

N, P, AND K BUDGETS ALONG NUTRIENT AVAILABILITY AND PRODUCTIVITY GRADIENTS IN WETLANDS

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Abstract. Nutrient enrichment in Western Europe is an important cause of wetland deterioration and the concomitant loss of biodiversity. We quantified nitrogen, phosphorus, and potassium budgets along biomass gradients in wet meadows and fens (44 field sites) to evaluate the importance of various nutrient flows (atmospheric deposition, flooding, groundwater flow, leaching, soil turnover rates) for availability of the growth-limiting nutrient(s). From the nutrient budgets, we assessed N, P, and K availabilities for plants and compared them with N, P, and K in aboveground biomass. Also, potential long-term effects of annual hay harvesting on nutrient limitation were assessed.

Comparing N, P, and K availabilities with N, P, and K amounts in the vegetation revealed that (1) the assessed availabilities could explain amounts and variation of nutrients in the vegetation along the biomass gradients, and (2) N was likely the major limiting nutrient along the gradients and P and K could (co)limit growth in some of the sites.

Increasing N availabilities along the biomass gradients were caused by increasing N turnover rates in the soil. The contribution of atmospheric N deposition ($43 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ at all sites) to N availability varied from ~63–76% in low-productivity meadows and fens to 24–42% in highly productive meadows and fens. P and K availabilities along the biomass gradients were primarily influenced by soil processes, as indicated by soil extractable nutrient pools. Flooding could explain 20–30% of K in aboveground higher plants but was less important for P or N availabilities. Nutrient input and output by groundwater flow were more or less negligible for nutrient availability.

At low-productivity sites, N output by hay harvesting just accounted for N input from atmospheric deposition, whereas there was net output of P and K. At highly productive sites, there was net output of all three nutrients. Compared to total N, P, and K pools in the top soil, net K output (1–20% of soil K pool) was at many sites much larger than that of P (generally 0.5–3%) or N (0–3%). Hay harvesting particularly seems to create K limitation.

Our results indicate that conservation or restoration of low productivity wetlands in Western Europe requires (1) stable site conditions controlling low N, P, and K turnover rates in the soil, and (2) in case of N limitation, annual removal of biomass by harvesting hay, or another management measure to counterbalance the N input from atmospheric deposition.

Key words: atmospheric deposition; eutrophication; flooding; groundwater; mineralization; nature management; nitrogen; nutrient cycling; phosphorus; potassium; soil nutrient turnover; wetlands.

INTRODUCTION

Even more than in other parts of the world, natural wetlands have largely disappeared in Western Europe, and many remaining ones are threatened by eutrophication. In many wet meadows and fens, also in areas protected and managed as nature reserves, shifts have occurred from low-productivity species-rich communities to highly productive and species-poorer communities (e.g., van Dijk 1991, Kooijman 1993, Alard et al. 1994, Fojt and Harding 1995, Rich and Woodruff

1996, Bollens 2000). The productivity increase can be considered as the result of increased availabilities of the potentially growth-limiting nutrients: nitrogen (N), phosphorus (P), and potassium (K; Bridgham et al. 1996, Verhoeven et al. 1996, Olde Venterink et al. 2001a). For a deliberate management and protection of these ecosystems, one should have insight into which of the three nutrients is limiting, whether its availability might increase, and the source by which the availability might increase. This potential increase can be predicted by analyzing the various nutrient flows operating in these systems. These flows include atmospheric deposition, nutrient supply by flooding and groundwater flow, nutrients leaching to groundwater, and denitrification, as well as grazing or harvesting natural products in the form of hay production. Increased availabilities of N, P, and K may also result from changes in soil nutrient turnover rates due to altered ecosystem prop-

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FIG. 1. Locations of research sites and weather stations in catchment areas of the Dommel River (The Netherlands) and the Zwarte Beek stream (Belgium).

erties. Soil nutrient turnover rates consist of decomposition, mineralization, weathering, chemical complexation, adsorption, or nutrient uptake by plants and soil organisms (e.g., Mengel 1982, Walbridge 1991, Marrs 1993).

The objective of this study was to quantify annual nutrient flows by atmospheric deposition, flooding, groundwater flow, leaching, and nutrient turnover rates in the soil, in 44 sites in wet meadows and fens, as well as to assess N, P, and K availabilities for plants by summation of these flows. These sites constituted a productivity gradient. We aimed to assess nutrient budgets along this productivity gradient in order to analyze the process of eutrophication in Western European fens and meadows. Additionally, we planned to assess the long-term consequences of hay-production on annual nutrient outputs and nutrient limitation.

METHODS

Study sites

The 44 sites (each 4 m²) in meadows and fens were located in seven nature reserves along the Dommel River (The Netherlands) and in three reserves along the Zwarte Beek (Belgium; Fig. 1). Five of the Dutch nature reserves were embedded in heavily fertilized

agricultural land, the other two and the three Belgian reserves were surrounded by forest or extensively used meadows. The fens and meadows were not fertilized and were annually mown for at least 10 yr, in most cases >20 yr. Hay was removed after mowing.

For comparability with other research, we divided the 44 sites into four types of meadows and three types of fens. We followed a classification based on plant species composition (cf. Wheeler 1988, Grootjans and Van Diggelen 1995). Species composition in the 44 sites was recorded in June 1995 by means of the Braun Blanquet method, and sites were clustered by means of Flexclus (van Tongeren 1986). We distinguished four types of meadows, *Molinia* meadows (*Junco-Molinia*), *Caltha* meadows (*Calthion palustris*), *Holcus* meadows (*Holcus lanatus* dominated degradation stage of *Calthion palustris*), and *Glyceria* meadows (*Valeriano-Filipenduletum*); as well as three types of fens, *Carex nigra* fens (*Caricion nigrae*), *Carex curta* fens (*Carici curtae-Agrostietum caninae*), and *Carex acuta* fens (*Caricion gracilis*; syntaxonomy: Schaminée et al. 1995, 1996, Stortelder et al. 1999). The *Carex acuta* fens were named after one of the dominant species, but could also be dominated by *Carex riparia* or *Scirpus sylvaticus*. A classification of our sites into various wetland types (cf. Mitsch et al. 1994) was less suited for our study—about the relationship between nutrient availability and productivity—since this classification is merely based on environmental conditions such as hydrology and acidity, and ignores differences in productivity (e.g., “wet meadows” and “rich fens” contain very wide productivity ranges). Nevertheless, in general our meadows and fens differed hydrologically. The fens were constantly wet, whereas meadows were generally dryer (except for the *Caltha* meadows in spring) and subjected to a more dynamic water regime (Table 1; cf. Mitsch et al. 1994). Additional information about the study sites is given in Olde Venterink et al. (2001b).

Based on Ellenberg's indication values of plant species (Ellenberg et al. 1991), the four types of meadows and three types of fens represent fertility gradients (Table 1). Moreover, during eutrophication, *Holcus* meadows can develop from *Molinia* meadows or *Caltha* meadows (e.g., Grootjans et al. 1985, 1986), *Glyceria* meadows can develop from *Caltha* meadows (Stortelder et al. 1999), and *Carex acuta* fens can develop from *Carex curta* or *Carex nigra* fens (Koerselman and Verhoeven 1992).

Aboveground biomass and productivity

Aboveground vegetation was harvested at all sites at the peak of the growing season (17–21 July 1995). The vegetation (living plus standing dead) was cut at 2 cm above the soil surface in three 0.25-m² plots within every 4-m² site. Additionally, bryophytes were collected. The samples of the three squares were combined and divided into graminoids and herbs. Dry masses of

TABLE 1. Habitat descriptors (mean \pm 1 SE) and characteristic plant species of the seven types of meadows and fens.

Wetland type	No. sites	Spring water level (cm)§	Water level dynamics (cm)	Soil moisture		Bulk density (g/cm ³)¶	Organic matter (%)¶	pH¶
				Content (%FW)§	Dynamics (%FW)			
Meadows†								
<i>Molinia</i>	8	40 \pm 6 ^a	73 \pm 8 ^{a-c}	63 \pm 6 ^{b-d}	13 \pm 3 ^{bc}	0.48 \pm 0.11 ^{a-c}	35 \pm 9 ^{a-d}	5.6 \pm 0.3 ^{a-c}
<i>Caltha</i>	7	23 \pm 3 ^a	73 \pm 3 ^b	81 \pm 1 ^a	15 \pm 2 ^b	0.20 \pm 0.01 ^c	63 \pm 2 ^d	5.6 \pm 0.1 ^b
<i>Holcus</i>	6	35 \pm 11 ^{ab}	68 \pm 8 ^{b-d}	56 \pm 4 ^d	15 \pm 4 ^{ab}	0.58 \pm 0.06 ^a	23 \pm 2 ^a	5.7 \pm 0.1 ^b
<i>Glyceria</i>	9	29 \pm 2 ^a	88 \pm 3 ^a	62 \pm 3 ^{cd}	25 \pm 2 ^a	0.52 \pm 0.04 ^a	29 \pm 2 ^b	5.1 \pm 0.1 ^c
Fens‡								
<i>Carex nigra</i>	6	7 \pm 2 ^c	47 \pm 7 ^d	75 \pm 2 ^b	6 \pm 1 ^d	0.32 \pm 0.03 ^b	38 \pm 3 ^c	5.9 \pm 0.1 ^a
<i>Carex curta</i>	3	11 \pm 1 ^{bc}	59 \pm 4 ^c	74 \pm 6 ^{a-c}	5 \pm 2 ^{cd}	0.30 \pm 0.07 ^{bc}	43 \pm 10 ^{b-d}	5.5 \pm 0.3 ^{a-c}
<i>Carex acuta</i>	5	5 \pm 2 ^c	60 \pm 7 ^{b-d}	76 \pm 4 ^{ab}	7 \pm 2 ^{cd}	0.28 \pm 0.05 ^{bc}	40 \pm 6 ^{bc}	5.7 \pm 0.1 ^b

Notes: Soil variables were measured in the top 10 cm of soil. Values with different letters are significantly different at $P < 0.05$ (Mann-Whitney U test).

