Biogeochemistry **12**: 135–148, 1991

Control of plant growth by nitrogen and phosphorus in mesotrophic fens

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Accepted 2 January 1991

Key words: fens, management, nitrogen, phosphorus, productivity, vegetation, wetlands

Abstract. A fertilization experiment was carried out in 3 mesotrophic fens to investigate whether plant growth in these systems is controlled by the availability of N, P or K. The fens are located in an area with high N inputs from precipitation. They are annually mown in the summer to prevent succession to woodland. Above-ground plant biomass increased significantly upon N fertilization in the two 'mid'-succession fens studied. In the 'late'-succession fen that had been mown for at least 60 years, however, plant biomass increased significantly upon P fertilization. The mowing regime depletes the P pool in the soil, while it keeps N inputs and outputs in balance. A long-term shift occurs from limitation of plant production by N toward limitation by P. Hence, mowing is a suitable management tool to conserve the mesothrophic character of the fens.

Introduction

In many upland and wetland ecosystems, plant growth is controlled by the availability of nutrients, in particular nitrogen, phosphorus and potassium (Chapin 1980; Shaver & Chapin 1980). Which of the major nutrients actually limits primary productivity depends on the chemical composition of the parent soil material, on the turn-over rate of the various nutrients and on the balances between their inputs and outputs (see Gorham et al. 1979). Ecosystems located in areas with intensive agriculture (particularly those with animal husbandry) are being gradually enriched with nitrogen due to increased atmospheric deposition and discharge of eutrophied ground and surface water (De Molenaar 1980). In The Netherlands, an extremely high atmospheric N deposition (about 10 times background values, Asman & Janssen 1987) has resulted in a rise in productivity and shifts in the dominance of species in heathlands (Berendse 1990), chalk grasslands (Bobbink et al. 1988) and wetlands (Vermeer & Berendse 1983).

Studies of nutrient dynamics of small mesotrophic fens in the Netherlands have revealed that fens in groundwater discharge areas have a total nitrogen input 4 times higher than under pristine conditions, whereas phosphorus inputs remain essentially unaffected (Koerselman et al. 1990a). Further, it was shown that the annual harvesting regime commonly applied in these fens results in a small annual net storage of N, and a net removal of P and K in the ecosystem. The fens studied are inhabited by different types of plant communities that characterize different successional stages and hydrological conditions: two vegetation types characterize a 'mid' and a 'late' successional stage in groundwater discharge areas, and a third type occurs in fens in groundwater recharge areas (Vermeer & Verhoeven 1987; Verhoeven et al. 1988).

This paper deals with fertilization experiments with N, P and K in fens of the three types mentioned. The study addresses two questions, one, is nitrogen still a growth-limiting factor at the present high input levels, and two, is the control of plant growth by N, P and/or K different in the three fen types and if so, can the differences be explained by factors related to hydrology, succession or management.

Study sites

The study has been carried out in the eastern 'Vechtplassen' area, The Netherlands. Here, complexes of fens have developed in narrow rectilinear ponds created by peat dredging in the 18th and the 19th century. The fens are located in an area of intensive livestock raising and receive large inputs of nutrients via the atmosphere and via groundwater (Verhoeven et al. 1983; Koerselman et al. 1988, 1990a). A further description of the study area and its hydrology is given by Verhoeven et al. (1983, 1988) and Beltman (1987). Many of the fens are annually mown, traditionally for thatch reed and hay, now mainly for the purpose of conservation.

The fertilization experiment was conducted in three fens differing in vegetation, successional stage and hydrology. They are representative examples of the three fen types distinguished in an earlier study (Verhoeven et al. 1988) and they are indicated as fen 1, 2 and 3, corresponding with the numbering of the types. Fen 1 and 2 were located in groundwater discharge areas (i.e. Westbroek Polder and Het Hol Kortenhoef, respectively) and received inputs of groundwater rich in calcium and bicarbonate (Beltman 1987; Beltman & Verhoeven 1988; Verhoeven et al. 1988).

