Journal of Vegetation Science 6: 5-16, 1995

Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems

Wassen, Martin J.[1*], **Olde Venterink, Harry G.M.**[2] & **de Swart, Evalyne O.A.M.**[3]

[1]*Department of Environmental Studies, Utrecht University, P.O. Box 80.115, 3508 TC Utrecht, The Netherlands;* [2]*National Institute for Public Health and Environmental Protection, P.O. Box 1, 3720 BA Bilthoven, The Netherlands;* [3]*IWACO, Consultants for Water and Environment, P.O. Box 8520, 3009 AM Rotterdam, The Netherlands;*
[*]*Corresponding author: Fax +31 30 540604; E-mail M.WASSEN@FRW.RUU.NL*

Abstract. The above-ground standing crop and nutrient concentrations in plant material were examined in 45 stands of mire vegetation in the Biebrza peatland, Poland. The stands included flood-plains, rich fens, transitional fens and bogs. The pattern in nutrient concentrations in the above-ground plant material resembled the pattern in nutrient concentrations in peatwater and peat which had been investigated in an earlier study. Concentrations of N were quite uniform along the gradient. P-concentrations were highest in the transitional fen. Critical nutrient concentrations were defined on the basis of a review of nutrient concentrations in plant material from peatlands in which a fertilization experiment had been carried out. Defined critical values for phanerogams were: 13-14 and 0.7 mg/g dry wt for N and P respectively. Concentrations lower than these values indicate deficiency. P/N ratios ≥ 0.07 indicate N-deficiency and P/N ratios ≤ 0.04 - 0.05 indicate P-deficiency. According to these values the Biebrza fens and bogs appear to be primarily deficient in N. The growth of the flood-plain vegetation does not appear to be restricted by nutrients.

Keywords: Biebrza; Bog; Fen; Flood-plain; P/N ratio; Peatland; Poland.

Nomenclature: Phanerogams: van der Meijden et al. (1983); Cryptogams: Margadant & During (1982); Syntaxa: Palczynski (1984).

Introduction

There has been much debate on whether nutrient concentrations in above-ground biomass reflect the nutrient availability of a site and whether this can be used to identify a particular nutrient that is in short supply. Vermeer & Berendse (1983) suggest that at the height of the growing season the nutrient concentration in the above-ground living biomass is a reliable indication of the total amount of nutrients available during the growing season. Other authors have found that there is considerable variability in nutrient concentration between, and even within, various mire types and that in many cases there is no relation or only a slight relation between the nutrient concentrations in the plant material and the nutrient concentrations in peatwater and peat (Tamm 1954; Malmer & Sjörs 1955; Malmer 1958; Goodman & Perkins 1968 a, b; Waughman 1980; Hayati & Proctor 1991; Beltman et al. 1992). Hayati & Proctor (1991) concluded that chemical analysis of plant material may be of only limited value as an indication of nutrient availability under natural conditions because there is a large intra- and inter-species variation in the nutrient concentration in plant tissue harvested in comparable habitats (Malmer 1958; Daniels 1975; Hayati & Proctor 1990, 1991). In other words, nutrient concentrations in plant material might be too dependent on the distribution of organs and tissues to be useful as generalized indicators of nutrient availability. For instance, the proportion of N-poor fibres will be very high in woody plants, grasses and cyperaceous plants, but low in most herbs.

However, it is common practice to define critical nutrient levels in *i.a.* some types of agricultural studies. De Wit et al. (1963) defined critical values for N, P and K-concentrations in above-ground plant material of agricultural grasslands in the Netherlands. These values were 14, 0.7 and 8 mg/g dry wt respectively. According to de Wit et al. concentrations lower than these values indicate nutrient-deficiency. Penning de Vries et al. (1980) and Penning de Vries & van Keulen (1982) suggested that the functional relation between N and P in plant cells makes the P/N ratio a useful parameter for determining whether N or P is in short supply, provided there is no other nutrient deficiency (for instance a shortage of K). In their fertilization experiments in Sahelian grasslands a ratio ≤ 0.04 indicates P-deficiency and one ≥ 0.15 indicates N-deficiency. Dividing de Wit's critical P-value by the critical N-value suggests a P/N ratio of 0.05, when both nutrients are in short supply. However, P/N ratios between 0.04 and 0.15 may just as well indicate neither N nor P-limitation. An attempt to analyse which nutrients were in short supply in Dutch fens using both the above-mentioned methods (N and P-content versus P/N ratio) showed that these criteria were not consistent (Wassen 1990).

Fertilization experiments are believed to reveal conclusive evidence about possible nutrient limitation. They are often used to determine which nutrients are deficient. A combination of fertilization experiments and the measurement of nutrient concentrations in plants may be useful for defining critical nutrient concentrations in plant material.

This study tries to discover which nutrients limit plant growth in various mire types in the Biebrza peatlands, Poland. Stands of flood-plain vegetation, rich fen, transitional fen and bog were analysed for nutrients in the living above-ground biomass (total phanerogams and total cryptogams) and in separate species. Critical N, P and K-concentrations and critical P/N ratios were derived from reports in the literature about the results of combined fertilization experiments with the measurement of nutrient concentrations in above-ground plant material. In order to define which nutrients limit plant growth at Biebrza, we compared these values with the concentrations measured in our study. The results will be discussed in relation to previous studies on nutrients in peatwater and peat (Wassen et al. 1990, 1992).

Study area and vegetation types

The valley of the river Biebrza which covers an area of ca. 1000 km^2 in northeastern Poland (22°30' - 23°60' E; 53°30'-53°75' N) contains many large undrained valley mires (Okruszko 1990; Succow & Jeschke 1986). The almost natural character of the Biebrza peatlands is reflected in a regular pattern of peat-forming plant communities which run along the length and width of the valley (Pałczynski 1984). The valley is bordered by morainic hills, the altitude of the valley ranges from ca. 130 to 100 m a.s.l., and the catchment area of ca. 7000 km^2 has a maximum altitude of 160 m (Byczkowski & Kicinski 1984). The mean annual precipitation is 583 mm, of which 244 mm falls in the summer. The mean annual temperature, 6.8 °C, is rather low and the growing season, ca. 200 days, is short for Polish conditions (Kossowska-Cezak 1984). Parts of the valley are mown or grazed by cattle, the rest is grazed and browsed by wildlife, particularly moose (*Alces alces*) and roe deer (*Capreolus capreolus*).

Vegetation composition and structure and hydrochemistry along three transverse transects, extending from the hills to the river, were studied in July 1987 (see Wassen et al. 1990, 1992). The locations were chosen on the basis of vegetation maps (Pałczynski 1984), in such a way that the main variation in vegetation types was covered in largely undisturbed parts of the valley.