† Characteristic plant species for meadows are as follows. *Molinia* meadows: *Molinia caerulea*, *Carex panicea*, *Juncus conglomeratus*, *Dactylorhiza* spp., *Festuca rubra*, *Agrostis canina*, *Cardamine pratensis*, and *Lychnis flos-cuculi*. *Caltha* meadows: *Caltha palustris*, *Juncus acutiflorus*, *Juncus filiformis*, *Pedicularis palustris*, *Festuca rubra*, *Agrostis canina*, *Cardamine pratensis*, and *Lychnis flos-cuculi*. *Holcus* meadows: *Holcus lanatus* (high cover), *Agrostis capillaris*, *Cardamine pratensis*, and *Lychnis flos-cuculi*. *Glyceria* meadows: *Glyceria maxima*, *Phalaris arundinacea*, *Deschampsia cespitosa*, *Carex vesicaria*, *Alopecurus pratensis*, and *Ranunculus repens*.

‡ Characteristic plant species for fens are as follows: *Carex nigra* fens: *Carex nigra*, *Carex panicea*, *Carex echinata*, *Carex lasiocarpa*, *Eriophorum angustifolium*, and *Menyanthes trifoliata*. *Carex curta* fens: *Carex rostrata*, *Carex curta*, and *Juncus filiformis*. *Carex acuta* fens: *Carex acuta*, *Carex riparia*, and *Scirpus sylvaticus*.

§ Mean of three measurements in the spring of 1996 (%FW = percentage freshwater, by mass). Because of a dry winter, the usual spring flooding did not occur. Therefore spring water levels are lower than normal, particularly in the usually flooded *Caltha* and *Glyceria* meadows.

|| Range of highest to lowest during one year (%FW = percentage freshwater, by mass).

¶ Mean of eight samples during one year; pH was measured in soil moisture.

Mix of five subsamples at every site, calculations are for the top 10 cm of soil.

†† Mean N-indication value of all plant species in a site after Ellenberg et al. (1991).

the samples were determined after drying for 48 h at 70°C. Since our sites are annually mown, biomass of vascular plants (graminoids plus herbs) can be considered as a measure for annual aboveground production. This measure of productivity underestimates total plant production because root production and biomass turnover within the growing season are not included. Bryophytes are not annually removed; its biomass is probably produced in several years (Paczynski and Stepa 1991).

External nutrient flows

Annual atmospheric deposition rates of N, P, and K in our meadows and fens were derived from the National Institute of Public Health and Environment (H. Olde Venterink, unpublished data). The mean flow rates for 1995 and 1996 for the whole research area were taken for all sites.

A part of the sites was flooded for some days during one flood event in May 1995. The flood water entered the meadows through a ditch connected to the river, until the flood water reached the water level of the river. Flooded meadows such as these are widespread in Europe; flooding is regulated by nature as in our sites, but may also be regulated artificially (e.g., Davidsson and Leonardson 1998). The flood water left our meadows again after lowering of the river water level. Hence, there was a single inflow and a single outflow

event of water in the meadows, instead of a continuous river water flux. The maximum flow rates of N, P, and K from river flooding to the sites was assessed by multiplying the measured volume of flood water (assessed from maximum flooding depth) with concentrations of NO₃⁻, NH₄⁺, soluble-reactive P, and K in the flood water. Because the soil was water saturated already before the flooding event, we assumed that flood water did not infiltrate (cf. Hooijer 1996). During the flood event, one sample was taken of the standing water at every flooded site. After centrifugation, NO₃⁻ and NH₄⁺ concentrations were measured colorimetrically with a continuous flow analyzer. Concentrations of soluble-reactive P and K were determined by inductively coupled plasma atomic emission spectrometry (ICP-AES). Inputs of N, P, and K in the flooded meadows by particulate N, P, or K, or by sedimentation were not measured. Furthermore, we note that the winter of 1995–1996 (within the measuring period of water tables at our sites; i.e., August 1995–September 1996), was dry and did not include the usual flooding. Therefore, the spring water levels in the *Caltha* meadows and *Glyceria* meadows (Table 1) were not above the surface level as one would expect from “flooded” meadows.

The volumes of water transported from the groundwater to the root zone, and out of the root zone to groundwater or ditches, were assessed by means of annual water balances for every site (see the Appen-

TABLE 1. Extended.

Total soil nutrients#			Legumes (% of total cover)	Ellenberg fertility index††
N (kg/ha)	P (kg/ha)	K (kg/ha)		
3252 ± 207 ^{bc}	307 ± 29 ^c	1314 ± 320 ^{ab}	3.8 ± 1.8 ^b	3.0 ± 0.1 ^d
4440 ± 143 ^a	553 ± 58 ^b	537 ± 38 ^b	12.1 ± 4.0 ^a	4.0 ± 0.1 ^b
3938 ± 240 ^{ab}	825 ± 77 ^a	577 ± 71 ^b	4.4 ± 0.9 ^{ab}	4.5 ± 0.2 ^b
4096 ± 338 ^a	716 ± 78 ^{ab}	1356 ± 177 ^a	0.3 ± 0.2 ^c	5.3 ± 0.2 ^a
3394 ± 224 ^{bc}	670 ± 183 ^{ab}	874 ± 235 ^{ab}	3.8 ± 1.5 ^{ab}	3.6 ± 0.1 ^c
3977 ± 331 ^{a-c}	448 ± 130 ^{a-c}	1597 ± 1035 ^{ab}	2.6 ± 2.6 ^{a-c}	4.1 ± 0.2 ^b
2816 ± 328 ^c	603 ± 210 ^{a-c}	911 ± 343 ^{ab}	1.8 ± 1.1 ^{bc}	4.9 ± 0.4 ^{ab}

dix). Annual flow rates of N, P, and K from groundwater to the root zone were calculated by multiplying NO_3^- , NH_4^+ , soluble-reactive P, and K concentrations in the groundwater with the annual volume of water coming into the root zone. Flow rates of N, P, and K out of the root zone to groundwater or ditches, was calculated by multiplying NO_3^- , NH_4^+ , soluble-reactive P, and K concentrations in the soil solution with the volume of water flowing out of the root zone. Groundwater and soil moisture were sampled eight times between August 1995 and September 1996 at every site. Groundwater samples were taken in piezometers at a depth of 80–120 cm below the surface level. Soil moisture was collected from the top 10 cm of soil using Rhizon soil moisture samplers (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). Mixed samples were taken from three samplers at every site. Nutrient concentrations were measured as in flood water. Since no temporal trends were observed, mean values of the eight samples were used for every site.

Annual N, P, and K output from hay harvesting was estimated by measuring the amounts of N, P, and K in the aboveground graminoids and herbs in the second half of July 1995 in all sites (see *Methods: Nutrients in aboveground vegetation*). The second half of July is the usual time for mowing of the 10 nature reserves.

Soil nutrient turnover

Annual net N, P, and K turnover rates in the soil were measured at every site between May 1995 and May 1996 by in situ soil incubation. In this paper, soil nutrient turnover rates are defined as the net release rates of inorganic N, P, or K in the top 10 cm of soil, regardless of the mechanism (e.g., mineralization of organic matter or release from chemically or physically bound nutrients). We followed the soil incubation technique as described in detail by Olff et al. (1994). Nutrient turnover rates in the soil were measured during five periods of 8 wk and one winter period of 12 wk. At the start of every period, one pair of soil cores (10 cm depth, 4.8 cm diameter) was taken at 1–5 cm from each other at every site. Soil cores were taken with sharpened PVC tubes. One of the paired tubes was incubated, the other one transported to the laboratory and extracted after a night at 2°C. Soil extractable N was determined by extraction with 1 mol/L KCl (Olff et al. 1994). Soil extractable P and ammonium-exchangeable K in the soil were determined by extraction with 0.1 mol/L NH_3 + 0.4 mol/L acetic acid + 0.1 mol/L lactic acid solution (ALA; cf. Scheffer and Schachtschabel 1989, Koerselman et al. 1993). Nutrient concentrations in the extracts were determined in a similar

TABLE 2. Assessed annual input flows of water and nutrients from flooding in seven types of meadows and fens between April 1995 and April 1996.

Habitat type	n	nf	Annual input flows by flooding			
			Water (1×10^4 L·ha ⁻¹ ·yr ⁻¹)	$\text{NO}_3^- + \text{NH}_4^+$ (kg N·ha ⁻¹ ·yr ⁻¹)	Dissolved P (kg P·ha ⁻¹ ·yr ⁻¹)	K (kg K·ha ⁻¹ ·yr ⁻¹)
Meadows						
<i>Molinia</i>	8	0	0 ^c	0 ^c	0 ^b	0 ^c
<i>Caltha</i>	7	7	49 ± 8 ^b	4.3 ± 0.7 ^b	0.31 ± 0.05 ^a	6.8 ± 1.1 ^b
<i>Holcus</i>	6	1	17 ± 17 ^c	0.1 ± 0.1 ^c	0.01 ± 0.01 ^b	0.4 ± 0.4 ^c
<i>Glyceria</i>	9	9	160 ± 20 ^a	11 ± 1.4 ^a	0.71 ± 0.14 ^a	21 ± 2.4 ^a
Fens						
<i>Carex nigra</i>	6	1	17 ± 17 ^c	0.1 ± 0.1 ^c	0.01 ± 0.01 ^b	0.4 ± 0.4 ^c
<i>Carex curta</i>	3	1	17 ± 17 ^c	0.3 ± 0.3 ^c	0.04 ± 0.04 ^b	0.7 ± 0.7 ^c
<i>Carex acuta</i>	5	2	40 ± 25 ^c	0.3 ± 0.2 ^c	0.03 ± 0.02 ^b	1.1 ± 0.7 ^c

Notes: Abbreviations are: n = number of sites; nf = number of flooded sites. Mean values (± 1 SE), including nonflooded sites, are shown. Values with different superscript letters are significantly different at $P < 0.05$ (Mann-Whitney U test).

