Applied Vegetation Science 9: 213-222, 2006

Comparison of nitrogen and phosphorus fluxes in some European fens and floodplains

Wassen, Martin J.[1*] **& Olde Venterink, Harry**[2]

[1]*Environmental Sciences, Copernicus Institute for Sustainable Development and Innovation, Utrecht University, PO Box 80115, 3508 TC Utrecht, The Netherlands;* [2]*Institute of Integrative Biology, ETH Zürich, CH-8092 Zürich, Switzerland;* [*]*Corresponding author; Fax +31 302532746; E-mail m.wassen@geo.uu.nl*

Abstract

Question: How do nitrogen and phosphorus budgets and balances differ between eutrophic fens and floodplains in western Europe and fens and floodplains in Poland, where we expect less eutrophication to occur?

Location: Wetlands along the rivers Dommel (The Netherlands), Zwarte Beek (Belgium) and Biebrza (NE Poland).

Methods: Assessment of external input and output fluxes as well as net N-mineralization rates. Annual N- and P-balances were estimated by the sum of all external input and output fluxes: atmospheric deposition, input of dissolved matter by flooding, input of sediment by flooding, input by groundwater, output by leaching, output by hay-making and for N also input by N_2-fixation. For N we also estimated net annual N-availability for plant growth, i.e. the N-budget, which includes net mineralization in soil.

Results: The studied wetland sites had a negative balance, which means that nutrients are depleted but only if mown annually, except for the Dutch/Belgian fens which had an equilibrium N-balance and the Polish fen which had an equilibrium P-balance. For the N-budget it appeared that atmospheric deposition added significantly to the budget of Dutch/Belgian fens and N-mineralization added significantly to fen and floodplain budgets, except for the Polish fens. Mineralization dominates the N-budget of the western European floodplains. Hay-making is the most important output pathway, particularly if practised annually. It seems to diminish N-enrichment in the Dutch fens and floodplains.

Conclusions: We conclude that western European fens and floodplains as well as Polish floodplains have a significant positive N-budget indicating that there is a surplus of N for plant growth. In the Polish fens this is less due to low atmospheric deposition and lower N-mineralization rates. The latter is associated with less drying out of the studied Polish ecosystems in summer. Our approach, although an approximate quantification, is helpful for assessing priorities focused on nutrient management.

Keywords: Atmospheric deposition; Belgium; Flooding; Groundwater; Mineralization; Netherlands; Nutrient balance; Nutrient budget; Poland.

Introduction

Eutrophication is one of the main factors for biodiversity loss in European and North American wetlands. As a result of increased nutrient availability shifts have occurred from low-productivity, species-rich communities to highly productive and species-poorer communities (Fojt & Harding 1995; Rich & Woodruff 1996). Such a productivity increase only occurs if the availability of the potentially growth-limiting nutrient increases. Generally, in aquatic freshwater wetlands of the temperate zone growth is limited by phosphorus (P) (Schlesinger 1997). Terrestrial wetlands such as bogs, fens and floodplains are generally limited by nitrogen (N) or phosphorus, or are co-limited by N and P in the temperate zone (Verhoeven et al. 1996a; Elser et al. 2000; Güsewell & Koerselman 2002, Olde Venterink et al. 2001a, 2003; Wassen et al. 2005).

Eutrophication can be a consequence of increased nutrient fluxes from external sources or the result of accelerated within-stand nutrient cycling through altered environmental conditions. Analysing which factor has increased availabilities of the growth limiting nutrient(s) is difficult since starting conditions are generally unknown and following the eutrophication process in time may require many years. In a previous paper we evaluated the contribution of various external and within-stand fluxes to eutrophication in western European fens and meadows by analysing them along a productivity gradient (Olde Venterink et al. 2002a). The disadvantage of this method is that nutrient fluxes that have increased over the whole gradient will not be detected as important factors for eutrophication. An example of such a factor in this respect is atmospheric N-deposition that has increased in western Europe from less than 10 $kg.ha^{-1}.a^{-1}$ before World War II to > 50 $kg.ha^{-1}.a^{-1}$ in the 1980s (Erisman & Draaijers 1995; Holland et al. 1999).