Fen 1 was in a 'mid'-successional stage: the pond in which it developed had been dredged after 1890 A.D. and had become overgrown with a floating mat in the 1940's. A regime of annual mowing in the summer started in the late 1960's. Fen 2 was much older: the pond in which it developed had been dredged prior to 1810 A.D. and had become overgrown around 1900 A.D. A regime of annual mowing in the summer started in the 1920's. This fen is considered to be in a 'late'-successional stage (Verhoeven et al. 1988; Segal 1966).

Fen 3 was located in the Molenpolder, an area of groundwater recharge which is supplied with polluted river water rich in nitrates and phosphates during dry spells in summer. It is similar to fen 1 in history with respect to dredging and mowing ('mid'-successional stage).

Table 1 gives information on the species composition of the fens. Fen 1 is dominated by *Carex rostrata, C. diandra* and *Potentilla palustris*, and the moderately developed moss layer mainly contains *Calliergon cordifolium* and *Calliergonella cuspidata*. Fen 2 is dominated by *Carex lasiocarpa, Molinia caerulea, Myrica gale* and *Erica tetralix*, whereas the moss layer is dominated by *Sphagnum fallax*. Fen 3 shows dominance of *Phragmites australis* and *Juncus subnodulosus*, and the thick moss layer is dominated by *Sphagnum* and *Polytrichum* species.

Methods

Five replicate sets of treatment plots were selected randomly in each of the fens. Each set contained five 50x50 cm plots for fertilization with N, P, K, all three of these elements and a control treatment, respectively. The spatial arrangements of treatment plots were randomized within each replicate set. Fertilization treatments consisted of 4 weekly applications of 1000 ml of fertilizing solution in April, 1987. The fertilizing solutions of NH_4NO_3 (N treatment), $NaHPO_4$ (P treatment), KCl (K treatment), and the three previous substances combined (NPK treatment) were brought to the field in concentrated form and were 10 times diluted with water from the ditches neighbouring the fens (the ditch water was tested and contained negligible quantities of N, P and K at the time). The control treatment received ditch water only. The quantities applied amounted to 200 kgN/ha, 50 kgP/ha and 160 kgK/ha, respectively.

Above-ground biomass of the plots was determined in August by clipping the phanerogams to ground level and removing living bryophyte material. Samples were sorted, dried (70 °C 48 h) and weighed. Total N, P and K content were determined by acid digestion of ground plant material with a mixture of sulphuric acid and salicylic acid. N and P contents of

Table 1. Dominant species in the fens studied. All species contributing more than 5% to the total above-ground biomass are listed.

Fen number	1	2	3
Carex rostrata	x		
Carex diandra	x		
Equisetum fluviatile	x		
Equisetum palustre	x		
Caltha palustris	x		
Lychnis flos-cuculi	x		
Calliergon cordifolium	x		
Calliergonella cuspidata	x		
Calamagrostis canescens	x		x
Potentilla palustris	x		x
Carex curta	x		x
Molinia caerulea		x	
Carex lasiocarpa		x	
Myrica gale		x	
Eriophorum angustifolium		x	
Carex echinata		x	
Drosera rotundifolia		x	
Carex panicea		x	
Cladium mariscus		x	
Scorpidium scorpioides		x	
Sphagnum fallax		x	
Juncus subnodulosus		x	x
Phragmites australis		x	x
Carex disticha		x	x
Sphagnum squarrosum			x
Sphagnum fimbriatum			x
Aulacomnium palustre			x
Lycopus europaeus			x
Thelypteris palustris			x
Carex acutiformis			x
Cirsium palustre			x
Alnus glutinosa seedlings			x
Holcus lanatus			x

digested samples were determined colorimetrically, the K content by flame emission spectroscopy.

The data for each fen were analyzed with ANOVA's (GLM procedure, SAS 1985). Statistical significance of differences among treatments was tested with the Tukey-Kramer test (Sokal & Rohlf 1981).