TABLE 3. Mean (± 1 SE) flow rates of water and nutrients from groundwater to the root zone, and flow rates out of the root zone to groundwater or ditches in seven types of meadows and fens between April 1995 and April 1996.

Habitat type	No. sites	Flow rates from groundwater to root zone			
		Water (1×10^4 L·ha ⁻¹ ·yr ⁻¹)	NO ₃ + NH ₄ (kg N·ha ⁻¹ ·yr ⁻¹)	Dissolved P (kg P·ha ⁻¹ ·yr ⁻¹)	K (kg K·ha ⁻¹ ·yr ⁻¹)
Meadows					
<i>Molinia</i>	8	107 \pm 6 ^c	0.4 \pm 0.0 ^c	0.03 \pm 0.01 ^b	1.5 \pm 0.6 ^{ab}
<i>Caltha</i>	7	111 \pm 8 ^c	0.5 \pm 0.1 ^c	0.27 \pm 0.12 ^a	2.6 \pm 0.8 ^{ab}
<i>Holcus</i>	6	210 \pm 27 ^{ab}	2.2 \pm 1.2 ^{ab}	0.28 \pm 0.18 ^{ab}	1.9 \pm 0.6 ^{ab}
<i>Glyceria</i>	9	159 \pm 5 ^b	1.0 \pm 0.1 ^b	0.15 \pm 0.11 ^{ab}	3.6 \pm 0.9 ^a
Fens					
<i>Carex nigra</i>	6	207 \pm 23 ^{ab}	1.8 \pm 0.8 ^{ab}	0.12 \pm 0.03 ^a	1.0 \pm 0.1 ^b
<i>Carex curta</i>	3	222 \pm 23 ^a	2.8 \pm 0.2 ^a	0.25 \pm 0.11 ^a	2.0 \pm 1.1 ^{ab}
<i>Carex acuta</i>	5	279 \pm 44 ^{ab}	1.3 \pm 0.2 ^b	0.12 \pm 0.03 ^a	1.7 \pm 0.5 ^{ab}

Notes: Calculations are based on a root zone depth of 30 cm. Values with different superscript letters are significantly different at $P < 0.05$ (Mann-Whitney U test).

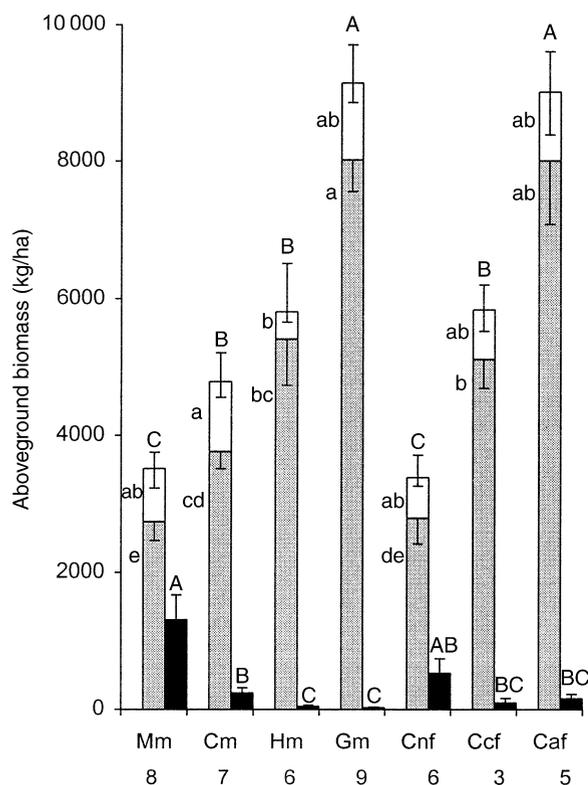


FIG. 2. Aboveground dry masses of vascular plants (graminoids, gray bars; herbs, white bars) and bryophytes (black bars) in July 1995 for four types of meadows and three types of fens: *Molinia* meadows (Mm), *Caltha* meadows (Cm), *Holcus* meadows (Hm), *Glyceria* meadows (Gm), *Carex nigra* fens (Cnf), *Carex curta* fens (Ccf), and *Carex acuta* fens (Caf). Histogram bars indicate means per meadow and fen type. Error bars on top of columns indicate +1 SE of the whole bar, error bars in the columns show -1 SE of graminoids and herbs. Significant differences ($P < 0.05$; Mann-Whitney U test) between the seven types are shown with different letters; capitals for whole bars and small letters for graminoids and herbs. The number of sites per type is shown under the abbreviations of names.

way as in flood water. Net nutrient turnover rates in the soil were calculated by subtracting soil extractable N, P, and K in the initial soil cores from that in the incubated cores, for the six periods. Values per unit area were calculated from values per unit dry soil and the mean bulk density of the top 10 cm of soil.

Nutrient availability

Nutrient availability for plants (N_a) was determined by the sum of the flow rates: atmospheric deposition (N_d), input by flooding (N_f), input by groundwater (N_g), output by leaching (N_l), and net N turnover rate in the soil (N_s ; Eq. 1). Eq. 1 is equal for N, P, and K. All flow rates are expressed in kg N, P or K·ha⁻¹·yr⁻¹. Denitrification and nitrogen fixation were not assessed for our meadows and fens, but their potential importance for plant-N availability will be discussed.

$$N_a = N_d + N_f + N_g - N_l + N_s \quad (1)$$

Although soil incubation techniques are often used to assess net N and P turnover rates in soil (Verhoeven et al. 1990, Berendse et al. 1994, Olf et al. 1994, Aerts et al. 1999) and occasionally also of K (Koerselman et al. 1993), other studies indicate that these techniques are less appropriate for assessment of net P turnover rates (Walbridge 1991, Walbridge and Vitousek 1987), or net K turnover rates (cf. Jungk and Claassen 1986). Therefore, soil extractable pool indices for P and K were estimated and used as a reference for within-stand P and K availability for plants in the soil, although these indices provide no information on turnover rates. Soil extractable P was determined by averaging ALA extracted P of the initial soils of the incubation study (see *Methods: Soil nutrient turnover*), and additionally in May 1995 by Bray II extractions (0.03 mol/L NH₄F + 0.1 mol/L HCl; Richardson and Marshall 1986). Both ALA and Bray II are in use as references for P availability for plants in the soil (Scheffer and Schachtschabel 1989). For assessment of plant-available K pools in the soil, we used two extractors: ammonium-exchangeable K and HCl-extractable K. The HCl-ex-

TABLE 3. Extended.

Flow rates out of root zone			
Water ($1 \times 10^4 \text{ L}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	$\text{NO}_3 + \text{NH}_4$ ($\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	Dissolved P ($\text{kg P}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	K ($\text{kg K}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)
55 ± 8 ^{bc}	0.4 ± 0.1 ^d	0.02 ± 0.01 ^{bc}	0.6 ± 0.3 ^{ab}
61 ± 10 ^{bc}	0.7 ± 0.2 ^{cd}	0.01 ± 0.00 ^c	0.3 ± 0.1 ^b
217 ± 24 ^a	11 ± 4.4 ^a	0.11 ± 0.03 ^a	2.5 ± 1.2 ^{ab}
46 ± 9 ^c	5.2 ± 2.4 ^{ab}	0.01 ± 0.00 ^c	1.1 ± 0.7 ^{ab}
93 ± 44 ^a	1.5 ± 0.7 ^{bc}	0.08 ± 0.04 ^{ab}	0.9 ± 0.4 ^{ab}
135 ± 67 ^{ab}	0.6 ± 0.3 ^{cd}	0.05 ± 0.03 ^{a-c}	0.6 ± 0.3 ^{ab}
119 ± 62 ^{a-c}	0.5 ± 0.3 ^{cd}	0.08 ± 0.05 ^{a-c}	5.7 ± 3.9 ^{ab}

tractable K pool includes both the ammonium-exchangeable K pool as well as an additional K fraction in the soil which is available for plants by soil acidification (Jungk and Claassen 1986). Ammonium-exchangeable K was determined by averaging ALA extracted K of the initial soils of the incubation study; 1 mol/L HCl-extractable K pools were measured in the same soils after 20 h without shaking at 50°C (Scheffer and Schachtschabel 1989).

Nutrients in aboveground vegetation

To relate N, P, and K availability for plants with N, P, and K in the aboveground vegetation, we ground the collected plant material (see Methods: Aboveground biomass and productivity) and digested it (using the Kjeldahl technique). Concentrations of N, P, and K in the digests were analyzed as in flood water. Aboveground biomass of graminoids, herbs, and bryophytes were multiplied by their N, P, and K concentrations to calculate amounts of N, P, and K in these parts of the vegetation at the peak of the growing season.

Total soil nutrient pools

To evaluate the long-term impact of annual N, P, and K output flows by hay harvesting for our meadow and

fen ecosystems, we compared them with annual input flows and with total N, P, and K pools in the top 10 cm of soil. Total N, P, and K pools were determined by taking five soil samples (10 cm deep × 4.8 cm diameter) within every 4-m² site in November 1995. The five samples were mixed, dried for 48 h at 70°C, and ground. Soil nutrient contents were determined by Kjeldahl digestion. Nutrient concentrations in the digests were determined as in flood water.