The transect in the flood-plain had a mean pH of 7.5 and a mean Ca^{2+} concentration of 102 mg/l (Wassen et al. 1990). It includes several highly productive plant communities of the *Phragmition* (Pałczynski 1984). The *Glycerietum maximae* covers large areas in the flood-plain; it is characterized by *Glyceria maxima*, *Rorippa amphibia*, *Rumex hydrolapathum* and *Utricularia vulgaris*. Where flooding lasts for a shorter time and occurs less frequently, the predominating vegetation consists of tall-sedge communities – the *Caricetum acutae* and *Caricetum elatae* – and in the occasionally flooded belt, the *Calamagrostidetum strictae*, a low vegetation of herbs and grasses. The latter community is characterized by *Calamagrostis stricta*, *Iris pseudacorus*, *Lysimachia vulgaris*, *Utricularia intermedia* and *Veronica scutellata*. It has a pH of 7.0 and a Ca^{2+} concentration of 51 mg/l.

The transects in the non-flooded zones traverse rich fen and transitional fen. The rich fen, with a pH of 7.2, and a Ca^{2+} concentration of 56 mg/l, contains two subassociations of the *Caricetum limoso-diandrae* (A and B), which consist of species-rich, sparse sedge vegetation with a well-developed layer of hypnaceous mosses. One of the two subassociations (A) has a higher presence and abundance of *Carex diandra*, *C. lepidocarpa* and *C. panicea*, whereas the other (B) has a higher abundance of *C. appropinquata*, *Peucedanum palustre* and *Salix repens*; it differs from the former by the presence of *Lysimachia vulgaris*, *Molinia caerulea* and *Ranunculus lingua*.

The dwarf-shrub vegetation of the transitional fen, a *Betuletum humilis* stand with a pH of 6.7 and a Ca^{2+} concentration of 24 mg/l, harbours fewer calciphytes than the other communities. Many of the above-mentioned calciphilous species are absent or rare. They are replaced by e.g. *Andromeda polifolia*, *Betula humilis*, *Drosera rotundifolia* and *Oxycoccus palustris*. In the moss layer species dominating in the *Caricetum limoso-diandrae* – *Campylium stellatum*, *Calliergon giganteum* and *Drepanocladus revolvens*, are absent or rare. They are replaced by e.g. *Aulacomnium palustre*, *Camptothecium nitens*, *Marchantia polymorpha* and *Sphagnum* cf. *flexuosum* (the latter taxon being rare, however). Some of the characteristic species of the *Betuletum humilis* are relatively nutrient-demanding, such as *Calla palustris*, *Epilobium palustre*, *Lychnis flos-cuculi* and *Rumex acetosa* (Wassen et al. 1990, 1992).

Six bog sites were sampled on the Pleistocene hills bordering the valley. pH-values in the bogs ranged from 2.6 to 3.4 and the mean Ca^{2+} concentration was 15 mg/l. These values were determined in water squeezed out from *Sphagnum* cushions and peat, which was filtered using a 0.45 υm-filter (de Swart & Olde Venterink 1991). The bog vegetation belongs to the *Vaccinio uliginosi-Pinetum typicum* (Pałczynski 1984). Characteristic species are *Pinus sylvestris*, *Vaccinium uliginosum* and also *Andromeda polifolia*, *Eriophorum vaginatum*, *Ledum palustre* and *Oxycoccus palustris*. The moss layer is dominated by *Sphagnum* spp., but it contains also *Dicranum bonjeani*, *Polytrichum commune* and *P. formosum*.

Methods

Biomass, nutrient contents and nutrient concentrations

The six plant communities included in the analysis ranged from the highly productive vegetation in the flood-plain – *Glycerietum maximae* – via three types of low-productive rich fen – *Calamagrostidetum strictae* and the two subassociations A and B of the *Caricetum limoso-diandrae*, to a transitional fen with *Betuletum humilis* and a bog with *Vaccinio uliginoso-Pinetum typicum*. For each plant community the living above-ground biomass was harvested at representative sites at the height of the growing season, i.e. the second half of July 1990. Results for the A and B sub-association of *Caricetum limoso-diandrae* were treated separately.

At each site three plots of 0.25 m^2 were clipped down to the peat surface. Phanerogams and cryptogams were kept separate, while dead plant material was removed. The plant species chosen were either characteristic of a certain plant community, or occurred in a (wide) range of plant communities (Wassen et al. 1990). 20 to 30 sterile, fully grown healthy shoots of these species were harvested within a range of 10 m from the centre of each site. In the case of herbs and *Betula humilis* only fully expanded healthy leaves were collected. The vegetation and plant samples were dried for 24 h at 70 °C, weighed and ground.

A sample of 0.2 - 0.3 g was taken at random from the ground plant material and digested in 4.4 ml acid digestion fluid (350 ml H_2O_2, 420 ml H_2SO_4, 14 g LiO_2, 0.42 g Se; Allen 1989) for 45 min. at 200 °C and 90 min. at 340 °C. $H_2PO_4^-$ was determined with the Molybdenum-blue method and N (as NH_4-N) by the Indophenol-blue method using a Skalar auto-analyser. Extinction was measured at 880 and 660 nm respectively. The K-concentration was determined by flame emission spectroscopy.

Statistics

Significant differences were tested at the $P < 0.05$ level between the six plant communities for the above-ground biomass (g dry wt/m^2) and for the N, P and K-concentrations in total above-ground biomass (mg/g dry wt) and in separately harvested species respectively, using Tukey's Studentized Range test within the General Linear Models (GLM) procedure (Anon. 1985).

To get a rough indication of the annual above-ground nutrient storage (g/m^2) we calculated the product of the living above-ground phanerogam biomass (g dry wt/m^2) and the nutrient concentration in the living above-ground phanerogam biomass (mg/g dry wt), both of which had been measured in July. For an estimation of the annual accumulation of N, P and K in mosses, data of Pałczynski & Stepa (1991) on annual biomass production of bryophytes in the Biebrza fens were used (7.36 g dry wt/yr). These were multiplied by the average nutrient concentrations measured in bryophytes in our study. This 'annual nutrient-storage' parameter may reflect the trophic status of a site in a better way than nutrient concentrations.

Differences between the six communities were tested as described above.

Table 1. Mean above-ground living biomass (g dry wt/m^2) ± 1 S.D. of five plant communities of the Biebrza Valley (Poland) and two bog areas located outside the valley, in July 1990. Significant differences in biomass at the $P < 0.05$ level are indicated by different letters (Tukey's Studentized Range test). *Phanerogams n = 7.

	Valley					Bogs
	Glycerietum maximae	*Calamagrostidetum strictae*	*Caricetum limoso-diandrae* (A)	*Caricetum limoso-diandrae* (B)	*Betuletum humilis*	*Vaccinio uliginosi-Pinetum typicum*
n	6	6*	9	8	9	6
Phanerogams	983 ± 315 a	354 ± 121 b	183 ± 49 b	225 ± 47 b	345 ± 396 b	204 ± 59 b
Cryptogams	0 c	46 ± 54 bc	350 ± 204 a	226 ± 93 ab	314 ± 167 a	341 ± 145 a
Total	983 ± 316 a	406 ± 83 b	534 ± 198 b	451 ± 107 b	660 ± 453 ab	545 ± 158 ab

Results

Above-ground biomass

The living biomass of the *Glycerietum maximae* phanerogams is ca. 1 kg dry wt/m^2. This is ca. 3 times as much as the phanerogam biomass of the *Calamagrostidetum* and the *Betuletum* and ca. 5 × as much as that of the other communities (Table 1). Both *Caricetum* types (A and B), the *Betuletum* and the bogs have a fairly large standing crop of mosses, which is zero or little in the *Glycerietum* and the *Calamagrostidetum*. This reduces the difference in total above-ground living biomass between the *Glycerietum* and the other communities to about a factor two.