Results

Above-ground biomass

The N and the NPK treatments resulted in significant increases in stand biomass in both 'mid'-succession fens (Fig. 1). In fen 1 the effects were significant both for total biomass and for vascular plant biomass, whereas

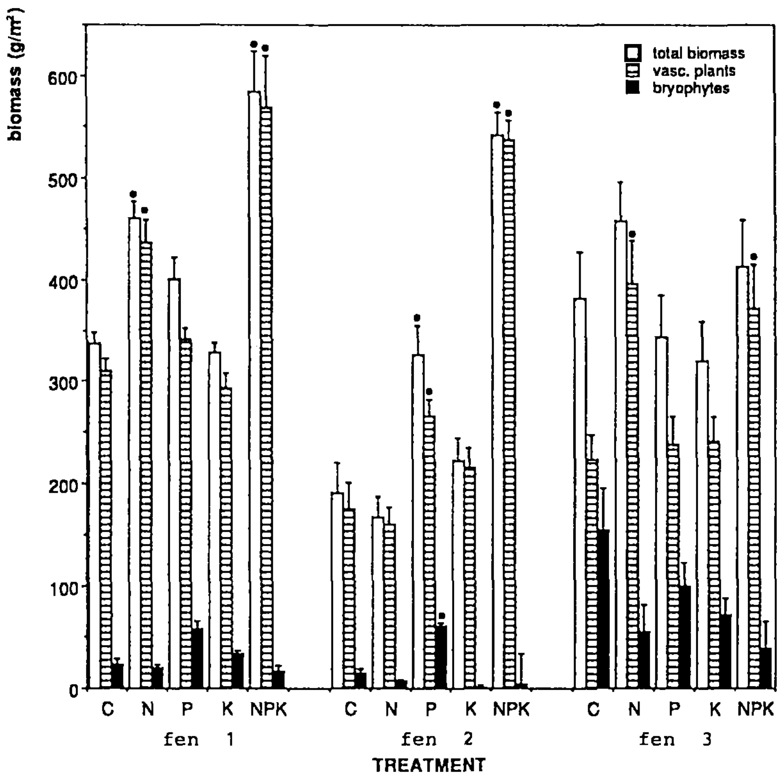

Fig. 1. Above-ground biomass (mean values with SE) of vascular plants and mosses in the treated plots in the three fens studied.

Fen 1 — 'Mid'-successional fen with groundwater discharge.
Fen 2 — 'Late'-successional fen with groundwater discharge.
Fen 3 — 'Mid'-successional fen with surface water inflow.
C — Control treatment
N — fertilized with N
P — fertilized with P
K — fertilized with K
NPK — fertilized with N, P and K

• significantly higher biomass than control ($p < 0.05$)

in fen 3 the effects were significant only for vascular plant biomass. In fen 2, biomass was significantly higher in the P and the NPK treatments. The difference with the control was significant for total above-ground biomass, vascular plant biomass as well as moss biomass in the P treatment, whereas there was no significant effect on moss biomass in the NPK treatment.

Total N, P and K in above-ground biomass

The amounts of N contained in the above-ground biomass (Fig. 2) were significantly higher than the control in the N and NPK treatments in the 'mid'-succession fens 1 and 3, particularly in the vascular plant material. In the 'late'-succession fen 2, there was more above-ground N in the P treatment and in the NPK treatment, whereas the N treatment did not result in a difference from the control.