The aim of this paper is to evaluate the importance of such historical increases of N- and P-fluxes on wetlands by comparing N- and P-budgets in the western

European sites of Olde Venterink et al. (2002a) with comparable sites in the Biebrza valley (NE Poland) where atmospheric N-deposition and other nutrient fluxes are expected to be near to natural background levels. We restricted our study to two important lowland wetland types: fens and river marginal floodplains. In these areas the following nutrient fluxes are considered important: atmospheric deposition, nutrient supply by flooding and groundwater flow, nutrient leaching to groundwater and, in the case of N, denitrification and N_2-fixation. In European nature reserves plant biomass is often harvested and exported with the aim of impoverishment of eutrophic ecosystems. Therefore, hay-making is also an important export flux (Koerselman & Verhoeven 1992; Olde Venterink et al. 2002a; van der Hoek et al. 2004). Increased availabilities of N and P may also result from increased mineralization of soil organic matter (e.g. Mengel 1982; Marrs 1993). The data presented here are a compilation of various previous studies and additional measurements. Interpretation of compiled data from different studies, areas and years, sometimes obtained by different methodologies requires care but potentially enables a comparison that goes beyond the possibilities of a single study.

Methods

Study sites

The western European sites were located in nature reserves along the river Dommel (The Netherlands) and in reserves along the Zwarte Beek (Belgium) (5°15' - 5°40' E and 51°05' - 51°45' N). The sites were not fertilized and have been annually mown for at least ten years, in most cases for over 20 years. Hay was removed after mowing. The Polish sites were located in the Biebrza National Park (22°30' - 23°60' E and 53°30' - 53°75' N). The sites were not fertilized and have been mown regularly for decades (frequency almost annually). Hay was removed after mowing. However, since World War 2 this practice has been abandoned in the floodplain and since then the fen sites we studied have been irregularly mowed.

In both areas the floodplains have highly productive, species-poor vegetation whereas the fens have lower above-ground standing crop of vascular plants and have a significant moss layer (Table 1). The species composition of the fens is characterized by low growing sedges such as *Carex nigra*, *C. panicea*, *C. diandra* and *C. limosa* and forbs such as *Menyanthes trifoliata* and *Potentilla palustris*. The western European floodplain vegetation consists of grassland dominated by *Glyceria maxima* and *Phalaris arundinacea* and other tall growing grasses. The Polish floodplain also contains these tall growing grasses and has a high cover of tall sedges such as *Carex acuta* and *C. elata* and tall growing forbs such as *Rumex hydrolapathum*, *Iris pseudacorus* and *Rorippa amphibia*.

The Polish floodplain was deeply flooded in spring; in the western European floodplains the flooding was less. In summer both the Polish floodplains and fens remained wetter than the western European ones. In the Polish fens organic matter content and bulk density were especially high and low, respectively, indicating a typical peat soil, not subjected to sedimentation or drainage. Total soil N and P contents showed large within-site variation (Table 1). Additional information about the study sites is given in Olde Venterink et al. (2001b, 2002a) (The Netherlands/Belgium) and Wassen et al. (1990, 1992, 2002) (Poland).

Vegetation

We recorded the species composition in June and determined above-ground standing crop at the peak of the growing season (end of July/beginning of August). Syntaxonomy followed Schaminée et al. (1995, 1996) (The Netherlands/Belgium) and Palczynski (1984) (Poland). Plant material was divided into vascular plants and mosses, dried for 48 h at 70°C and weighed. Plant material was digested (Kjeldahl); N-concentrations in the digests were analysed colorimetrically, P-concentrations by means of an Inductively Coupled Plasma technique (ICP). The western European data are from Olde Venterink et al. (2001b, 2002a), the Polish data from Wassen et al. (1990, 1995).

Assessment of nutrient fluxes

Atmospheric deposition

For the western European sites annual atmospheric deposition rates of N and P were derived from the National Institute of Public Health and Environment (unpubl. data). These rates are based on extrapolations from measured wet and dry deposition rates in the area (Erisman & Bobbink 1997). We used mean values for 1995 and 1996 for the whole research area. For Poland we used on site measured rates of dry and wet atmospheric deposition as measured by means of through fall gutters at six locations (unpubl. data W. Bleuten).

Input from groundwater / Output by leaching

To assess annual nutrient fluxes between soil moisture and groundwater and *vice versa*, we assessed the

Table 1. Vegetation types, characteristic species, standing crop and site conditions (mean ± 1 SD) of some European fens and flood-plains. Soil variables were measured in the top 10-cm soil. Different characters indicate significant differences ($P < 0.05$; one-way ANOVA, Tukey).