Annual above-ground storage of nutrients

The estimated annual storage of nutrients in the above-ground biomass is much higher in the *Glycerietum* than in the other communities (Table 2).

Nutrient concentrations in plant material

N-concentration in the above-ground living biomass is fairly equal in the various communities. The *Sphagnum* spp. of the bogs are an exception in that they have lower N-values than the *Hypnaceae* in the other communities (Table 3). P and K-concentrations differ more between the communities. P-concentrations are lowest in both mosses and phanerogams of the *Caricetum* types and the bogs. K-concentrations are also low in the *Caricetum* types and the bogs.

In most communities, except for the bogs, mosses have a higher N-concentration than phanerogams. P-concentrations do not differ much between mosses and phanerogams. K-concentrations in the mosses are about half the concentration in the phanerogams, except in the bogs where vascular plants and mosses have equal K-concentrations.

Concentrations in the separately harvested species occurring along the gradient in three or more fen types (Table 4) show a trend which is similar to that of the total phanerogam biomass. These species generally have equal N-concentrations, whereas P-concentrations are significantly lower in the *Caricetum* types in most species and highest in the *Glycerietum* and the *Betuletum*. K-concentrations are lowest in the *Caricetum*-B subassociation. *Menyanthes trifoliata* has higher nutrient concentrations than other species. The sedges have the lowest nutrient concentrations.

Characteristic species of the *Glycerietum* – *Glyceria maxima*, *Rumex hydrolapathum* – have high nutrient concentrations. Those of the *Caricetum* – *Carex diandra*, *C. lasiocarpa*, *C. lepidocarpa*, *C. panicea* and *Molinia caerulea* – have especially low P-concentrations. Species of the *Betuletum* have high P-concentrations; *Rumex acetosa* and *Lychnis flos-cuculi* also have high K-concentrations.

Only one species, *C. rostrata*, grows in both the fens and the bogs, so for this species it is possible to compare the nutrient concentrations. Its N-concentration is significantly higher in the bogs than in the *Caricetum* fen types. Its P-concentration in the bogs is significantly lower than in the *Betuletum* transitional fen but equals the concentrations measured in the other fen types. *Eriophorum vaginatum*, which is characteristic of the bog, has nutrient concentrations which do not deviate much from those of many sedges and grasses in the fens.

P/N ratios in plant material

Both phanerogams and cryptogams have significantly higher P/N ratios in the *Betuletum* and *Glycerietum* communities than in the other fen communities (Table 3). The values are lowest in the *Caricetum* types; but not significantly lower than in the *Calamagrostidetum*. The species present in most fen types which were analysed separately present the same picture as the total phanerogam living biomass of phanerogams, but in this case the difference from the *Calamagrostidetum* is significant for *Menyanthes trifoliata*, *Equisetum fluviatile*, *Carex lasiocarpa* and *Carex diandra*. P/N ratios exceeding 0.15 are encountered only in the *Betuletum humilis*.

Discussion

Above-ground biomass and estimated annual nutrient storage

Only the above-ground biomass was harvested. Nutrient concentrations in the below-ground biomass might differ from those of the above-ground parts (see Beltman et al. 1992). The ratio between above and below-ground biomass differs greatly between species and may also differ between the various vegetation types (Aerts et al. 1992a). Because there is a 'functional equilibrium' between roots and rhizomes on the one hand and shoots on the other hand (Veerkamp et al 1980; Brouwer 1983; Konings 1989; Lambers & Poorter 1992) species from the relatively nutrient-rich sites (such as those from the *Glycerietum maximae*) are expected to have lower below-ground/above-ground biomass ratios than species from nutrient-poor sites (such as those from the *Caricetum limoso-diandrae*). Therefore, total biomass production as shown in Table 1 might be underestimated for the latter type. Differences in the way that

Table 2. Estimated annual nutrient storage in the above-ground living biomass (g/m^2) ± 1 S.D. in five plant communities of the Biebrza Valley (Poland) and two bog areas located outside the valley. Annual nutrient storage was estimated by calculating the product of the living above-ground biomass (g dry wt/m^2) and the nutrient concentration in the living above-ground biomass (mg/g dry wt) both measured in July 1990. Above-ground living biomass of the cryptogams was divided by 3, assuming the cryptogam living biomass is the sum of the production of ca. 3 yr. Significant differences at the $P < 0.05$ level are indicated by different letters (Tukey's Studentized Range test).

	Valley					Bogs
	Glycerietum maximae	*Calamagrostidetum strictae*	*Caricetum limoso-diandrae* (A)	*Caricetum limoso-diandrae* (B)	*Betuletum humilis*	*Vaccinio uliginosi-Pinetum typicum*
n	6	7	9	8	9	6
N	15.0 ± 7.6 a	4.8 ± 1.1 b	2.9 ± 0.8 b	3.0 ± 0.7 b	4.8 ± 5.3 b	2.7 ± 0.9 b
P	1.71 ± 0.59 a	0.34 ± 0.1 b	0.14 ± 0.04 b	0.13 ± 0.03 b	0.75 ± 0.98 ab	0.20 ± 0.06 b
K	13.0 ± 4.3 a	4.4 ± 1.6 b	1.6 ± 0.4 b	1.8 ± 0.4 b	3.3 ± 3.2 b	1.6 ± 0.6 b

species adapt to oxygen deficiency may also cause a variation in this ratio. Furthermore, Wheeler & Shaw (1991) showed that turnover rates of *Glyceria maxima* leaves are high. This may have caused a larger underestimation of the annual above-ground biomass production of the *Glycerietum maximae* compared to the other vegetation types, since we only harvested once at the height of the growing season.

The annual storage of nutrients in the above-ground plant material is only estimated very roughly. The collected data do not allow for a more precise estimate. Nevertheless, the results show that nutrient storage in the flood-plain's *Glycerietum* is much higher than in the other communities. This points to a much higher nutrient availability in the flood-plain than in the fens (and bogs). A similar difference was found by Haslam (1965) between valley fens and headwater fens, respectively.

Nutrient concentrations in above-ground plant material

If we assume with Vermeer & Berendse (1983) that the nutrient concentration in the above-ground living biomass at the height of the growing season is a trustworthy indication of the total amount of nutrients available during the growing season (Vermeer & Berendse 1983) we can draw conclusions about the relative differences in nutrient availability in the various mire types. K is more readily available in the regularly flooded *Glycerietum maximae* and in the occasionally flooded *Calamagrostidetum strictae* than in the non-flooded fen communities and the bogs. This corresponds to the differences in the concentrations found in the peatwater (Wassen et al. 1990). P-availability is much lower in the groundwater-fed *Caricetum limoso-diandrae* and in the

Table 3. Mean nitrogen, phosphorus and potassium concentrations (mg/g dry wt) ± 1 S.D. and P/N ratios of phanerogams and cryptogams in five plant communities of the Biebrza Valley and two bog areas located outside the valley in July 1990. Significant differences at the $P < 0.05$ level are indicated by different letters (Tukey's Studentized Range test).