Data evaluation and statistics

In order to evaluate whether the various external nutrient flows and soil nutrient turnover could contribute significantly to differences in nutrient availabilities across wetland types, differences in the various external flow rates, soil turnover rates, and soil extractable nutrient pools were tested between the seven meadow and fen types. Moreover, we used nonparametric Mann-Whitney *U* tests to overcome problems of nonnormal distributions and unequal variances among types. Subsequently, the importance of the various external flows and soil turnover for their absolute contributions (kg nutrient·ha⁻¹·yr⁻¹) to differences in nutrient availabilities across types and along the productivity gradients was evaluated by comparing their absolute values.

TABLE 4. Net annual turnover rates of N, P, and K in the top 10 cm soil (mean ± 1 SE) in seven types of meadows and fens between May 1995 and May 1996.

Habitat type	No. sites	Soil N turnover [†] ($\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	Soil P turnover [‡] ($\text{kg P}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	Soil K turnover [§] ($\text{kg K}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)
Meadows				
<i>Molinia</i>	8	29 ± 6 ^d	-3 ± 3 ^a	4.8 ± 14 ^b
<i>Caltha</i>	7	45 ± 14 ^{cd}	0 ± 9 ^a	48 ± 10 ^a
<i>Holcus</i>	6	108 ± 24 ^{ab}	8 ± 9 ^a	19 ± 6.8 ^{ab}
<i>Glyceria</i>	9	133 ± 23 ^a	-5 ± 35 ^a	14 ± 19 ^{ab}
Fens				
<i>Carex nigra</i>	6	19 ± 9 ^d	-25 ± 22 ^a	7.5 ± 10 ^b
<i>Carex curta</i>	3	43 ± 13 ^{b-d}	6 ± 14 ^a	12 ± 12 ^{ab}
<i>Carex acuta</i>	5	58 ± 10 ^{bc}	-15 ± 12 ^a	42 ± 23 ^{ab}

Notes: Turnover rates are the sum of six periods and were determined by subtracting extractable N, P, and K of fresh soil from that of in situ incubated soil. Values with different superscript letters are significantly different at $P < 0.05$ (Mann-Whitney *U* test).

[†] Net turnover rate of KCl-extractable $\text{NH}_4 + \text{NO}_3$.

[‡] Net turnover rate of ammonium lactic-acid acetic-acid extractable P.

[§] Net turnover rate of NH_4 -exchangeable K as extracted with ammonium lactic-acid acetic-acid.

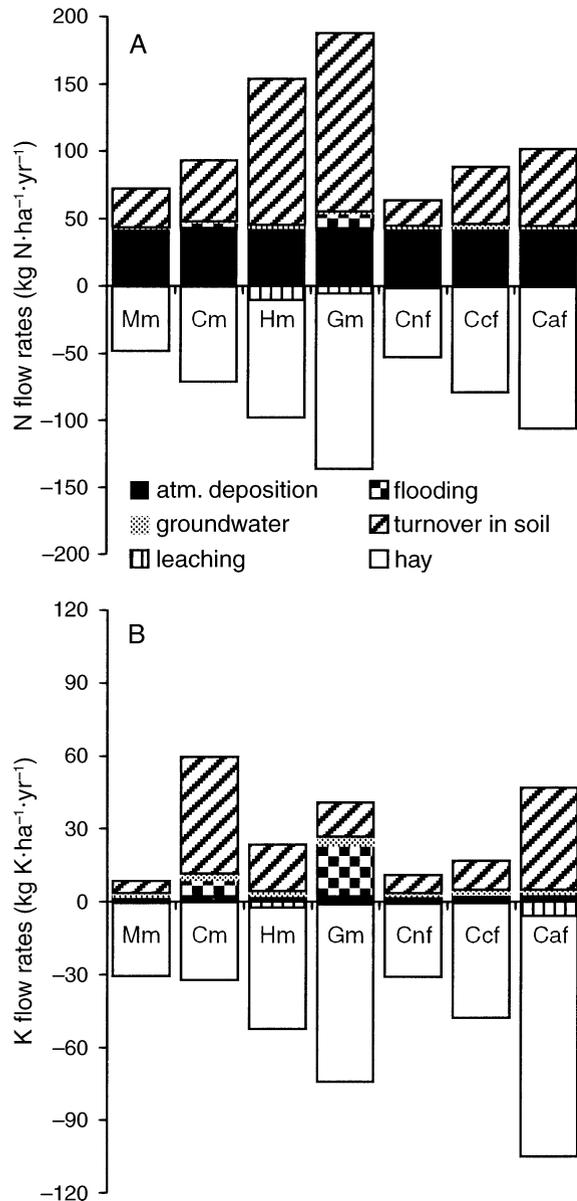


FIG. 3. Mean flow rates of (A) nitrogen and (B) potassium in four types of meadows and three types of fens by atmospheric deposition, groundwater supply, flooding, and soil nutrient turnover vs. output flow rates by haymaking and leaching to groundwater or ditches. Letters in the bars refer to *Molinia* meadows (Mm), *Caltha* meadows (Cm), *Holcus* meadows (Hm), *Glyceria* meadows (Gm), *Carex nigra* fens (Cnf), *Carex curta* fens (Ccf), and *Carex acuta* fens (Caf).

Additionally, first order (linear, logarithmic, inverse) regressions were carried out between measures for nutrient availabilities (sum of all flow rates and turnover rates or soil extractable nutrient pools) vs. aboveground biomass, as well as vs. N, P, and K in the biomass. These regressions were carried out to verify the overall reliability of our assessments of external nutrient flows and turnover rates; i.e., since the nutrients N, P, and/

or K are generally growth limiting in our types of meadows and fens (cf. Verhoeven et al. 1996, Olde Venterink et al. 2001a) significant correlations were expected between aboveground biomass and the availability of at least one of the nutrients N, P, and/or K. If such a relationship was observed for only one or two of the three nutrients, this provided an indication about the kind of nutrient limitation.

Net nutrient outputs by hay (i.e., output by hay minus nutrient inputs from external sources) were divided by the total nutrient pools in the top soil, to enable a comparison between the soil exhaustion times of the nutrients N, P, and K, and hence to evaluate the impact of hay harvesting on nutrient limitation and productivity.

We note that rates of external nutrient flows and soil nutrient turnover were assessed without within-site replication. Replication across wetland types was created by clustering sites into meadow and fen types. Nutrient concentrations in groundwater, soil moisture, and soil extractable pool indices for P and K availabilities were determined seven or eight times during a year at every site. Mean values of these variables were calculated per site, since no general temporal trends were observed.

RESULTS

Aboveground biomass

The meadow and fen types of this study represent gradients of aboveground biomass of vascular plants (Fig. 2). Since biomass of vascular plants is produced in one growing season in the annually mown sites, these biomass gradients can also be considered as productivity gradients. The biomass gradients were primarily determined by differences in biomass of graminoids. Mean biomass of bryophytes decreased with increasing biomass of vascular plants ($R^2 = 0.60$, $P = 0.042$).

External nutrient flows

Atmospheric deposition rates were assessed at $43 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $0.15 \text{ kg P}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and $2.2 \text{ kg K}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for all sites.

Flooding primarily occurred in the *Caltha* meadows and *Glyceria* meadows, during one flood event in May 1995. Nutrient input from flooding in these meadow types was estimated at $4.3\text{--}11 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $0.3\text{--}0.7 \text{ kg P}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and $6.8\text{--}21 \text{ kg K}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Table 2). Input flow rates of water and therefore also of nutrients were significantly higher in the *Glyceria* meadows. Mean nutrient input from flooding was negligible in the other types.

Nitrogen input and output flow rates by groundwater ranged on average between $0.4\text{--}2.2 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ and $4\text{--}11 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively (Table 3). The relatively high output flow rates in the *Glyceria* and *Holcus* meadows were caused by much higher nitrate concentrations in soil moisture ($5\text{--}10 \text{ mg N/L}$) compared to

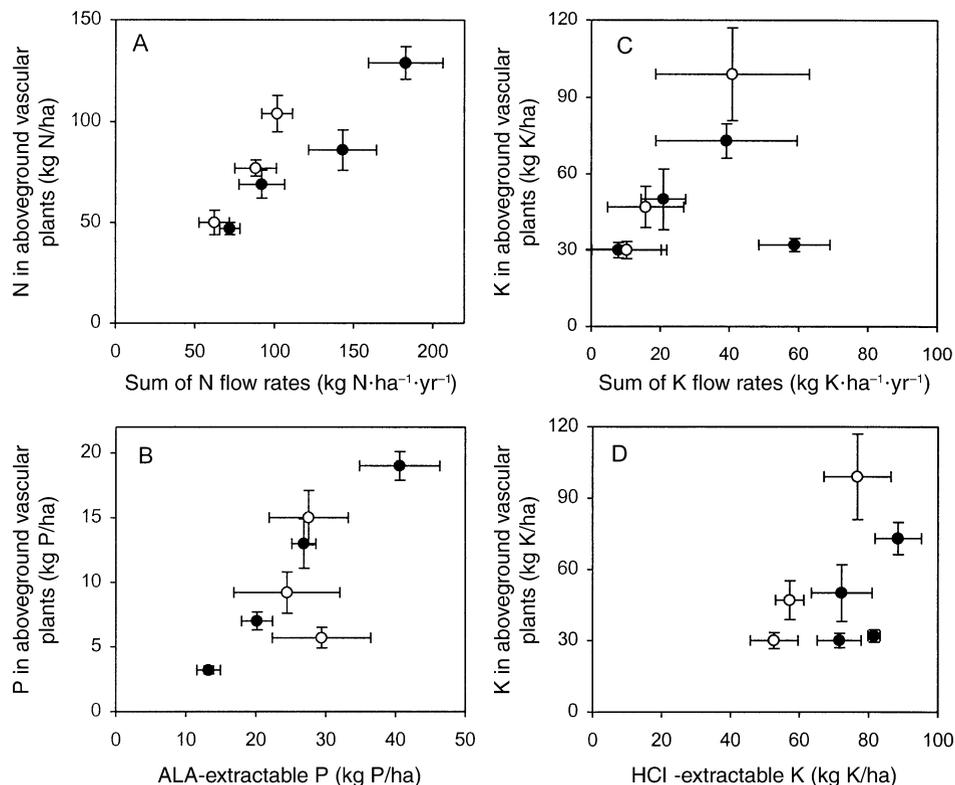


FIG. 4. Amounts of N, P, or K in aboveground biomass of vascular plants at the peak of the growing season (July 1995) vs. assessed N, P, and K availabilities for plants. Panels (A) and (C) show N and K in vegetation vs. sum of annual flow rates of various external flows and soil nutrient turnover rates; panels (B) and (D) show P and K in vegetation vs. extractable pool indices (see Table 6). Filled circles are meadow types; open circles are fen types. Error bars represent ± 1 SE.

