·68±0·58* |
| | Moderate-rich fen | | | Floodplain rich fen | | |
| Fen type | Total | Phan | Bryo | Total | Phan | Bryo |
| Control | 3·49±0·79 | 3·49±0·40 | 3·32±1·20 | 1·30±0·07 | 1·28±0·07 | 1·60±0·10 |
| N | 3·31±0·42 | 3·39±0·51 | 2·92±0·15 | 1·25±0·30 | 1·25±0·31 | 1·32±0·76 |
| P | 3·79±0·52 | 3·74±0·18 | 3·82±0·93 | 1·42±0·14 | 1·36±0·12 | 2·65±0·65* |
| K | 3·56±0·58 | 3·78±0·26 | 4·00±1·98 | 1·05±0·19 | 1·05±0·18 | 1·37±0·29 |
| NPK | 3·23±0·73 | 3·06±0·92 | 3·78±0·36 | 1·30±0·27 | 1·23±0·21 | 2·26±1·14* |

Values in mg P/g dry weight ±SD ($n=5$). * = Value significantly different from that in control treatment (one-way ANOVA and Dunnet's test, $P<0.05$). Vertical lines are SD.

**Table 3.** Potassium concentrations in total living above-ground biomass and in living phanerogam and bryophyte above-ground material in the different fertilization treatments

| | Rich fen 1 | | | Rich fen 2 | | |
|---|---|---|---|---|---|---|
| Fen type | Total | Phan | Bryo | Total | Phan | Bryo |
| Control | 6·4±0·5 | 7·2±0·9 | 3·7±2·0 | 8·4±2·2 | 11·2±0·9 | 3·6±0·6 |
| N | 6·6±1·4 | 7·1±1·6 | 3·7±0·3 | 7·0±1·8 | 10·1±2·0 | 3·0±0·4 |
| P | 6·6±1·4 | 7·7±1·6 | 3·8±0·7 | 7·5±2·3 | 10·8±2·6 | 4·1±2·0 |
| K | 9·7±1·2* | 11·3±1·9* | 5·1±0·8 | 8·5±3·6 | 11·7±0·8 | 6·3±6·3 |
| NPK | 10·5±2·0* | 12·0±2·3* | 3·9±0·6 | 10·2±1·2 | 11·9±1·0 | 5·0±1·3 |
| | Moderate-rich fen | | | Floodplain rich fen | | |
| Fen type | Total | Phan | Bryo | Total | Phan | Bryo |
| Control | 11·6±1·4 | 14·7±2·6 | 7·9±0·7 | 11·3±1·2 | 11·5±1·2 | 7·6±0·8 |
| N | 11·7±1·9 | 13·2±2·0 | 6·8±0·7 | 13·4±2·3 | 13·7±2·3 | 4·9±3·1 |
| P | 13·4±2·8 | 15·7±2·9 | 8·5±2·1 | 10·9±2·0 | 11·1±2·1 | 6·0±1·2 |
| K | 15·3±2·2 | 16·6±1·1 | 12·2±3·0* | 13·6±1·6 | 13·9±1·7 | 6·9±1·5 |
| NPK | 12·5±3·5 | 13·1±4·0 | 11·1±1·4 | 14·0±0·8 | 14·2±0·6 | 6·5±3·1 |

Values in mg K/g dry weight SD ($n=5$). * = Value significantly different from that in control treatment (one-way ANOVA and Dunnet's test, $P<0·05$). Vertical lines are SD.

### *Groundwater and peat*

In April water levels were at or above the peat surface (Table 4). The spring flooding of the floodplain-rich fen was of particularly great magnitude. In July water levels had fallen to about 0·5 m below the surface in the floodplain. Water levels also dropped in

**Table 4.** Site conditions in four fen types at Biebrza in April and July 1992. Values are mean ± SD (number of samples between parentheses). Water samples were taken as close to the surface as possible (see water level for sampling depth). Peat samples were taken at a depth of 5–15 cm.