	Valley					Bogs
	Glycerietum maximae	*Calamagrostidetum strictae*	*Caricetum limoso-diandrae* (A)	*Caricetum limoso-diandrae* (B)	*Betuletum humilis*	*Vaccinio uliginosi-Pinetum typicum*
Phanerogams						
n	6	7	9	8	9	6
N	14.77 ± 3.02 a	13.78 ± 2.05 a	15.22 ± 0.98 a	12.63 ± 0.80 a	13.86 ± 1.88 a	12.83 ± 3.08 a
P	1.74 ± 0.22 a	0.98 ± 0.14 b	0.74 ± 0.07 b	0.57 ± 0.08 b	2.03 ± 0.70 a	0.99 ± 0.23 b
K	13.25 ± 1.54 a	12.49 ± 0.95 a	8.50 ± 0.78 bc	7.70 ± 0.82 c	10.12 ± 1.50 b	7.74 ± 2.18 bc
P/N	0.121 ± 0.021 a	0.071 ± 0.009 b	0.048 ± 0.004 b	0.045 ± 0.006 b	0.146 ± 0.040 b	0.081 ± 0.026ab
Cryptogams						
n	0	5	9	8	9	6
N		19.53 ± 3.26 a	17.15 ± 2.78 a	18.59 ± 1.26 a	16.55 ± 2.09 a	12.13 ± 1.38 b
P		1.53 ± 0.31 ab	0.99 ± 0.43 b	0.78 ± 0.11 b	1.98 ± 0.66 a	0.77 ± 0.36 b
K		7.64 ± 1.12 a	4.00 ± 1.08 b	3.35 ± 0.62 b	6.58 ± 1.99 a	6.55 ± 2.96 a
P/N		0.078 ± 0.006 b	0.058 ± 0.020 b	0.0.42 ± 0.004 b	0.119 ± 0.035 a	0.064 ± 0.031 b

Table 4. Mean nitrogen, phosphorus and potassium concentrations in July 1990 (mg/g dry wt) ± 1 S.D. and P/N ratios of sterile shoots (leaves from herbs and *Betula humilis*) in five plant communities in the Biebrza Valley (Poland) and two bog areas outside the valley. Significant differences in N, P and K-concentrations ($P < 0.05$) are indicated by different letters (Tukey's Studentized Range test). Numbers on the same line as the species name refer to the number of harvested sites (n). Significant differences are shown when $n \geq 3$ for more than one plant community.

	Valley					Bogs
	Glycerietum maximae	*Calamagrostidetum strictae*	*Caricetum limoso-diandrae* (A)	*Caricetum limoso-diandrae* (B)	*Betuletum humilis*	*Vaccinio uliginosi-Pinetum typicum*
Carex elata	3	4	5	4	1	0
N (mg/g)	13.95 ± 0.78 a	13.21 ± 1.75 a	15.29 ± 1.81 a	12.42 ± 1.44 a	18.19	
P (mg/g)	1.42 ± 0.47 a	0.87 ± 0.06 b	0.97 ± 0.19 ab	0.74 ± 0.07 b	1.63	
K (mg/g)	11.43 ± 2.90 a	10.41 ± 3.10 a	11.08 ± 1.61 a	7.35 ± 0.69 a	9.16	
P/N ratio	0.101 ± 0.029 a	0.066 ± 0.010 b	0.063 ± 0.008 b	0.060 ± 0.006 b	0.090	
Menyanthes trifoliata	1	7	5	3	3	0
N (mg/g)	31.02	29.87 ± 4.08 a	27.88 ± 1.26 a	25.11 ± 1.85 a	26.76 ± 1.61 a	
P (mg/g)	4.00	2.80 ± 0.55 a	2.14 ± 0.18 b	1.73 ± 0.12 b	3.34 ± 0.01 a	
K (mg/g)	24.24	19.99 ± 2.98 a	15.68 ± 2.01 b	8.36 ± 1.58 c	15.83 ± 1.80 ab	
P/N ratio	0.129	0.093 ± 0.010 b	0.077 ± 0.006 c	0.069 ± 0.004 c	0.125 ± 0.005 a	
Potentilla palustris	0	6	4	4	4	0
N (mg/g)		18.67 ± 1.85 a	19.96 ± 1.57 a	18.48 ± 2.03 ab	17.84 ± 3.15 a	
P (mg/g)		1.48 ± 0.12 b	1.43 ± 0.22 bc	0.97 ± 0.16 c	2.44 ± 0.39 a	
K (mg/g)		10.88 ± 1.13 b	12.64 ± 0.92 a	9.01 ± 0.73 c	13.37 ± 0.61 a	
P/N ratio		0.079 ± 0.007 b	0.072 ± 0.007 bc	0.052 ± 0.007 c	0.138 ± 0.027 a	
Equisetum fluviatile	0	6	5	4	4	0
N (mg/g)		15.72 ± 2.87 b	19.00 ± 1.40 ab	17.26 ± 2.03 ab	20.43 ± 1.53 a	
P (mg/g)		1.68 ± 0.41 b	1.56 ± 0.17 b	1.26 ± 0.16 b	2.66 ± 0.27 a	
K (mg/g)		15.54 ± 3.92 a	19.15 ± 2.81 a	12.83 ± 2.60 a	14.46 ± 3.88 a	
P/N ratio		0.106 ± 0.010 b	0.082 ± 0.004 c	0.073 ± 0.001 c	0.130 ± 0.013 a	
Carex rostrata	0	2	6	3	4	4
N (mg/g)		13.03 ± 0.08	12.51 ± 1.13 a	11.57 ± 1.06	14.09 ± 1.35 a	16.55 ± 2.75 a
P (mg/g)		1.01 ± 0.14	0.81 ± 0.14 b	0.74 ± 0.14 b	2.08 ± 0.44 a	1.09 ± 0.25 b
K (mg/g)		9.80 ± 0.74	8.80 ± 1.07 a	6.24 ± 1.03 a	9.78 ± 4.32 a	12.00 ± 3.94 a
P/N ratio		0.077 ± 0.010	0.065 ± 0.010 b	0.065 ± 0.017 b	0.148 ± 0.036 a	0.067 ± 0.016 b
Carex appropinquata	0	2	3	4	3	0
N (mg/g)		10.99 ± 0.17	12.60 ± 2.95 a	11.04 ± 0.62 a	12.14 ± 0.37 a	
P (mg/g)		0.79 ± 0.10	0.74 ± 0.18 ab	0.61 ± 0.11 b	1.95 ± 0.96 a	
K (mg/g)		10.68 ± 1.53	10.47 ± 1.59 a	9.58 ± 1.54 a	10.47 ± 0.37 a	
P/N ratio		0.072 ± 0.08	0.059 ± 0.003 ab	0.055 ± 0.011 b	0.163 ± 0.083 a	
Carex lasiocarpa	0	5	6	4	0	0
N (mg/g)		11.55 ± 1.12 a	11.49 ± 1.18 a	10.23 ± 0.83 a		
P (mg/g)		0.84 ± 0.17 a	0.58 ± 0.12 b	0.55 ± 0.13 b		
K (mg/g)		8.78 ± 2.03 a	6.31 ± 0.82 b	5.49 ± 1.52 b		
P/N ratio		0.073 ± 0.015 a	0.050 ± 0.008 b	0.054 ± 0.008 b		
Glyceria maxima	6	0	0	0	0	0
N (mg/g)	23.06 ± 5.99					
P (mg/g)	1.78 ± 0.42					
K (mg/g)	10.79 ± 3.16					
P/N ratio	0.079 ± 0.016					
Rumex hydrolapathum	2	3	0	0	0	0
N (mg/g)	26.33 ± 9.21	17.56 ± 3.15				
P (mg/g)	3.06 ± 1.70	1.79 ± 0.56				
K (mg/g)	29.33 ± 3.42	23.36 ± 7.95				
P/N ratio	0.112 ± 0.026	0.102 ± 0.024				
Lysimachia vulgaris	1	5	0	1	1	0
N (mg/g)	26.94	21.04 ± 1.44		15.48	21.07	
P (mg/g)	2.39	1.70 ± 0.13		1.65	2.42	
K (mg/g)	8.04	12.65 ± 1.05		14.28	7.77	
P/N ratio	0.089	0.081 ± 0.005		0.107	0.115	
Iris pseudacorus	0	7	0	0	0	0
N (mg/g)		11.58 ± 2.46				
P (mg/g)		1.17 ± 0.34				
K (mg/g)		19.41 ± 2.83				
P/N ratio		0.104 ± 0.035				