nitrate concentrations in soil moisture in the other types or in groundwater (0.1–0.7 mg N/L). Phosphorus input and output flow rates by groundwater ranged between 0.03–0.28 kg P·ha⁻¹·yr⁻¹ and 0.01–0.11 kg P·ha⁻¹·yr⁻¹, respectively. Potassium input and output rates by groundwater flow ranged between 1.0–5.6 and 0.3–5.7 kg K·ha⁻¹·yr⁻¹, respectively.

Soil nutrient turnover

Mean turnover rates of nitrogen in the soil ranged between 19 and 133 kg N·ha⁻¹·yr⁻¹ in the various wetland types, and were significantly higher in the highly productive meadows and fens than in low productivity ones (Table 4). Mean P turnover rates in the soil had relatively large standard errors and ranged around zero in both meadows and fens. Mean K turnover rates were relatively high in *Caltha* meadows and *Carex acuta* fens (48–42 kg K·ha⁻¹·yr⁻¹), and were 5–10 times higher than in *Molinia* meadows and *Carex nigra* fens. Variation in K turnover rates was, however, just as for P turnover rates relatively large.

Nutrient availability and nutrients in vegetation

Atmospheric N deposition and N turnover rates in the soil were the most important sources for N availability (Fig. 3). Atmospheric deposition determined up

to 63–76% of N availability in the low productivity *Molinia* meadows and *Carex nigra* fens, whereas differences in N availability between the sites were primarily determined by differences in N turnover rates in the soil. Mean N availability for plants in our meadow and fen types ranged between 60 and 180 kg N·ha⁻¹·yr⁻¹, whereas N in the aboveground vascular plants at the peak of the growing season was 50–130 kg N/ha (Fig. 4A). Moreover, N in vascular plants increased significantly with increasing N availability (Table 5).

According to the amounts of P in the aboveground vascular plants, P availability for plants must have been at least in the range of 2.5 kg P·ha⁻¹·yr⁻¹ in the low productivity *Molinia* meadows to 19 kg P·ha⁻¹·yr⁻¹ in the highly productive *Glyceria* meadows (Fig. 4B). This range of P availability was ~20 times higher than the sum of flow rates of P from external sources (0.16–1.0 kg P·ha⁻¹·yr⁻¹). Including soil turnover rates in calculations of P availability yielded negative P availabilities for four of the seven vegetation types (cf. Table 4). So, true P turnover rates in soil were not appropriately assessed. As an alternative measure for soil-P availability, we also measured soil extractable-P pools. Biomass of vascular plants, and amounts of P in it, increased significantly with increasing soil extractable-

TABLE 5. Relationships between aboveground biomass of vascular plants at the peak of the growing season, or N, P, and K in aboveground biomass, vs. N, P, and K availabilities.

Parameter	Aboveground biomass vascular plants			N, P, or K in vascular plants		
	Meadows (df = 28)	Fens (df = 12)	Whole set (df = 42)	Meadows (df = 28)	Fens (df = 12)	Whole set (df = 42)
Sum of N flow rates	0.44¶***	0.44 **	0.39¶***	0.42¶***	0.46¶**	0.42¶***
Sum of P flow rates	NS	NS	NS	NS	NS	NS
Sum of K flow rates	NS	0.26§†	NS	NS	0.35 *	NS
P pool ALA‡	0.27 **	NS	0.09 *	0.44 ***	NS	0.31 ***
P pool Bray II‡	0.32¶***	NS	0.14¶*	0.50 ***	NS	0.34¶***
K pool ALA‡	NS	0.24†	0.12§*	0.13§†	0.37§*	0.17§**
K pool HCl‡	NS	0.42 *	0.15§*	NS	0.59§***	0.10§*

Notes: Availabilities were assessed by summation of annual rates of external flows and soil turnover (for N, P, and K), and additionally by Bray II- or ALA-extractable soil pools (for P), and ALA- or HCl-extractable soil pools (for K). Amounts of N, P, or K in biomass (in kg/ha) were regressed vs. N, P, or K availability, respectively. Values represent R^2 values of linear, logarithmic, or inverse regressions (highest R^2 values of the three regressions is shown).

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.1$.

‡ See Table 6.

§ Linear regression.

|| Logarithmic regression.

¶ Inverse regression.

P pools (both Bray-II and ALA) in meadows, but not in fens (Table 5). Mean ALA-extractable P pools resembled amounts of P in the vascular plants more than Bray-II pools (cf. Fig. 4B and Table 6).

In the *Caltha* meadows, the sum of K annually supplied by the various external flows and soil turnover (60 kg K/ha) was higher than K in aboveground vascular plants at the peak of the growing season (32 kg K/ha; Fig. 4C). In the other meadow and fen types this sum (8–40 kg K/ha) was two to four times lower than K in aboveground vascular plants (30–100 kg K/ha; Fig. 4C). Mean HCl-extractable K pools in the soil, however, ranged between 50–90 kg K/ha (Table 6), which indicates that plant available K in the soil was higher than the K turnover rates we measured. Biomass of vascular plants, and amounts of K in them, were significantly related to particularly HCl-extractable K pools in fens, but not in meadows (Table 5). The only

important external input flow for K was flooding; it could explain 20–30% of K in aboveground vascular plants in the *Caltha* meadows and *Glyceria* meadows.

Impact of hay harvest

Annual N output by hay harvesting was more or less equal to annual N input by atmospheric deposition in the low productivity meadows and fens. Hay harvesting therefore prevents enrichment by removing N, but does not decrease the soil N pool in these ecosystems (Fig. 5A). In the more highly productive sites, there was a net annual N output up to 100 kg N·ha⁻¹·yr⁻¹, which removed <3% of the total amount of N from the top 10 cm soil (Fig. 5A). Outputs of P and K by hay harvesting were larger than external inputs of P and K at all sites, hence harvesting reduces the pools of P and K in the soil. Net P output ranged from 2 to 23 kg P·ha⁻¹·yr⁻¹, which represented 0.5–3% (a few sites 7%)

TABLE 6. Extractable P and K pools in the top 10 cm of soil (mean ± 1 SE) in seven types of meadows and fens.

Habitat type	No. sites	ALA-extractable P† (kg P/ha)	Bray II-extractable P‡ (kg P/ha)	NH ₄ -exchangeable K§ (kg K/ha)	HCl-extractable K (kg K/ha)
Meadows					
<i>Molinia</i>	8	13.3 ± 1.7 ^c	9.9 ± 1.3 ^c	34.4 ± 2.4 ^{a-c}	71.5 ± 6.4 ^{b-d}
<i>Caltha</i>	7	20.2 ± 2.2 ^b	20.1 ± 5.8 ^{bc}	29.2 ± 1.3 ^{b-d}	81.6 ± 1.8 ^{ab}
<i>Holcus</i>	6	26.9 ± 1.7 ^b	92.4 ± 9.6 ^a	24.4 ± 1.8 ^e	72.3 ± 8.8 ^{a-d}
<i>Glyceria</i>	9	40.6 ± 5.8 ^a	95.2 ± 28.7 ^a	40.9 ± 4.7 ^{ab}	88.5 ± 6.7 ^{a-c}
Fens					
<i>Carex nigra</i>	6	29.4 ± 7.0 ^{a-c}	166.0 ± 66.3 ^{a-c}	25.3 ± 4.2 ^{cd}	52.7 ± 6.9 ^d
<i>Carex curta</i>	3	24.4 ± 7.6 ^{a-c}	69.8 ± 34.0 ^{a-c}	23.4 ± 3.0 ^{de}	57.2 ± 4.1 ^{cd}
<i>Carex acuta</i>	5	27.5 ± 5.7 ^{a-c}	108.6 ± 39.8 ^{a-c}	36.9 ± 4.6 ^{a-d}	76.8 ± 9.7 ^{a-d}

Notes: Values with different superscript letters are significantly different at $P < 0.05$ (Mann-Whitney U test).

† Ammonium lactic-acid acetic-acid extractable P, determined seven times at every site between May 1995 and June 1996.

‡ Bray II extractable P, determined in May 1995.

§ NH₄-exchangeable K as extracted with ammonium lactic-acid acetic-acid, determined seven times at every site between May 1995 and June 1996.

|| HCl-extractable K representing NH₄-exchangeable K + actively acquirable K by plants, determined seven times at every site between May 1995 and June 1996.