All additions of P (P and NPK treatments) resulted in significant effects

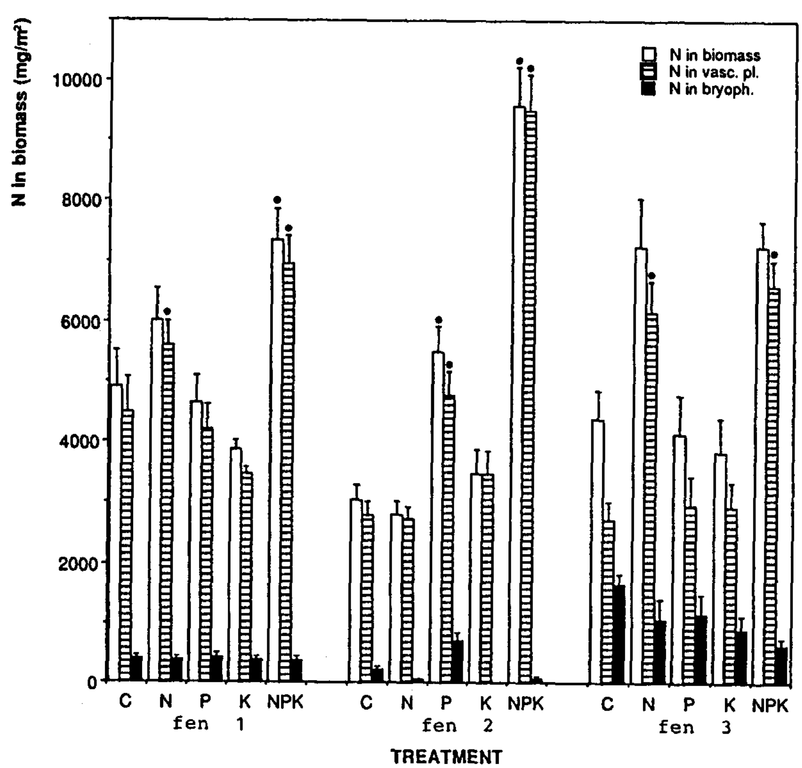

Fig. 2. Total amount of N in the above-ground biomass (Mean values with SE). For a key to the symbols see Fig. 1.

on the amounts of P in the above-ground biomass (Fig. 3). The differences from the control were significant for total biomass in all cases, for vascular plant biomass in all but one case, and for moss biomass in two of the P treatments.

The amounts of K in the biomass were significantly higher than the control treatment in the NPK treatments only (Fig. 4).

N, P and K concentrations in plant material

None of the treatments resulted in higher concentrations of N in the plant material (Table 2). P concentrations were significantly higher in vascular plant material in all P and NPK treatments (Table 3). P concentrations were also higher in the mosses in the P treatments in fens 2 and 3 and in the NPK treatment in fen 3. K concentrations were significantly higher than the control in the K and NPK treatments in vascular plants in fen 1 and in mosses in fen 3 (Table 4).