Table 4, cont.

	Valley					Bogs
	Glycerietum maximae	*Calamagrostidetum strictae*	*Caricetum limoso-diandrae* (A)	*Caricetum limoso-diandrae* (B)	*Betuletum humilis*	*Vaccinio uliginosi-Pinetum typicum*
Calamagrostis stricta	0	7	0	1	3	0
N (mg/g)		10.75 ± 1.30 b		8.99	12.85 ± 1.00 a	
P (mg/g)		0.92 ± 0.15 b		0.74	2.59 ± 0.96 a	
K (mg/g)		11.57 ± 0.98 a		8.22	10.40 ± 2.31 a	
P/N ratio		0.087 ± 0.018		0.082	0.202 ± 0.077 a	
Carex diandra	0	4	6	0	5	0
N (mg/g)		11.38 ± 0.40 a	12.98 ± 1.35 a		12.45 ± 0.85 a	
P (mg/g)		1.12 ± 0.16 ab	0.85 ± 0.18 b		1.83 ± 0.84 a	
K (mg/g)		11.39 ± 1.55 ab	8.30 ± 1.85 b		11.62 ± 2.84 a	
P/N ratio		0.098 ± 0.012 ab	0.066 ± 0.017 b		0.146 ± 0.064 a	
Carex panicea	0	0	6	0	0	0
N (mg/g)			13.21 ± 1.63			
P (mg/g)			0.70 ± 0.06			
K (mg/g)			10.83 ± 2.79			
P/N ratio			0.053 ± 0.007			
Carex lepidocarpa	0	0	6	0	0	0
N (mg/g)			12.79 ± 1.03			
P (mg/g)			0.65 ± 0.06			
K (mg/g)			10.01 ± 0.82			
P/N ratio			0.051 ± 0.008			
Molinia caerulea	0	0	0	3	1	0
N (mg/g)				11.89 ± 0.46	15.32	
P (mg/g)				0.69 ± 0.16	2.42	
K (mg/g)				9.22 ± 1.54	6.61	
P/N ratio				0.058 ± 0.012	0.078	
Betula humilis	0	0	1	0	3	0
N (mg/g)			18.27		20.79 ± 1.56	
P (mg/g)			1.09		3.26 ± 0.81	
K (mg/g)			6.55		9.73 ± 1.24	
P/N ratio			0.060		0.155 ± 0.027	
Rumex acetosa	0	0	0	0	3	0
N (mg/g)					19.17 ± 4.41	
P (mg/g)					3.54 ± 2.11	
K (mg/g)					30.34 ± 6.77	
P/N ratio					0.178 ± 0.074	
Lychnis flos-cuculi	0	0	0	0	3	0
N (mg/g)					16.64 ± 1.97	
P (mg/g)					4.51 ± 0.73	
K (mg/g)					44.85 ± 19.58	
P/N ratio					0.273 ± 0.046	
Eriophorum vaginatum	0	0	0	0		6
N (mg/g)						13.47 ± 1.11
P (mg/g)						0.89 ± 0.36
K (mg/g)						8.81 ± 0.70
P/N ratio						0.067 ± 0.030

rainwater-fed bogs than in the flood-plain fed by seasonal river floods or the *Betuletum humilis* predominantly fed by rainwater. No evidence was found to support the hypothesis that K-availability is a limiting factor for plant growth in the *Betuletum humilis*. This hypothesis was based on the low K-concentrations in the peatwater of this community (Wassen et al. 1990). K-concentration in the plant material of the *Betuletum* is not particularly low. On the contrary, it is extremely high in two of the three characteristic species of the *Betuletum*. A Canonical Correspondence Analysis (CCA) performed on earlier data (Wassen et al. 1990) showed that both N in peat and N in peatwater were unrelated to the mire's vegetation gradients (Wassen et al. 1990). The absence of a trend in N-concentration in the analysed plant material along the gradient (Table 3, 4) supports the CCA-results of this previous study.

We found that the nutrient concentration pattern in the above-ground plant material measured in this study largely resembles the observed pattern of nutrient concentration in peatwater and peat (Wassen et al. 1990). Both point to a large K and P-availability in the flood-

Table 5. Nutrient concentrations in plant material for sites in which fertilization experiments have been carried out by various authors (Col. 1), and the limiting nutrient(s) revealed by the experiments (Col. 4; parentheses indicate unclear results). *n* = number of observations. Nutrient concentrations (mg/g dry wt) and P/N ratio are from the unfertilized control plots.