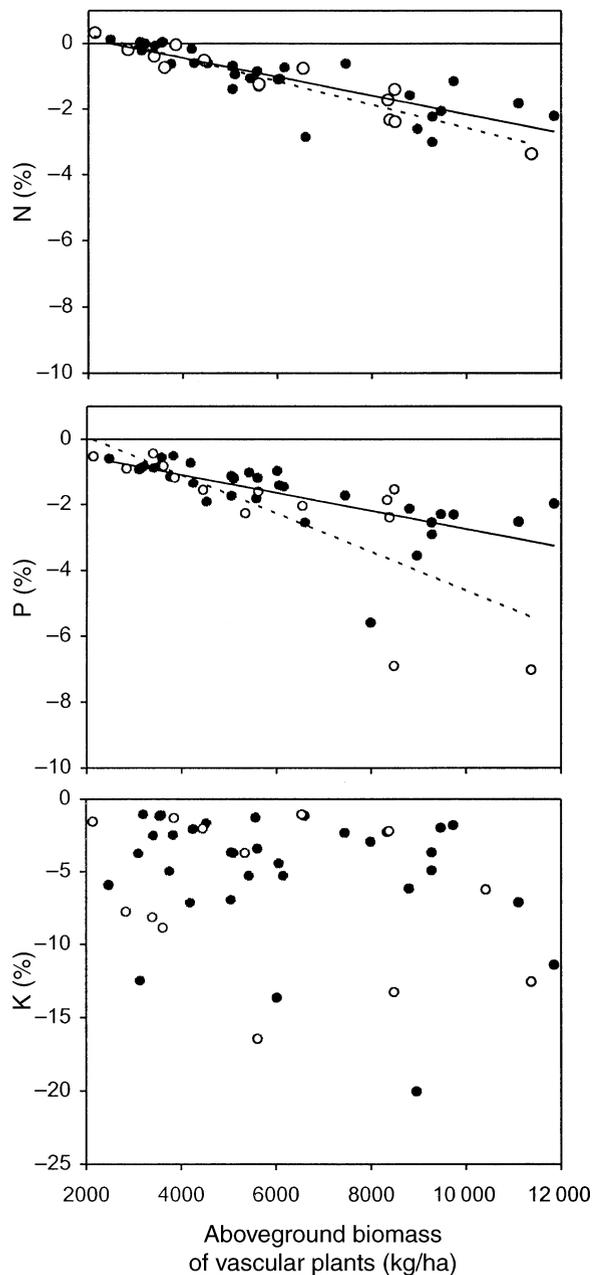


FIG. 5. Net annual output of N, P, and K by hay removal as a percentage of the total amounts of N, P, and K in the top 10 cm of soil, plotted against aboveground biomass of vascular plants in meadows (filled circles) and fens (open circles). Hay removal was assessed by cutting vegetation in the second half of July, the usual time of hay harvesting. Solid lines show linear regressions for the meadows (N, $R^2 = 0.46$, $P < 0.001$; P, $R^2 = 0.88$, $P < 0.001$), and dashed lines for fens (top panel, $R^2 = 0.43$, $P < 0.001$; middle panel, $R^2 = 0.58$, $P = 0.002$). Regressions for K were not significant ($P > 0.1$). Note the different scale of the y-axis for K.

of the total amount of P in the top 10 cm soil (Fig. 5B). Net K output ranged from 8 to 120 kg K·ha⁻¹·yr⁻¹. At half of the sites, net K output was larger than 5% of the total amount of K in the top 10 cm of soil; at most it reached 20% (Fig. 5C).

DISCUSSION

N, P, and K availabilities along biomass gradients

The objective of this study was to evaluate the importance of various nutrient flows for N, P, and K availabilities for plants, along biomass gradients in wet meadows and fens in Western Europe. Our results (Fig. 6) show the relative importance of nutrient flows by atmospheric deposition, flooding, groundwater flow, and soil turnover rates in both low-productivity meadows and high-productivity meadows. Atmospheric deposition was a very important source of nitrogen in both low-productivity and high-productivity meadows, and there were much higher soil nutrient turnover rates in the highly productive meadows. The amounts of P and K in hay that was removed from the sites, in both the low-productivity and high-productivity meadows, indicated substantial annual P and K availabilities which were not supplied by P and K inputs from external sources, suggesting relatively large P and K turnover rates in the soil. Such important soil nutrient turnover rates could not (phosphorus) or only partly (potassium) be demonstrated by soil incubation techniques, but were supported by soil extractable P and K pools (Table 4, Fig. 4).

We assessed nutrient budgets along biomass gradients in order to analyze the process of eutrophication in Western European meadows and fens. Alternative to measuring changes of nutrient flows in time, we studied spatial variation to obtain insight in the possible mechanisms involved in a temporal availability increase of the growth-limiting nutrient. Analogously to the eutrophication process, there was a shift in species composition along our biomass gradients (Table 1), and biomass of vascular plants (particularly of graminoids) increased, whereas biomass of bryophytes decreased (Fig. 2). Together with this aboveground indication of nutrient enrichment, we also found increasing "availabilities" of N, P, and K along our gradients.

Aboveground biomass of vascular plants, and the amount of N in it, increased significantly with increasing N availability (sum of external flows and soil turnover; Fig. 4A, Table 5). The amount of N in the aboveground biomass was on average ~75% of the assessed N availability (Fig. 4A). We conclude that N availability was assessed fairly well. The fact that the amount of N in biomass was lower than the assessed N availability is most likely due to underestimation of total plant productivity and total plant uptake, because growth and nutrient uptake by roots was not included, nor was the vegetation's turnover of biomass and nutrients within the growing season. The availabilities of

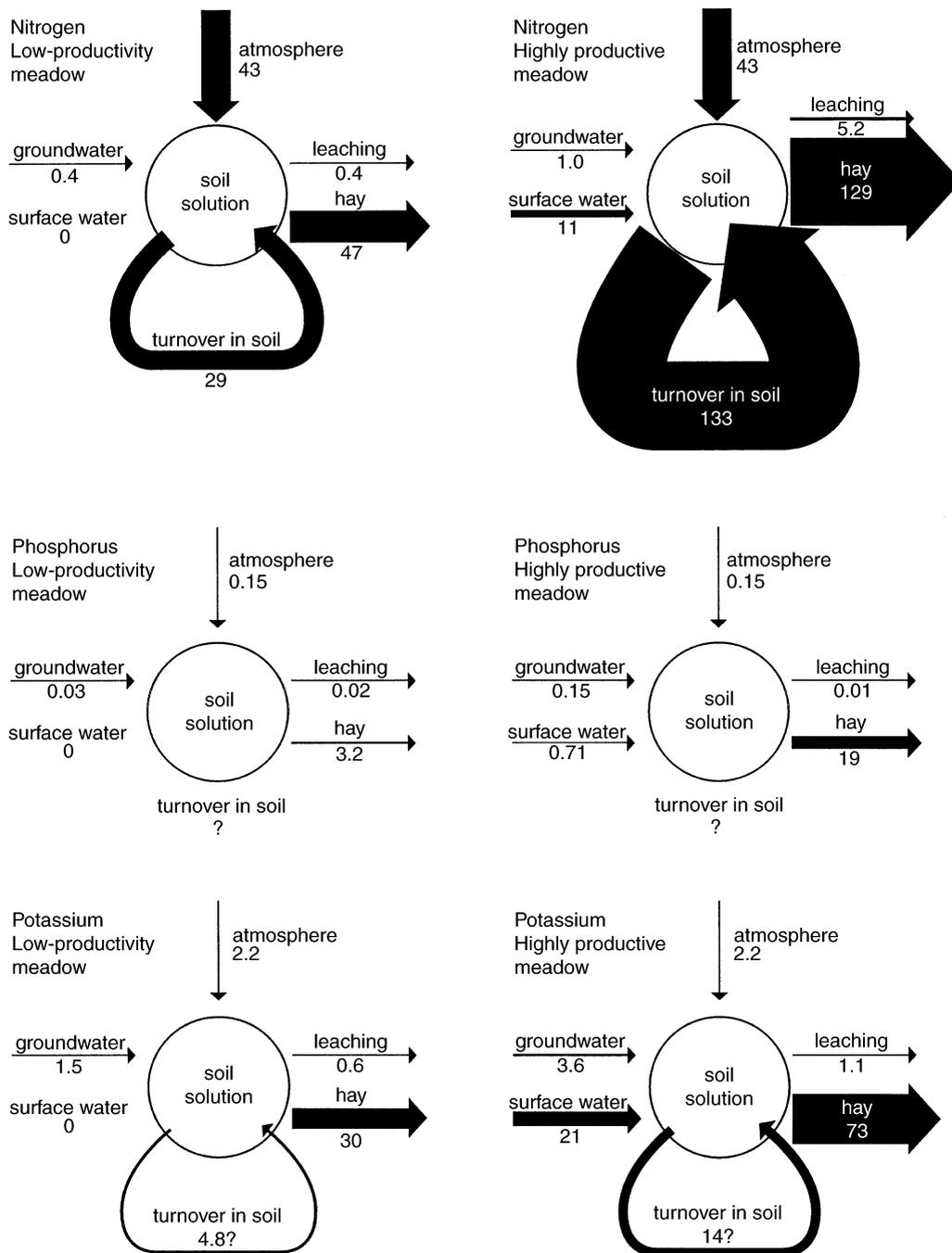


FIG. 6. Schematic representation of annual N, P, and K flows into, out of, and within the root zone of low-productivity *Molinia* meadows and highly productive *Glyceria* meadows. All flows are shown in kg N, P or K per hectare per year. Arrow thickness corresponds to flow size, except for flows <2 kg·ha⁻¹·yr⁻¹. Data are from Tables 2, 3, and 4 and Fig. 4. Soil nutrient turnover rates were not reliably assessed for phosphorus and are likely to be underestimated for potassium in this study.