| | Rich fen 1 | | Rich fen 2 | | Moderate-rich fen | | Floodplain rich fen | |
|---|---|---|---|---|---|---|---|---|
| | April | July | April | July | April | July | April | July |
| Water level (cm above mire surface) | +19 ± 3(51)$^{a}$ | −8 ± 3(17)$^{p}$ | 0 ± 3(51)$^{b}$ | −33 ± 6(17)$^{q}$ | +2 ± 4(51)$^{b}$ | −24 ± 4(17)$^{q}$ | +27 ± 6(6)$^{a}$ | −52 ± 3(6)$^{r}$ |
| E7 (mV) | −49 ± 32(16) | −16 ± 20(12)$^{q}$ | 30 ± 69(17) | 339 ± 57(17)$^{p}$ | 105 ± 70(17) | 265 ± 83(17)$^{p}$ | — | — |
| $pH_{peat\ water}$ | 6·72 ± 0·03(4)$^{b}$ | 7·14 ± 0·25(4)$^{p}$ | 6·03 ± 0·25(4)$^{c}$ | 6·17 ± 0·09(4)$^{q}$ | 5·41 ± 0·07(3)$^{d}$ | 6·52 ± 0·20(3)$^{pq}$ | 7·90 ± 0·24(6)$^{a}$ | 6·76 ± 0·10(6)$^{pq}$ |
| $Ca_{peat\ water}$ (mg $l^{-1}$) | 39 ± 4(25)$^{b}$ | 58 ± 121(4) | 45 ± 2(25)$^{b}$ | 75 ± 3(4) | 21 ± 2(23)$^{c}$ | 58 ± 13(3) | 76 ± 2(6)$^{a}$ | 66 ± 22(6) |
| $K_{peat\ water}$ (mg $l^{-1}$) | 0·37 ± 0·44(25)$^{b}$ | 2·68 ± 0·76(4)$^{p}$ | 2·21 ± 1·49(25)$^{a}$ | 1·05 ± 0·54(4)$^{pq}$ | 2·26 ± 1·19(23)$^{a}$ | 0·95 ± 0·46(3)$^{q}$ | 2·75 ± 0·26(6)$^{a}$ | 1·85 ± 1·48(6)$^{p}$ |
| $NO_{3\ peat\ water}$ (mg $l^{-1}$) | 0·26 ± 0·10(25)$^{b}$ | 1·41 ± 0·93(4)$^{q}$ | 0·52 ± 0·29(25)$^{a}$ | 0·39 ± 0·51(4)$^{q}$ | 0·68 ± 0·48(23)$^{a}$ | 2·28 ± 3·94(3)$^{q}$ | 0·70 ± 0·00(6)$^{a}$ | 21·88 ± 0·83(6)$^{p}$ |
| $NH_{4\ peat\ water}$ (mg $l^{-1}$) | 0·31 ± 0·20(25) | 0·43 ± 0·07(4) | 0·57 ± 0·35(25) | 0·34 ± 0·24(4) | 0·60 ± 0·39(23) | 0·41 ± 0·13(3) | 0·84 ± 0·64(5) | 3·71 ± 5·16(5) |
| $PO_{4\ peat\ water}$ (mg $l^{-1}$) | 0·30 ± 1·09(25)$^{b}$ | 0·10 ± 0·06(3)$^{q}$ | 0·56 ± 0·43(25)$^{b}$ | 0·31 ± 0·26(3)$^{pq}$ | 6·00 ± 2·93(23)$^{a}$ | 7·09 ± 6·53(3)$^{p}$ | 0·25 ± 0·19(5)$^{b}$ | 0·37 ± 0·48(5)$^{pq}$ |
| Organic matter content peat (% of dry weight) | — | 88 ± 1(6) | — | 81 ± 2(6) | — | 80 ± 5(6) | — | 86 ± 1(6) |
| Water content peat (% of fresh weight) | — | 87 ± 2(6) | — | 83 ± 1(6) | — | 87 ± 1(6) | — | 85 ± 2(6) |
| $p_{lime\ peat}$ | — | 4·75(1) | — | 4·97(1) | — | 3·50(1) | — | 4·30(1) |
| $N_{tot\ peat}$ (% of dry weight) | — | 2·01 ± 0·39(6)$^{pq}$ | — | 1·84 ± 0·28(6)$^{q}$ | — | 2·74 ± 0·69(5)$^{p}$ | — | 2·91 ± 0·35(6)$^{p}$ |
| $P_{tot\ peat}$ (% of dry weight) | — | 0·08 ± 0·01(6)$^{q}$ | — | 0·08 ± 0·01(6)$^{q}$ | — | 0·49 ± 0·23(5)$^{p}$ | — | — |
| $K_{tot\ peat}$ (% of dry weight) | — | 0·09 ± 0·08(6) | — | 0·07 ± 0·05(6) | — | 0·04 ± 0·05(5) | — | — |
| Available $PO_4$–P (mg $PO_4$ $kg^{-1}$ dry weight) | — | 587(1) | — | 302(1) | — | 8890(1) | — | 1080(1) |
| Nutrient release (mg/$dm^3$/4 weeks): | | | | | | | | |
| N | — | 0·27 ± 0·25(3)$^{q}$ | — | 1·36 ± 1·08(3)$^{q}$ | — | 2·54 ± 0·78(3)$^{p}$ | — | 4·69 ± 3·09(3)$^{p}$ |
| P | — | 0·14 ± 0·15(3)$^{q}$ | — | 0·00 ± 0·07(3)$^{q}$ | — | 3·09 ± 2·41(3)$^{p}$ | — | 0·49 ± 0·63(3)$^{q}$ |
| K | — | 3·38 ± 3·52(3)$^{q}$ | — | 4·52 ± 3·36(3)$^{q}$ | — | 12·18 ± 6·60(3)$^{p}$ | — | 7·42 ± 5·13(3)$^{pq}$ |