	Dutch/Belgian Fen	Dutch Flood-plain	Polish Fen	Polish Flood-plain
Vegetation type	*Caricetum nigrae*	*Glycerietum maximae*	*Caricetum limoso-diandrae*	*Glycerietum maximae / Caricetum gracilis*
Characteristic species	*Carex nigra* *Carex panicea* *Carex echinata* *Carex lasiocarpa* *Eriophorum angustifolium* *Menyanthes trifoliata*	*Glyceria maxima* *Phalaris arundinacea* *Deschampsia cespitosa* *Carex vesicaria* *Alopecurus pratensis* *Ranunculus repens*	*Carex diandra* *Carex panicea* *Carex limosa* *Carex lepidocarpa* *Calamagrostis stricta* *Menyanthes trifoliata*	*Glyceria maxima* *Phalaris arundinacea* *Carex acuta* *Carex elata* *Equisetum fluviatile* *Rumex hydrolapathum*
Standing crop vascular plants (kg.ha^{-1} dry wt)	3387 ± 807 b	9149 ± 1676 a	1868 ± 304 b	8785 ± 1616 a
Standing crop bryophytes (kg.ha^{-1} dry wt)	532 ± 525 b	27 ± 33 b	2563 ± 2000 a	57 ± 5 b
Water level flood period (cm – surface)	-2 ± 4 bc	-16 ± 6 b	1 ± 3 c	-47 ± 19 a
Water level summer (cm – surface)	47 ± 15 b	110 ± 13 a	7 ± 4 c	25 ± 21 c
Organic matter (%)	37 ± 7 b	29 ± 7 b	82 ± 7 a	53 ± 43 a
Bulk density (g.cm^{-3} dry wt)	0.32 ± 0.06 b	0.52 ± 0.11 a	0.15 ± 0.04 c	0.18 ± 0.11 c
Total soil N (kg.ha^{-1})	3394 ± 548 a	4096 ± 1014 a	3522 ± 1193 a	4454 ± 1337 a
Total soil P (kg.ha^{-1})	670 ± 449 a	716 ± 233 a	583 ± 813 a	119 ± 44 a
Soil extr. P (kg.ha^{-1})	29.4 ± 17.2 ab	40.6 ± 17.2 a	6.6 ± 0.3 c	8.1 ± 1.0 bc
Number of sites	6	9	7-10	7-19

annual water fluxes between the top 30 cm soil layer and the groundwater below, and multiplied them with the mean concentrations of nitrate, ammonium and dissolved P in it. In the western European sites, the water fluxes were based on measured and extrapolated rates of precipitation, evapotranspiration and changes in groundwater levels and soil moisture (cf. Olde Venterink et al. 2002a). For Poland we used the dynamic models MODFLOW and SIMGRO for assessing the mean annual groundwater fluxes to and from the root zone (Mioduszewski & Querner 2002; Batelaan & Kuntohadi 2002). Groundwater samples were taken in piezometers at 80 cm to > 250 cm below the surface level. Soil moisture was collected from the top 10 cm - 20 cm by means of shallow piezometers (Polish sites) or Rhizon soil moisture samplers (Eijkelkamp, Giesbeek; Dutch and Belgian sites); mean concentrations of 8-12 samples were used. The sampling periods were August 1995-September 1996 (Dutch and Belgian sites) and July 1987-August 1999 (Polish sites). Water samples were centrifuged and NO_3^- and NH_4^+ concentrations were measured colorimetrically, dissolved P (also called soluble-reactive P) by means of an ICP.

Input from flooding

In the floodplains, the maximum input of nutrients by floodwater was determined using a worst case assessment: it was assumed that all nutrients in the maximum column of standing floodwater in the floodplain would be available for the plants. To assess N and P input fluxes per square metre the volume of water at maximum flood depth was multiplied with the nutrient concentrations in the flood water (cf. Olde Venterink et al. 2002a). Flood depth and flood water samples were recorded and taken in May 1995 (Dutch/Belgian sites) and in April 1992 and 1993 (Polish sites). Additionally, in the Polish floodplain, inputs of N and P attached to sediment deposited in the floodplain was measured. Net sediment deposition was determined using sediment traps in the form of 50 cm × 50 cm plastic mats (cf. Middelkoop & Asselman 1998). Four replicate traps were placed at three places in the Polish floodplain in autumn 2001 and removed after the spring flood of 2002. The traps were rinsed with tap water under high pressure, and the suspension was collected in a bucket. After 72 hours the standing water was separated from the residue. The residue was dried for 48 h at 70 ºC, and ground. Nutrient contents were determined after Kjeldahl digestion; nutrient concentrations in the digests were determined as in water.