P and K were more difficult to assess by summation of external flow rates and soil nutrient turnover rates, because soil incubation techniques did not yield proper or full estimates of P and K turnover rates. For P, this may be due to microbial immobilization of released P or because of the complex P equilibrium dynamics with

Ca or Fe in the soil (cf. Richardson and Marshall 1986, Walbridge 1991). Underestimation of K turnover rates in the soil was likely due to exclusion of soil acidification and subsequent K solubilization by plant roots (cf. Jungk and Claassen 1986). The alternative measures for P and K avail-

TABLE 7. Growth-limiting nutrients in seven types of meadows and fens as indicated by the ratios of N, P, and K concentrations in the aboveground biomass of vascular plants.

Habitat type	Nutrient ratios in vascular plants		Growth limiting nutrient
	N:P	N:K	
Meadows			
<i>Molinia</i>	15.1 ± 0.6 ^a	1.7 ± 0.2 ^{a-c}	N and/or P
<i>Caltha</i>	10.0 ± 0.8 ^b	2.2 ± 0.2 ^a	N and/or K
<i>Holcus</i>	6.8 ± 0.3 ^c	2.0 ± 0.3 ^{ab}	N and/or K
<i>Glyceria</i>	6.9 ± 0.3 ^c	1.9 ± 0.2 ^{ab}	N
Fens			
<i>Carex nigra</i>	9.3 ± 1.0 ^b	1.7 ± 0.1 ^b	N
<i>Carex curta</i>	8.8 ± 1.2 ^b	1.7 ± 0.2 ^{a-c}	N
<i>Carex acuta</i>	7.1 ± 0.5 ^c	1.1 ± 0.2 ^c	N

Notes: Critical values of the N:P and N:K ratios are ~15 and ~2.1 respectively (Wassen et al. 1995, Koerselman and Meuleman 1996, Olde Venterink 2000). Values with different superscript letters are significantly different at $P < 0.05$ (Mann-Whitney U test).

abilities in the soil-extractable P and K pools (1) increased significantly with P or K in vascular plants (in meadows or fens, Table 5), and (2) could, in contrast to P and K supply from external sources, account for the amounts of P and K in vascular plants (Fig. 4).

The significant relationships between biomass of vascular plants and N availability (sum of all external flows and soil turnover), and extractable P and K pools (Table 5) indicate that all three nutrients could control growth in at least a part of our sites. Fertilization experiments have shown that N is the most frequently growth-limiting nutrient in Western European wetlands, but P and/or K (co)limitation also occur (Verhoeven et al. 1996, Olde Venterink et al. 2001a). Consistently, ratios of N:P and N:K in the vegetation indicated that N was the major growth-limiting nutrient in our meadows and fens, but also indicated possible (co)limitation of P and K in a part of the sites (Table 7).

Soil nutrient turnover

The dominant role of soil processes for differences in nutrient availability along our biomass gradients, as indicated by both N and K turnover rates (Figs. 3, 6) and soil extractable P and K pools (Fig. 4), agrees well with the importance of soil processes for availabilities of nutrients in other meadows (Grootjans et al. 1985, 1986, Berendse et al. 1994, Olf et al. 1994), fens (Richardson and Marshall 1986, Walbridge 1991, Koerselman and Verhoeven 1992), as well as other terrestrial ecosystems as tundra (Chapin et al. 1978), heathlands (Rozé 1988), bogs (Hemond 1980), and forests (Pastor et al. 1984, Birk and Vitousek 1986; see also Table 8). Moreover, it should be noted that we would have found even a greater importance of soil processes for nutrient availability in our sites, if we had made our measurements and calculations for a larger root zone than the top 10-cm soil layer.

The dominant role of soil processes in setting nutrient availability also demonstrates that human alterations of site conditions, resulting in increased soil nutrient turnover rates by, for instance, increased min-

eralization, may influence nutrient availabilities for plants that can go far beyond effects of increased nutrient inputs from external sources. Lowering of groundwater tables, a usual phenomenon in Western Europe, is an example of an altered site condition that can cause severe nutrient enrichment through increased aeration of wetland soil and subsequent increased mineralization rates (e.g., Grootjans et al. 1985, Laine et al. 1995, Bridgham et al. 1998). Alterations in soil acidity, soil redox status, or even soil compaction as a consequence of management with heavy machinery, are other examples of changed site conditions that may lead to increased soil nutrient turnover rates and internal eutrophication (e.g., Koerselman et al. 1993, Lamers et al. 1998, Olde Venterink 2000).

External nutrient flows

External nutrient flows were of different importance for availabilities of N, P, or K. They seemed negligible for P availability, of moderate importance for K availability (flooding), but could be very important for N availability (atmospheric deposition). In the low-productivity meadows and fens, N deposition of 43 kg N·ha⁻¹·yr⁻¹ made up 63–76% of N availability. We did not have the facility to measure differences in atmospheric N deposition among sites, but current estimates span 30–70 kg N·ha⁻¹·yr⁻¹ for the region (Erisman and Bobbink 1997). N deposition has increased from 5–20 kg N·ha⁻¹·yr⁻¹ before the 1950s (Erisman and Draaijers 1995). Hence, from a historical point of view, atmospheric N deposition has likely increased N availability, and may have caused eutrophication, in our N-limited sites as well as other N-limited meadows, fens, heathlands, and bogs in Western Europe (Bobbink et al. 1998). Atmospheric N deposition in other parts of the world (7–20 kg N·ha⁻¹·yr⁻¹; Table 8) are clearly lower than in our area, but might obviously cause eutrophication in N limited ecosystems when the N input is not accompanied by a comparable annual N output, for instance in our sites with hay removal.

Flooding was almost completely restricted to the

TABLE 8. Nutrient flow rates from and to external sources (kg·ha⁻¹·yr⁻¹), soil nutrient turnover rates (kg·ha⁻¹·yr⁻¹), soil extractable nutrient pools (kg/ha), and nutrients in vegetation (kg/ha) in wetlands and grasslands.

Ecosystem†	Input and output flow rates					
	Atmospheric deposition	N fixation	Denitrification	Surface water in	Ground-water in	Surface water out
Nitrogen						
Bog (USA)	7.5	10	0–4
Bog (USA)	7.3	0.5	1.8	...	5.4	6.4
Bog (UK)	8.2	2.9–17.5‡
Bog (IRE)	24	7.5–17‡
Fens (NL)	42–44	2.1–13	1.1–1.4	1.3–7.3	0–20	9.3–21
Fen (NL)	42–48	20	...	10–12	0	...
Intertidal marsh (USA)	8–11	3–68	4–140	570–670	...	540–650
Heathland (UK)	8.1	1–4
Savanna (IC)	19	10
Pampa (ARG)	7.5
Meadows (NL)
Meadows (NL)	60	<1	16–18
Wet meadow (DK)	21	...	31	...	39	...
Grassland (USA)	9–10	0–26
Prairie (USA)	10
Artificial flood meadows (S)	20	...	220–460	270–700	...	230–610
Herbaceous wetlands	10–20	0–30	0–10‡	0–50
This study‡	43	0–11	0.4–2.8	...
Phosphorus						
Bog (USA)	0.6	0.5	0.5
Bog (UK)	0.5–0.7	0.4–0.8‡
Bog (IRE)	0.7	0.1–0.5‡
Fens (NL)	0.5–0.7	0.1–0.5	0–0.5	0.7–1.0
Fen (NL)	0.1–0.5	0.3–0.5	0	...
Fen (USA)	0.3
Riparian marshes (USA)	5.4–31‡	...	0.6–11
Cypress swamp (USA)	1.1	36‡	0.1	...
Tundra (USA)	0.01
Wet meadow (DK)	2.4	0.5	...
Pampa (ARG)	0.4
Grassland (USA)	~0
This study‡	0.15	0–0.7	0.03–0.3	...
This study‡
Potassium						
Bog (USA)	0.9
Bog (USA)	4.0	6.1
Bog (UK)	3.1	7.0	9–11‡
Bog (IRE)	18	3.1–7.4‡
Fens (NL)	6.1–6.2	3.9–19	...	13–22
Fen (NL)	2–18	52–71	0–5.9	...
Various wetlands (USA)
This study‡	2.2	0–21
This study‡	1.0–3.6	...

Note: Nutrient flow rates by surface water or groundwater are based on water budgets for the root zone (RZ) or for whole areas (A).

† USA, United States; UK, United Kingdom; IRE, Ireland; NL, Netherlands; IC, Ivory Coast; ARG, Argentina; DK, Denmark; S, Sweden.

‡ Refers to a note following the reference.

§ 1, Hemond (1980, 1983). 2, Verry and Timmons (1982); Urban and Eisenreich (1988). 3, Crisp (1966); low values are estimates for mineral NPK in surface water outflow; high values include NPK from erosion. 4, Burke (1975); calculated from annual water budgets and three months NPK measurements in drained and undrained plots. 5, Koerselman and Verhoeven (1992); soil turnover rates (0–20 cm) from Verhoeven and Arts (1987); ALA-extractable P and K pools (5–15 cm) from Koerselman et al. (1999). 6, van Wirdum (1991). 7, Morris (1991). 8, Rozé (1998). 9, de Mazancourt et al. (1999). 10, Chaneton et al. (1996); soil turnover rates calculated from 150-d nutrient budgets. 11, Olf et al. (1994). 12, Berendse et al. (1994). 13, Hoffman (1998); soil turnover rates calculated for 100 d; P turnover calculated from ammonification rate. 14, Woodmansee and Duncan (1980); soil turnover rate based on budgets. 15, Risser and Parton (1982); soil turnover rate from simulation. 16, Davidsson and Leonardson (1998). 17, usual range in wetlands from a review by Bowden (1987). 18, Richardson and Marshall (1986); Bray II P pool. 19, Mitsch et al. (1995); P inflow from surface water includes sediment P. 20, Mitsch et al. (1979); P inflow from surface water includes sediment P. 21, Chapin et al. (1978); value for leaching was run-off, Bray II P pool. 22, Bridgham et al. (1998); NH₄-exchangeable K. 23, ranges of mean values for seven meadow and fen types of this study, data from Fig. 4, Tables 2, 3, and 4 and ALA P and K pools from Table 6. 24, as 23 but Bray II-extractable P pools and HCL-extractable K pools from Table 6.