—: not measured. Differences between fen types were tested separately for April and July (Tukey's Studentized range test). Significant differences at the $P<0·05$ level are indicated by different letters (a–d April; p–r July).

rich fen 2 and the moderate-rich fen water, whereas they remained near the surface in rich fen 1. Nevertheless, the water content of the peat was high at all sites in July. Redox potentials dropped only in the fens where water levels sunk.

All rich fens had a fairly constant circum-neutral pH. In spring pH and Ca-concentrations were lowest in the moderate-rich fen and highest in the floodplain, indicating the influence of rainwater and river water, respectively. Nitrate-concentrations were very high in the floodplain in July, when water levels were lowest. The moderate-rich fen had high P-concentrations in groundwater and in peat, both total contents and easily extractable contents.

*Nutrient release*

Nutrient release rates were higher in the moderate-rich fen and the floodplain-rich fen than in rich fens 1 and 2. P-release was very high in the moderate-rich fen (Table 4).

## DISCUSSION

Pałczynski & Stepa (1991) measured at Biebrza annual growth rates for mosses of 7·36 g dry wt $m^{-2}$ $year^{-1}$ in fens not flooded by the river. This is very low compared to the living standing crop of mosses as harvested by us in these fens (*c*. 50–200 g dry wt $m^{-2}$) which implies that most of the bryophyte material we harvested was produced in earlier years. The fact that we did not detect a significant growth response of mosses on nutrient addition after 3 months is thus probably an artefact of our method. For this reason only the results of the phanerogam-group will be discussed. There were also difficulties in comparing the experiments carried out in two different years. The floodplain-rich fen was fertilized in 1993, instead of 1992 as in the other sites. In 1992 the fertilized site of the floodplain had a water level of +27 and −52 cm relative to the surface in April and July, respectively (Table 4). In 1993 this was +25 and −10 respectively. Thus, summer water levels were higher in 1993. Furthermore, the differences in fertilization method, solutions and grains, respectively, may at first sight render a direct comparison difficult. However, as all nutrients had leached out of the grains in July, and because there was no visible water current in the floodplain-rich fen site when fertilized and because water levels dropped below the surface in the first half of May, we assume that the nutrients became available to the vegetation in the same doses as at the other sites.

Vascular plants were N-limited in the three non-flooded fen communities as shown by the positive growth response on N-fertilization. The fact that N-concentrations in the plant material did not significantly increase after N-fertilization is further evidence for this conclusion, as this suggests that the supplied N was invested in extra growth.

The phanerogam results compare well with the hypotheses of Wassen *et al.* (1995) on expected nutrient limitation of fens in the Biebrza valley. They based their hypotheses on two related variables measured in non-fertilized plant material. First, they stated that N-, P- and K-concentration values in the aboveground biomass below 14, 0·7 and 8 mg $g^{-1}$ dry weight respectively indicate a limitation by that nutrient (cf. De Wit *et al.* 1963). Their second variable was the P/N-quotient, defined by the quotient of the P-concentration and the N-concentration, with a value lower than 0·04 suggesting P-limitation, whereas a value higher than 0·08 was supposed to be indicative of N-limitation. However, when the values for the nutrient concentrations in the vascular plants of our control plots are compared with the values defined by de Wit *et al.* (1963), it could be concluded that only rich fen 1 is N- (and K-)limited and the floodplain-rich fen is N-limited, whereas in the fertilization experiment N-limitation was found for both rich fens and the moderately-rich fen, and no nutrient-limited growth was detected in the floodplain-rich fen. Also, if P/N-quotients are calculated it seems that the vascular plants of rich fens 1 and 2 are not clearly limited by nutrients, or they are colimited by N and P 0·069 and 0·074 resp. P/N-quotients of the vascular plants in the moderate-rich fen and the floodplain-rich fen indicate N-limitation 0·21 and 0·097 resp. As these results do not compare well with the results of our fertilization experiment, the critical nutrient concentration and the P/N-quotient should be regarded as rough indicators. We agree with Verhoeven *et al.* (1996b) that fertilization experiments have proved successful in determining the growth-limiting nutrient in mires, but with Pegtel *et al.* (1996) we are sceptical about the reliability of the P/N-quotient of the aboveground biomass as an index of the degree to which N or P has been limited (Verhoeven *et al.* 1996b; Koerselman & Meuleman 1996; Boeye *et al.* 1997).