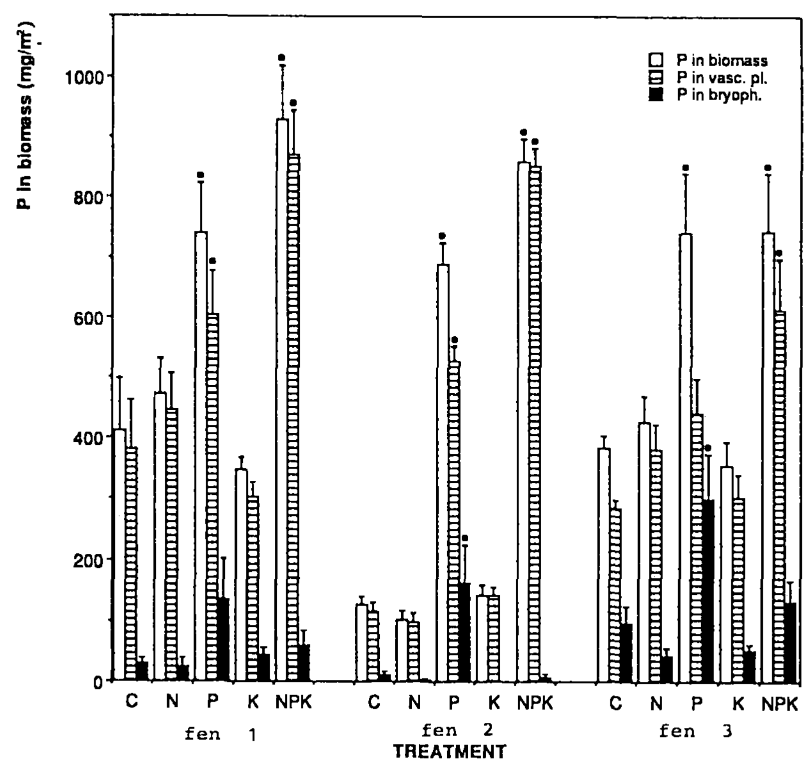

Fig. 3. Total amount of P in the above-ground biomass (Mean values with SE). For a key to the symbols see Fig. 1.

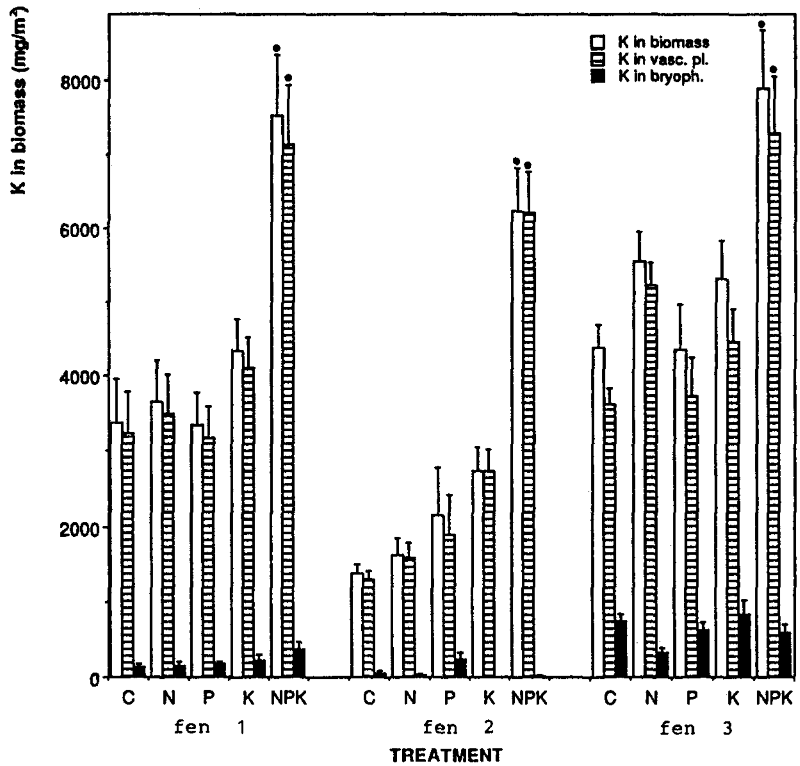

Fig. 4. Total amount of K in the above-ground biomass (Mean values with SE). For a key to the symbols see Fig. 1.

Discussion

The significant growth responses to the fertilization treatments show that nitrogen is the key element controlling plant growth in fens 1 and 3 and that phosphorus is the limiting factor in fen 2. The fact that N uptake by plants was higher under P-enriched conditions in fen 2 is further evidence that P is in short supply here. Potassium does not play a growth-limiting role in any of the fens studied.

Extra N uptake always resulted in extra growth, and no luxury consumption of N took place. All P fertilizations, however, resulted in higher P uptake, regardless of responses of plant growth, as is commonly found in similar experiments with P fertilization (Solander 1983). A higher K uptake occurred in most K treatments, although not always statistically significant.

Table 2. Nitrogen concentrations in phanerogam (phan) and bryophyte (bryo) material in relation to fertilization treatment.

Fen nr.	----------1----------		----------2----------		----------3----------	
	phan	bryo	phan	bryo	phan	bryo
Control	13.6	14.7	16.5	13.0	12.2	11.9
N	14.8	13.0	17.4	12.6	15.4	20.4
P	12.6	18.7	17.8	12.6	12.5	11.4
K	13.3	17.3	16.1	13.3	12.0	13.1
NPK	13.1	19.5	17.7	13.9	11.2	16.2

Values are given as mgN/g dry weight. * — value significantly different from that in control treatment. For keys to sites and treatments, see Fig. 1.