Authors	Ecosystem type	Material	Limiting nutrient	*n*	K	N	P	P/N
Tamm (1954)	Bog	*Eriophorum vaginatum*	P	8	7.6	11.5	0.50	0.043
Loach (1968)	*Molinietum*	*Molinia caerulea*	P	6	11.4	12.2	0.57	0.046
	Wet heath		P	6	10.5	11.4	0.45	0.039
	Valley bog		P	6	5.9	9.6	0.32	0.033
Hayati & Proctor (1990)	Wet heath	*Molinia caerulea*	N, P	97	18.4	17.2	0.94	0.055
Hayati & Proctor (1991)	Wet heath	*Molinia caerulea*	N, P	10	18.1	12.9	1.15	0.089
	Wet heath		N, P	3	9.6	8.5	0.50	0.059
	Upland blanket bog		N, P, K	3	8.7	10.3	1.03	0.100
	Upland poor fen		(N), (P)	3	13.2	8.2	0.69	0.084
	Upland poor fen		(N), (P)	3	10.7	10.7	0.81	0.076
	Upland poor fen		(N), (P)	3	15.4	8.7	1.38	0.159
	Wet heath	*Carex panicea*	N, P	3	16.0	7.5	0.65	0.087
	Upland poor fen		(N, (P)	3	14.5	6.3	1.26	0.200
	Upland poor fen		(N), (P)	3	13.9	8.2	0.50	0.061
Verhoeven & Schmitz (1991)	*Caricion davallianae*-rich fen	Phanerogams	N	5	9.2	13.6	1.11	0.082
		Cryptogams	N	5	5.0	14.7	1.07	0.073
	Cirsio-Molinietum poor fen	Phanerogams	P	5	7.8	16.5	0.69	0.042
		Cryptogams	P	5	3.7	13.0	0.59	0.045
	Juncus-Sphagnum intermediate fen	Phanerogams	N	5	16.4	12.2	1.30	0.107
		Cryptogams	N	5	5.4	11.9	0.75	0.063
Vermeer (1986)	*Caricion davallianae*-rich fen	Total above-ground biomass	N	5	6.0	12.0	0.85	0.071
Boyer & Wheeler (1989)	Short vegetation in spring-fed rich fen	*Juncus subnodulosus*	P	15	16.1	11.0	0.5	0.045
			P	15	11.2	10.8	0.2	0.019
	Tall vegetation in spring-fed rich fen		?	15	17.9	13.1	0.9	0.069
				15	11.6	8.0	0.6	0.075

plain with *Glycerietum maximae*, a low P-availability in the groundwater-fed *Caricetum* types and a high P-availability in the predominantly rainwater-fed *Betuletum humilis*. The availability of N is quite uniform along the gradient, which agrees with the results of Waughman (1980), who showed that in southern Germany total nitrogen in both vegetation and peat was not related to the mire vegetation gradient.

These conclusions give only an indication of relative differences in nutrient availability along the gradient flood-plain → rich fen → transitional fen → bog. This does not necessarily imply that a certain nutrient having a low concentration in peat, peatwater and above-ground living biomass is indeed in short supply. The absence of differences in N-concentrations along the studied gradient for instance, can equally well imply that N is in short supply in all the fen types and the bogs as it can imply that it is not.

Defining critical nutrient concentrations in plant material

A review of nutrient concentrations in above-ground plant material from wet heaths and peatlands for which a fertilization experiment has been carried out (Table 5) shows that, with respect to mosses, our present knowledge is not sufficient to define critical nutrient levels in plant tissue. For phanerogams we may conclude that P is limiting if the P-concentration in the above-ground living plant material is lower than 0.7 mg/g dry wt and the P/N ratio does not exceed 0.04 - 0.05. In N-limited systems the N-concentration in the above-ground living biomass is lower than 13 - 14 mg/g dry wt and the P/N ratio exceeds 0.07. Dividing the critical P-value by the critical N-value gives a critical P/N ratio of ca. 0.05.

The results summarized above suggest that both critical values defined by de Wit et al. (1963), i.e. 14 and 0.8 mg/g dry wt for N and P respectively, are valid for mires. The P/N ratio that Penning de Vries et al. (1980)

defined as indicative of N-limitation (≥ 0.15) seems to be too high for mires. It should rather be 0.07. However, the P/N ratio indicative of P-limitation (≤ 0.04) seems accurate.

Furthermore it is obvious that although Tamm (1954), Loach (1968) and Boyer & Wheeler (1989) demonstrated P-deficiency, the N-concentrations mentioned by them are also below the critical level. Tamm (1954) wondered whether the quantity of nitrogen applied (50 kg/ha) was too low. This may well be the case since normally N-doses of 200 kg/ha are applied (Vermeer 1986; Verhoeven & Schmitz 1991). Loach (1968) added quantities roughly corresponding to agricultural applications. Boyer & Wheeler (1989) carried out a P-fertilization experiment only, which may imply that *Juncus subnodulosus* was not only P-limited but also N-limited (co-limitation) in calcareous spring-fed fens. The critical value for P defined above (0.7 mg/g dry wt) is in line with a value indicative of P-deficiency as defined by Loach (1968; 60 mg/100 g dry wt).

Comparing the Biebrza nutrient concentration data with defined critical values

A comparison of the above-mentioned critical values with our results shows that the two methods for determining nutrient-deficiency (N and P-concentrations versus P/N ratio) lead to different conclusions. On the basis of N and P-concentrations in the above-ground phanerogam biomass one can conclude that the *Caricetum*-B subtype is N and P-deficient and that the bogs are N-deficient. P/N ratios suggest that the *Caricetum*-B subtype is P-limited and the *Glycerietum*, *Calamagrostidetum*, *Betuletum* and bogs are N-limited (Table 3).

According to the N-concentration in the leaves of separately harvested species, most species are N-limited in one or more fen types (Table 4). Only *Carex appropinquata*, *C. lasiocarpa*, *C. panicea*, *C. lepidocarpa* and *Molinia caerulea* are N and P-limited in the *Caricetum limoso-diandrae*.

In 10 out of 17 cases of separately clipped species which are, according to its N and P-concentration, N-limited only, P/N ratios also indicate N-limitation. In the other six cases P-concentrations are just above the critical P-value, which yields a value for the P/N ratio between 0.04 - 0.05 and 0.07. P/N ratios further indicate N-limitation for 23 out of 29 cases which were neither N nor P-limited according to the N and P-concentrations. These are all cases where the P-concentration is ca. 2 × the critical level of 0.7. P/N ratios seem inadequate for defining nutrient deficiency in cases where the concentration of a nutrient is well above the critical value.

Remarkably, the nutrient concentrations in the total biomass are lower than the concentrations in the leaves or shoots of separately harvested characteristic species (Tables 3, 4). The lower concentrations in the total biomass might be due to dilution in flowering stems, which are known to have low nutrient concentrations (Aerts 1989).

The Biebrza fens and bogs appear to be primarily N-limited. The highly productive flood-plain vegetation, judged by critical values in above-ground biomass, does not seem to be restricted by nutrient availability. The same holds for some common fen species which are abundant throughout the entire fen area. Examples are *Menyanthes trifoliata*, *Potentilla palustris* and *Equisetum fluviatile*. Some characteristic species of the *Caricetum limoso-diandrae* appear to be limited in growth by both N and P but only in this specific fen type (*Carex appropinquata*, *C. lasiocarpa*, *C. panicea*, *C. lepidocarpa*, *Molinea caerulea*) for which P-availability was shown to be lower than in the other fen types (Wassen et al. 1990).