Examples of fertilization experiments in floodplains were not found in the literature. The reason for the lack of nutrient limitation in the floodplain vegetation is probably that the seasonal river floods bring an excess of nutrients to the vegetation, which are captured by the benphyton algae in the shallow water layer. The algae die and are rapidly mineralized in summer (Okruszko 1991), as reflected in the high inorganic N-concentrations in our samples. N-release from peat was also high in the floodplain. Hooijer (1996) gives a review of ecohydrological studies showing that flood duration is a key factor for vegetation development in fairly undisturbed floodplains. In floodplains largely influenced by man this relationship is less clear (Girel 1994; Van den Brink *et al.* 1993; Large *et al.* 1994; Trémolières *et al.* 1994). We hypothesize that in the Biebrza floodplain flood duration and light conditions are more important factors in determining species composition of plant communities than nutrient availability.

Limitation by N is commonly found in a wide range of wet and moist ecosystems such as grassland, fen, marsh, tundra and dune slack (for reviews see Verhoeven *et al.* 1993, 1996b; Wassen *et al.* 1995). A co-limitation of N and P has been found for vegetation in subarctic Swedish lakes (Solander 1983) and Alaskan wetlands (Sanville 1988), while P was the limiting factor in long-mown ecosystems (Egloff 1983; Vermeer 1985; Verhoeven & Schmitz 1991). The importance of mowing for nutrient limitation has been shown by Koerselman *et al.* (1990) in a nutrient budget study in an area with atmospheric deposition of *c.* 50 kg N $ha^{-1}$ $year^{-1}$. They found that annual mowing leads to net exports for P and K, rather than N. This means that after a period of mowing P (or K) may become deficient. Aerts *et al.* (1992) showed that *Sphagnum* growth in bogs was N-limited in an area with low atmospheric N-deposition, but P-limited in a high N-deposition area, suggesting that changes in atmospheric nutrient deposition may cause a shift in nutrient limitation. Boyer & Wheeler (1989) found P-limitation in a spring-fed, calcareous low-productive rich fen in England. Compared with the other fen studies, they worked in an area with a very high Ca-content (in excess of 80 mg $l^{-1}$). In their fen P coprecipitated with calcite and was rendered unavailable for the vegetation (Boyer & Wheeler 1989). However, in less calcareous rich fens Fe and Al appear to play a more important role in reducing P availability (Wassen *et al.* 1995; De Mars *et al.* 1996; Boeye *et al.* 1997). Hence, there is little hard evidence for a causal relationship between (moderately) calcium- and base-rich water (as in the Biebrza fens) and low P-availability (Wassen *et al.* 1996). The very high P-concentrations in our moderate-rich fen (inorganic in water and total and extractable in peat) can neither be explained by the somewhat lower calcium concentrations and the slightly acidic conditions nor by the $Fe_{tot}$ concentrations, which are relatively high (averages of 1·79 to 4·1 mg $l^{-1}$; Wassen *et al.* 1990; De Mars *et al.* 1997). Although P-release from sediments is optimal in the pH-range between 5·5 and 6·0 (Richardson & Marshall 1986), the origin of the extremely high P-availability in the moderate-rich fen needs further research.

The fens studied at Biebrza have not been mown since World War II. Only rich fen 2 and the floodplain-rich fen are irregularly grazed by cattle and the floodplain is sometimes mown in extremely dry summers. The two other sites are grazed and browsed at low intensity by elk and roe-deer. Therefore a shift towards P- and/or K-limitation is not expected. We did not detect obvious differences in the total N-concentrations in the peat water or in the peat of the fens, except for the floodplain in summer which also had higher N-release rates. Supply of N from the atmosphere is low (*c.* 10 kg $ha^{-1}$ $year^{-1}$) in N.E. Poland. The N-input and mineralization may therefore simply be not sufficiently large in the non-flooded fens to counterbalance N-limitation. If input levels for N remain at the present level and as long as the fens are not drained or mown regularly, then N will continue to be the controlling factor for the non-flooded fen communities.

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