Table 3. Phosphorus concentrations in phanerogam and bryophyte material in relation to fertilization treatment.

Fen nr.	----------1----------		----------2----------		----------3----------	
	phan	bryo	phan	bryo	phan	bryo
Control	1.11	1.07	0.69	0.59	1.30	0.75
N	1.14	0.86	0.62	0.12	0.96	0.87
P	1.91*	2.75	1.99*	2.89*	1.85*	3.11*
K	1.20	1.39	0.67	0.11	1.24	0.88
NPK	1.64*	2.73	1.59*	0.38	1.85*	3.36*

Values are given as mgP/g dry weight. * — value significantly different from that in control treatment. For keys to sites and symbols, see Fig. 1.

Table 4. Potassium concentrations in phanerogam and bryophyte material in relation to fertilization treatment.

Fen nr.	----------1----------		----------2----------		----------3----------	
	phan	bryo	phan	bryo	phan	bryo
Control	9.2	5.0	7.8	3.7	16.4	5.4
N	8.7	4.6	10.0	1.7	13.4	6.2
P	9.2	6.1	7.3	3.5	15.8	6.5
K	14.8*	11.6	12.6	1.1	18.6	18.4*
NPK	13.2*	12.8	11.6	1.1	19.9	16.1*

Values are given as mgK/g dry weight. * — value significantly different from that in control treatment. For keys to sites and treatments, see Fig. 1.

The experiment shows that limitation of plant growth by N still occurs in Dutch fens in spite of the strongly increased nitrogen inputs. The two fens in which N was found to be limiting strongly differ in hydrology: Fen 1 is located in a groundwater discharge area and receives 100 cm of groundwater and 11 cm of surface water per year, whereas fen 3 is located in a groundwater recharge area: it loses 6 cm to the groundwater and receives 31 cm of surface water per year (Koerselman 1989). The relatively greater importance of rain water in fen 3 is clearly reflected in the chemistry of the fen water and the species composition of the vegetation (Koerselman et al. 1990b). The two fens are similar in age and land use history, which is probably of key importance in explaining their similar reaction to the fertilization treatments. In fen 2, the distinct response of biomass production to P fertilization indicates that plant growth is P-controlled. This fen is similar in hydrology to fen 1 but it is much 'older' than fens 1 and 3 and has a longer history of annual summer mowing (Verhoeven et al. 1988).

The responses of the three fens studied suggest that a shift from N- to P-limited plant growth takes place in the course of succession. Long-term processes of storage, release and loss of earlier accumulated nutrients play a role here. A nutrient balance study carried out in fens in the same area has shown that inputs more or less equal outputs for N but that there are substantial annual P losses in these annually mown systems (Koerselman et al. 1990a). The most important nutrient outputs from the system are losses due to the removal of the hay.

The results suggest the following general picture of control of plant growth by N and P in fens undergoing succession in the study area. In early successional stages, luxuriant plant growth occurs in floating rafts and shore stands of large helophytes. These stages are characterized by a rapid flow-through of groundwater and surface water. Plant growth is primarily controlled by nutrients carried to the system by water flow and precipitation, and N is probably the limiting factor (see also Bowden 1987; Barko & Smart 1978; Neely & Davis 1985). In the 'mid'-successional stage, the vegetation has formed a continuous thick floating mat of rhizome material and loose peat, in which large amounts of organic C, N and P have accumulated (Vermeer & Verhoeven 1987; Verhoeven 1986). At the same time, water flow-through rates have declined as a result of increased hydraulic resistance, and recycling of nutrients in the mat is the primary source for uptake by the vegetation (Verhoeven et al. 1988; Koerselman et al. 1990a). Although N availability is gradually increasing as a result of the mineralizaton of steadily higher amounts of organic N, this element still controls plant growth in this stage (Vermeer 1986).