A conceptual model for nutrient availability in the Biebrza fens and bogs

Fertilization experiments by Vermeer (1986) and Verhoeven & Schmitz (1991) in low-productivity subneutral rich fens, fairly productive subneutral intermediate fens and low productivity acidic poor fens in the Netherlands showed that growth of above-ground biomass was N-limited in the rich fen and the intermediate fen and P-limited in the poor fen. The poor fen investigated by Verhoeven & Schmitz (1991) was in a later phase of succession than the rich fen; it had been mown annually for over 60 yr, whereas the rich fen had been mown only for 30 yr. Koerselman et al. (1990) showed that mowing results in a net removal of P and K in these fens and in a small annual net storage of N. The area has a high atmospheric N-input (ca. 40 kg ha^{-1} yr^{-1}; Koerselman 1989) which is ca. 10 × the background values (Asman & Janssen 1987). Aerts et al. (1992b) showed with their fertilization experiments in *Sphagnum*-dominated bogs in Sweden that *Sphagnum* productivity was N-limited in an area with low atmospheric N-deposition but P-limited in a high N-deposition area.

The atmospheric N-deposition in the Biebrza area is relatively low by European standards (5 - 10 kg ha^{-1} yr^{-1}; pers. comm. W. Bleuten). Most of the sites studied here had not been mown or grazed since World War II or had been mown or grazed only occasionally (pers. comm. local farmers). Combination of this information with our results (this study and Wassen et al. 1990, 1992) leads us to develop a conceptual model for nutrient-availability in the Biebrza fens and bogs.

Due to the low atmospheric N-deposition the Biebrza fens and bogs are N-limited. In the rich fens which are fed by calcareous groundwater, P-availability is restricted too. The Biebrza transitional fen recently evolved from rich fen (less than 100 yr ago; Wassen & Joosten mscr.). The infiltration of rainwater into the transitional fen peat led to leaching of Ca and consequently to mobilization of the calcium-phosphate pool (Wassen et al. 1990). This P-pool is not exported by annual harvesting. As a consequence P-availability is, and will remain, high in the transitional fen. The bogs which have been ombrotrophic for a long time do not have such a large P-pool as the transitional fens, since the atmosphere supplies only low amounts of P.

It is uncertain how long atmospheric N-deposition and input of N by groundwater flow will remain low in the Biebrza area; agriculture has intensified in the last few years. Increase in the N-input might lead to a shift from N to P-limitation in the rich fens. Boyer & Wheeler (1989) stated that discharge of groundwater with high NO_3-loading in the spring-fed calcareous P-limited fens they studied, need not be associated with an increase in vegetation productivity or loss of floristic quality. P-co-precipitation with calcite would provide a natural mechanism for the maintenance of low-productivity spring-fen vegetation and may largely account for the survival of examples of this fen type in close proximity to high-intensity arable farming (Wheeler & Shaw 1990). In our transitional fen the P-co-precipitation mechanism suggested by Boyer & Wheeler (1989) obviously does not work because the fens are less calcareous. Increase in the atmospheric N-supply in the transitional fen will inevitably lead to a larger biomass production and a change in species composition unless regular harvesting of biomass is practised again. This has been shown for sub-neutral fens in the Vecht river-plain which have been mown for decades (Koerselman et al. 1990).

Waughman (1980) suggests that plants growing on acidic mires may encounter problems of phosphorus uptake rather than phosphorus supply. However, in our bogs and especially in our transitional fen there are no indications of nutrient uptake problems. The presence of typical nutrient-demanding species like *Poa pratensis*, *Lychnis flos-cuculi*, *Rumex acetosa*, and *Epilobium palustre* in our transitional fen is a further illustration of the relatively nutrient-rich conditions (Wassen et al 1990). pH-values in our transitional fen are only slightly acid (hummocks 4.5 - 5.5; hollows 5.8 - 6.3) but the bog has pH-values < 3.5 (de Swart & Olde Venterink 1991). Nevertheless, nutrient concentrations in the bog plant material are not lower than in the rich fen plant material. P-concentrations in the phanerogams and K-concentrations in the mosses are even higher.

The fact that the Biebrza transitional fen evolved recently from a rich fen by succession combined with the fact that it is only slightly acidified makes it in principle not comparable to the acidic and rainwater-fed wet heaths, blanket bogs and bogs studied by Tamm (1954), Loach (1968), Goodman & Perkins (1968 a, b) and Hayati & Proctor (1990, 1991). A comparison of nutrient concentrations in plant material or a comparison of the results of fertilization experiments only makes sense if attention is paid to vegetation succession. Water sources and consequently hydrochemistry and nutrient availability of the investigated sites strongly depend on the successional phase, especially in fens (see Gorham et al. 1987; Giller & Wheeler 1988; Succow 1988; Glaser et al. 1990; van Diggelen et al. 1991; Wassen & Barendregt 1992).

Acknowledgements. We thank Dr. J.T. de Smidt and three referees for their suggestions for improving the manuscript. We thank Sheila MacNab for correcting the English.

References

Anon. 1985. *User's guide: statistics*, 5th ed. SAS Institute Inc., Cary, NC.

Aerts, R. 1989. Above-ground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. *Oikos* 56: 31-38.

Aerts, R., de Caluwe, H. & Konings, H. 1992a. Seasonal allocation of biomass and nitrogen in four *Carex* species from mesotrophic and eutrophic fens as affected by nitrogen supply. *J. Ecol.* 80: 653-664.

Aerts, R., Wallén, B. & Malmer, N. 1992b. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *J. Ecol.* 80: 131-140.

Allen, S.E. 1989. *Chemical analysis of ecological materials.* 2nd ed. Blackwell, Oxford.

Asman, W.A.H. & Janssen, A.J. 1987. A long-range transport model for ammonia and ammonium for Europe. *Atm. Environ.* 21: 2099-2119.

Beltman, B., Kooijman, A.M., Ellers, J. & Oosterbeek B.J. 1992. Nutrient availability and plant species composition of rich fens in the dune complex at Dooaghtry, Co. Mayo, Ireland. In: Carter, R.W.G., Curtis, T.F.G. & Sheehy-Skeffington, M.J. (eds.) *Coastal Dunes*, pp. 283-296. Balkema, Rotterdam.

Boyer, M.L.H. & Wheeler, B.D. 1989. Vegetation patterns in spring-fed calcareous fens: Calcite precipitation and constraints on fertility. *J. Ecol.* 77: 597-609.

Brouwer, R. 1983. Functional equilibrium: sense or nonsense. *Neth. J. Agric. Sci.* 31: 335-348.

Byczkowski, A. & Kicinski, T. 1984. Surface waters in the Biebrza drainage basin. *Pol. Ecol. Stud.* 10: 271-299.

Daniels, R.E. 1975. Observations on the performance of *Narthecium ossifragum* (L.) Huds. and *Phragmites communis* Trin. *J. Ecol.* 63: 965-977.

de Swart, E. & Olde Venterink, H. 1991. *Above-ground biomass production and nutrient concentrations in plant* *material of peatlands in and around the Biebrza Valley in relation to hydrochemical conditions in the root-zone.* Report 7/91, Department of Environmental Studies, Utrecht University, Utrecht (in Dutch with English summary).

de Wit, C.T., Dijkshoorn, W. & Noggle, J.G. 1963. *Ionic balance and growth of plants.* Verslagen van Landbouwkundige Onderzoeken, 69.15. Pudoc, Wageningen.