TABLE 8. Extended.

Input and output flow rates		Soil				Vegetation aboveground	Reference§
Leaching	Budget for	Depth (cm)	Turnover rate	Extractable nutrient pool			
2-3	RZ	0-20	26	...	30	1	
...	RZ	2	
...	A	3	
...	RZ	4	
0.3-1.0	RZ	0-20	67-320	...	54-120	5	
7-8	RZ	0-20	28-170	...	38-140	6	
...	A	?	180-200	...	160-230	7	
3-4	RZ	?	39-150	...	45-144	8	
5.5	RZ	?	79	...	20	9	
...	...	0-12	64-71‡	...	11-23	10	
...	...	0-10	61-180	...	72-110	11	
0-3	RZ	0-10	160-200	...	140-170	12	
2	A	?	110-140‡	...	90	13	
...	...	0-30	83-130	...	36-65	14	
...	...	0-20	48-53‡	...	40-52	15	
...	A	...	high	...	65-110	16	
...	20-180	...	~30-350	17	
0.4-11	RZ	0-10	19-133	3-11	47-129	23	
...	RZ	2	
...	A	3	
...	RZ	4	
0.02-0.1	RZ	...	3.4-44‡	1.2-1.7‡	3-11	5	
1.2-1.3	RZ	0-20	-0.1-3.2	...	1.6-8.9	6	
...	...	0-20	0.6	9‡	6	18	
...	A	11-47	19	
3.4	A	0-24	8.7-33	20	
0.002‡	RZ	0-20	1.5	34‡	2.8	21	
0.1	A	?	12-16‡	...	11	13	
...	...	0-12	4.7-6.5‡	2.3-2.5	1.1-2.4	10	
...	...	0-30	13-15	23-60	9.12	14	
0.01-0.1	RZ	0-10	?	13-41‡	3.2-18.8	23	
...	...	0-10	...	10-95‡	...	24	
1.1	RZ	0-20	1	
...	RZ	2	
...	A	3	
...	RZ	4	
0.1-2.0	RZ	5-15	...	4.0-17‡	28-70	5	
60-87	RZ	0-20	-9-85	...	46-120	6	
...	...	0-10	...	22-108	...	22	
0.3-5.7	RZ	0-10	4.8-48	23-41‡	30-99	23	
...	...	0-10	...	53-89‡	...	24	

Caltha meadows and *Glyceria* meadows (Table 2). At very high river discharges these meadows are subjected to flooding events. We assessed nutrient input from the only flooding event in the measuring period (in May 1995) without correcting for the amounts of nutrients that returned to the river later (see *Methods*). This worst-case assessment showed that flooding might be a relevant input source for K—it could account for 20–30% of K in aboveground vascular plants—but it seemed of minor importance for N and P availability. Obviously, the importance of flooding will be larger in ecosystems with higher flooding frequencies, or continuous input and output flows of river water, such as intertidal marshes, riparian zones, or artificially flooded

meadows (cf. Table 8). Furthermore, it should be noted that input of nutrients adsorbed to sediment was not included in the assessment, which could be of particular importance for P availability in riparian wetlands (Mitsch et al. 1979, 1995: Table 8).

Contributions of nutrient input and output by groundwater flow to nutrient availability in the meadows and fens were more or less negligible, despite decades of heavy fertilization in the water infiltration areas. Taking into account that we modeled water flow for a root zone of 30 cm, the amounts of water and nutrients in it were within the range of assessments for other fens (Koerselman et al. 1990) and bogs (Verry and Timmons 1982), although our assessments were

made for a dry year (see Appendix). Higher estimates of nutrient supply by groundwater flows in the literature are all estimates for entire riparian areas (regardless of the soil depth; cf. Table 8), which do not provide information for the root zone and consequently availability for plants. In fact, our conclusion that inflow from groundwater hardly contributes to nutrient availability is consistent with the observations that N in groundwater descending from agricultural land disappeared by denitrification before reaching the root zone (Lowrance et al. 1983, Hill 1996, Hoffmann 1998), that P was adsorbed to the soil near the agricultural land (Hoffmann 1998, Olde Venterink et al. 1999), and that K was present in deeper groundwater but had not reached the root zone (Olde Venterink et al. 1999).

Unquantified nutrient flows

Denitrification rates in the root zone of freshwater wetlands are usually in the range of 0–10 kg N·ha⁻¹·yr⁻¹ (Bowden 1987). Our N availability assessment should, however, not be diminished with such a value because denitrification was implicitly included in the measurements of net soil N turnover. The accumulation of N in the incubated soil cores was the result of ammonification and nitrification minus denitrification. We note that the N output flow by denitrification may have been different in incubated cores than in the field due to N accumulation or altered pore space and moisture conditions in the cores (cf. Olde Venterink 2000). Nevertheless, since denitrification depends on soil nitrate concentrations, which were only high in the *Holcus* and *Glyceria* meadows, relatively high denitrification rates of 10 kg N·ha⁻¹·yr⁻¹ likely only occurred in sites with a high N availability (150–180 kg N·ha⁻¹·yr⁻¹). Therefore the contribution of denitrification to the annual N budgets likely did not exceed 5–10%.

Atmospheric N₂ fixation was not included in our budgets. Boring et al. (1988) assessed nonsymbiotic N₂ fixation at <1–5 kg N·ha⁻¹·yr⁻¹, and symbiotic N₂ fixation, particularly in forests, at ~10–160 kg N·ha⁻¹·yr⁻¹. In our sites, legumes were generally not abundant. The mean percentage cover by legumes (of total cover) was, at 12%, the highest in the *Caltha* meadows (Table 1). Assuming that 12% of all N in aboveground vascular plants was derived from this process, symbiotic N₂ fixation would account for 8 kg N·ha⁻¹·yr⁻¹, corresponding to 8% of N availability, in these meadows. A rate of 8 kg N·ha⁻¹·yr⁻¹ matches with reported N₂ fixation rates for herbaceous ecosystems (cf. Table 8). N₂ fixation seems less important in the other meadows and fens since cover of legumes was 3–40 times lower than in the *Caltha* meadows (Table 1).

Impact of hay harvesting

Considerable amounts of N, P, and K were annually removed from our sites by mowing and removal of the vegetation near the peak of the growing season (Figs. 3 and 4). In the low-productivity meadows and fens,

N output by hay was more or less equal to N input from atmospheric deposition, whereas P and K output by hay were larger than external P and K inputs (e.g., Figs. 5 and 6). So annual hay harvesting prevents N enrichment, and seems to induce P and/or K limitation in the longer term (e.g., Koerselman et al. 1990). However, to evaluate the impact of hay removal on the type of nutrient limitation in the longer term, nutrient output flows should not only be compared with nutrient input flows, but also with sizes of total nutrient pools in the soil. By comparison, the relative net output of N and P were of similar orders of magnitude (generally 0–3% of total pools) along the biomass gradients, whereas relative net K output was much larger in half of the sites (up to 20% of the total K pool; Fig. 5). We conclude that hay removal may reduce K availability and cause K limitation within ~10 yr, whereas reduction of N and P availability will likely require a three to four times longer period of hay removal. This is consistent with Oomes et al. (1996) who observed a decreased K concentration in meadow vegetation after 9 yr of hay harvesting while N and P concentrations were not changed, and with Olf et al. (1994) who found that N mineralization rates were reduced after 26–45 yr of annual hay removal in meadows.

CONCLUSIONS

Variation in nutrient availability across a gradient of low- to high-productivity wetlands in our study was caused by soil processes, not by variability in nutrient inputs across the sites. Based on this result, we conclude that alterations of environmental conditions in the root zones is probably the major stimulating factor for nutrient enrichment and eutrophication in wetlands, although historical nutrient inputs from external sources may also have stimulated soil nutrient turnover rates. Hence, conservation or restoration of low-productivity and species-rich wetlands primarily requires stable site conditions controlling low N, P, and K turnover rates in the soil.

The analysis of spatial differences in nutrient flows and availabilities along productivity gradients does not allow for the effect of a temporal increase in a nutrient input flow operating on a large geographical scale, such as the increased atmospheric N deposition in Western Europe. On average, atmospheric N deposition made up 63–76% of the availability of this important growth-limiting nutrient in our low-productivity meadows and fens. It is obvious that atmospheric N deposition causes eutrophication in many low-productivity wetlands in Western Europe and other regions, particularly when the N input is not accompanied by a comparable annual N output, like in our sites with hay-harvesting.

Annual nutrient output by hay harvesting seemed an effective management measure to compensate for annual N input from external sources as deposition. However, long-term hay removal likely affects the kind of nutrient limitation; i.e., net annual outputs of P and K

were much larger than that of N in our low-productivity sites. Accounting for the net N, P, and K output by hay harvesting revealed that hay harvesting may induce K limitation. Hay harvesting may therefore have a large impact on species composition and productivity in wetlands, through its effect on the kind of nutrient limitation (cf. Olde Venterink 2000).

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APPENDIX

A description of the calculation of water balance is available in ESA's Electronic Data Archive: *Ecological Archives* A012-099-A1.