The annual mowing of the fen, that starts in the 'mid'-successional stage as soon as the mat can support light machinery, removes N, P and K from the system. The annual inputs of N to the fens exceed or more or less balance the amounts removed in the hay, but the P and K inputs can only account for about one fourth the amounts removed (Koerselman et al. 1990a). Thus, the system is gradually depleted of P and K. This is probably the main reason for the shift from N limitation toward P limitation after prolonged annual mowing.

The difference in hydrology between the 'mid'-succession fens is apparently of lesser importance here. Both the groundwater flowing into fen 1 and the surface water supplied to fen 3 carry sufficient N, P and K to be significant as input sources (Koerselman et al. 1990a). Both N and P mineralization rates are faster in fen 3 than in fen 1 (Verhoeven & Arts 1987), probably as a result of the surface water inflow into the former fen and the predominance of *Sphagnum* litter in the soil. Orthophosphate concentrations in the fen water are significantly higher in fen 3, whereas there are no differences for inorganic nitrogen (Koerselman et al. 1990b). Orthophosphates are probably adsorbed on or precipitated with calcium ions that are continually supplied by groundwater inflows in fen 1 (see Boyer & Wheeler 1989).

In the fens studied, the shift from limitation by N towards limitation by P was primarily caused by the combination of high atmospheric N deposition and anthropogenic management. Would such a shift also occur in peat-forming wetlands in other regions in the absence of mowing? Although data on control of plant growth by nutrients in freshwater wetlands are scarce in the literature, they suggest that this may be true. Primary production in freshwater marshes is primarily controlled by the availability of N (Barko & Smart 1978, 1986; Neely & David 1985). Fens comparable with our 'late'-succession site that are under the influence of Ca-or Al-rich groundwater or surface water show P-controlled plant growth, as a result of immobilization of phosphates into inorganic bound P pools (Richardson & Marshall 1986; Boyer & Wheeler 1989). In these cases, it is not so much the high P output that limits P availability but rather the high storage rates into inaccessible pools.

The results of our study have some important implications for the management of fens in The Netherlands. A primary concern is the increase in productivity that may be caused by nitrogen enrichment, as such an increase has been shown to lead to loss of rare species and shifts in species dominances (Vermeer & Berendse 1983; Vermeer & Verhoeven 1987). A regime of annual mowing in the summer and removal of the hay in 'mid'-succession fens will lead to a shift from N-limited towards P-limited plant growth within 3 to 4 decades. As a result of this shift, the enlarged N inputs through precipitation and inflows of groundwater and surface water will cease to affect the productivity and species richness of the fens. Productivity may eventually decrease again as a result of P depletion, as indicated by the low biomass in the control treatment in fen 2 compared to fens 1 and 3 (Fig. 1).

If, however, the hydrological management of the landscape is altered to the extent that river water has to be supplied in the summer, previously groundwater-fed fens will start to remobilize the large bound inorganic P stores ("internal eutrophication"), primarily as a result of physicochemical desorption and dissolution caused by the changes in water chemistry; then, drastic increases in productivity accompanied with changes in the species composition and loss of rare species, are to be expected (Verhoeven et al. 1988). Thus, a consistent regime of annual mowing and a hydrological regime ensuring groundwater discharge in the fens are both vital to the long-term conservation of 'late'-succession fen vegetation.

Acknowledgements

We are indebted to prof. dr. P. J. M. van der Aart, dr. R. Aerts, dr. B. Beltman, dr. W. Koerselman, dr. D. F. Whigham, drs. A. M. Kooijman, drs. C. Mesters and H. de Caluwe for their critical comments on the manuscript. We thank 'Natuurmonumenten' and the National Forest Service for permissons to carry out the experiments on their property. The manuscript was written during a stay of the first author at the Smithsonian Environmental Research Center at Edgewater, Md, USA supported by a Smithsonian Senior Postdoctoral Fellowship and a grant from the Netherlands Organization for Scientific Research (NWO).

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