Giller, K.E. & Wheeler, B.D. 1988. Acidification and succession in a flood-plain mire in the Norfolk Broadland, U.K. *J. Ecol.* 76: 849-866.

Glaser, P.H., Janssens, J.A. & Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, Northern Minnesota. *J. Ecol. 78*: 1021-1048.

Goodman, G.T. & Perkins, D.F. 1968a. The role of mineral nutrients in *Eriophorum* communities. III. Growth response to added inorganic elements in two *Eriophorum vaginatum* communities. *J. Ecol.* 56: 667-683.

Goodman, G.T. & Perkins, D.F. 1968b. The role of mineral nutrients in *Eriophorum* communities. IV. Potassium supply as a limiting factor in an *Eriophorum vaginatum* community. *J. Ecol.* 56: 685-696.

Gorham, E., Janssens, J.A., Wheeler, G.A. & Glaser, P.H. 1987. The natural and anthropogenic acidification of peatlands. In: Hutchinson, T.C. & Meema, K.M. (eds.) *Effects of atmospheric pollutants on forests, wetlands and agricultural ecosystems*, pp. 493-512. NATO ASI Series Vol. 16, Springer-Verlag, Berlin.

Hayati, A.A. & Proctor, M.C.F. 1990. Plant distribution in relation to mineral nutrient availability and uptake on a wet-heath site in south-west England. *J. Ecol.* 78: 134-151.

Hayati, A.A. & Proctor, M.C.F. 1991. Limiting nutrients in acid-mire vegetation: peat and plant analysis and experiments on plant responses to added nutrients. *J. Ecol.* 79: 75-95.

Koerselman, W. 1989. *Hydrology and nutrient budgets of fens in an agricultural landscape.* Ph.D. Thesis, Utrecht University, Utrecht.

Koerselman, W., Bakker, S.A. & Blom, A. 1990. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *J. Ecol.* 78: 428-442.

Konings, H. 1989. Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. In: Lambers, H., Cambridge, M.L., Konings, H. & Pons, T.L. (eds.) *Causes and consequences of variation in growth rate and productivity of higher plants*, pp. 101-123. SPB Academic Publishing, Den Haag.

Kossowska-Cezak, U. 1984. Climate of the Biebrza ice-marginal valley. *Pol. Ecol. Stud.* 10: 253-270.

Lambers, H. & Poorter, H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23: 187-261.

Loach, K. 1968. Relations between soil nutrients and vegetation in wet-heaths. II. Nutrient uptake by the major species in the field and in controlled conditions. *J. Ecol.* 56: 117-127.

Malmer, N. 1958. Notes on the relation between chemical composition of mire plants and peat. *Bot. Not.* 111: 274-288.

Malmer, N. & Sjörs, H. 1955. Some determinations of elementary constituents in mire plants and peat. *Bot. Not.* 108: 46-80.

Margadant, W.D. & During, H.J. 1982. *Beknopte flora van de Nederlandse blad- en levermossen.* Thieme, Zutphen.

Okruszko, H. 1990. *Wetlands of the Biebrza Valley, their value and future management.* Polish Academy of Sciences, Warszawa.

Pałczynski, A. 1984. Natural differentiation of plant communities in relation to hydrological conditions of the Biebrza Valley. *Pol. Ecol. Stud.* 10: 347-385.

Pałczynski, A. & Stepa, T. 1991. Biomass production in main plant associations of the Biebrza Valley with respect to soil conditions. *Pol. Ecol. Stud.* 17: 53-62.

Penning de Vries, F.W.T. & van Keulen, H. 1982. La production actuelle et l'action de l'azote et de phosphore. In: Penning de Vries, F.W.T. & Djitèye, M.A. (eds.) *La productivité des pâurages sahéliens. Une étude des sols, des végétations et de l'exploitation de cette resource naturelle*, pp. 196-226. Pudoc, Wageningen.

Penning de Vries, F.W.T., Krul, J.M. & van Keulen, H. 1980. Productivity of sahelien rangelands in relation to the availability of nitrogen and phosphorus from the soil. In: Rosswall, T. (ed.) *Nitrogen cycling in West African Ecosystems*, pp. 95-113. Royal Swedish Academy of Sciences, Stockholm.

Succow, M. 1988. *Landschaftsökologische Moorkunde.* Gebr. Borntraeger, Berlin.

Succow, M. & Jeschke, L. 1986. *Moore in der Landschaft.* Urania Verlag, Leipzig.

Tamm, C.O. 1954. Some observations on the nutrient turnover in a bog community dominated by *Eriophorum vaginatum* L. *Oikos* 5: 189-194.

van der Meijden, R., Weeda, E.J., Adema, F.A.C.B. & de Joncheere, G.J. 1983. *Flora van Nederland.* Wolters-Noordhoff, Groningen.

van Diggelen, R., Grootjans, A.P., Kemmers, R.H., Kooijman, A.M., Succow, M., de Vries N.P.J. & van Wirdum, G. 1991. Hydro-ecological analysis of the fen system Lieper Posse, eastern Germany. *J. Veg. Sci.* 2: 465-476.

Veerkamp, M.T., Corré, W.J., Atwell, B.J. & Kuiper, P.J.C. 1980. Growth rate and phosphate utilization of some *Carex* species from a range of oligotrophic to eutrophic swamp habitats. *Physiol. Plant.* 50: 237-240.

Verhoeven, J.T.A. & Schmitz, M.B. 1991. Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochemistry* 12: 135-148.

Vermeer, J.G. 1986. The effect of nutrients on shoot biomass and species composition of wetland and hayfield communities. *Oecol. Plant.* 7: 31-41.

Vermeer, J.G. & Berendse, F. 1983. The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. *Vegetatio* 53: 121-126.

Wassen, M.J. 1990. *Water flow as a major landscape ecological factor in fen development.* Ph.D. Thesis, Utrecht University, Utrecht.

Wassen, M.J. & Barendregt, A. 1992. Topographic position and water chemistry of fens in a Dutch river plain. *J. Veg. Sci.* 3: 447-456.

Wassen, M.J., Barendregt, A., Pałczynski, A., de Smidt, J.T. and 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, M.J., Barendregt, A., Pałczynski, A., de Smidt, J.T. & de Mars, H. 1992. Hydro-ecological analysis of the Biebrza mire (Poland). *Wetlands Ecol. Manage.* 2: 119-134.

Waughman, G.J. 1980. Chemical aspects of the ecology of some South German peatlands. *J. Ecol.* 68: 1025-1046.

Wheeler, B.D. & Shaw, S.C. 1990. Dereliction and eutrophication in calcareous seepage fens. In: Hiller, S.H., Walton, D.W.H. & Wells, D. (eds.) *Calcareous Grasslands - Ecology and Management*, pp. 154-160. Bluntisham Books, Huntingdon.

Wheeler, B.D. & Shaw, S.C. 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.

Received 28 December 1993;
Revision received 25 April 1994;
Accepted 1 June 1994.