Estimate of N_2-fixation

N_2-fixation was not measured. We estimated what could have been the 'maximum' fixation rate by assuming that all N in the above-ground vegetation of leguminous species at a site was derived from N_2-fixation. We calculated this by multiplying N in above-ground vegetation with the % of vegetation that was made up by legumes (based on cover). Hence, this is a very rough 'maximum' estimate since it does not include the amount of fixed N in roots nor does it account for different N-concentrations in legumes and non-legumes and loss of N through litter production.

Output by hay-harvesting

Annual N- and P-output from hay harvesting were estimated by multiplying the above-ground biomass of vascular plants by their N- and P-concentration. Plant biomass was harvested in the second half of July or beginning of August which is the normal time for hay-making in these areas.

Net N-mineralization

Annual net N-mineralization was measured at every site by *in situ* soil incubation of the top 10cm soil following the technique described by Olff et al. (1994). Net N-mineralization was measured during four or five periods of eight weeks and one winter period of 12-26 weeks between May 1995-April 1996 (Dutch and Belgian sites) and June 2002-July 2003 (Polish sites). Net mineralization rates were calculated by subtracting values in 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 soil.

Data from the Dutch and Belgian sites are from Olde Venterink et al. (2001b, 2002a). The Polish data have not been published before.

Nutrient balances and budgets for the vegetation

Annual N- and P-balances were determined by the sum of all external input and output fluxes: atmospheric deposition (Natm), input of dissolved matter by flooding (Nfd), input of sediment by flooding (Nfs), input by groundwater (Ng), output by leaching (Nl), output by hay-making (Nh), and for N also input by N_2-fixation (Nfix). Output of denitrification could not be included because data were lacking. All fluxes are expressed in kg-N or kg-P.$ha^{-1}.a^{-1}$. The balance is completed with a change in storage pool (dNs). This term indicates if an ecosystem is losing nutrients or is subject to nutrient loading. Thus for N and P respectively we calculated the balances as follows:

$$\text{Natm} + \text{Nfix} + \text{Nfd} + \text{Nfs} + \text{Ng} + \text{dNs} = \text{Nl} + \text{Nh} \quad (1)$$

$$\text{Patm} + \text{Pfd} + \text{Pfs} + \text{Pg} + \text{dPs} = \text{Pl} + \text{Ph} \quad (2)$$

Nitrogen budgets for plants (Nbudget) were determined by the sum of all the external fluxes except output by hay. Thus, the budget does not include output by hay or changes in root biomass. The budget is considered as an estimate of net annual N-availability for plant growth. Hay-making is not included since this is (except for growth of roots and losses) largely what has been available. Net mineralization in soil (Nm) was included in the budget. Thus for N we calculated the budgets as follows:

$$\text{Nbudget} = \text{Natm} + \text{Nfix} + \text{Nfd} + \text{Nfs} + \text{Ng} + \text{Nm} - \text{Nl} \quad (3)$$

Ignoring changes in root biomass is an unknown source of error in the balance as well as in the budget. For P, calculating budgets does not make sense since we have no estimate for annual soil P release which is expected to be, quantitatively, an important P-flux of the budget. For soil P, we only assessed total and extractable contents of samples taken once (see below).

Soil nutrient pools

Total N- and P-pools in the top 10cm soil were determined by taking five soil samples (10 cm depth × 4.8 cm diameter) within every site (November 1995 in the Dutch and Belgian sites; July 1990 in the Polish sites). The five samples were mixed, dried for 48 h at 70 ºC and ground. Soil nutrient contents were determined after Kjeldahl digestion. Nutrient concentrations in the digests were determined as in water.

The plant available P pool in the top 10cm soil was assessed at every site by soil extraction with ALA (0.1M NH_3 + 0.4M acetic acid + 0.1M lactic acid solution; cf. Scheffer & Schachtschabel 1989; Koerselman et al. 1993; Olde Venterink et al. 2002a). The ALA extractions were carried out with every initial soil core of the N-mineralization experiment (six samples per site).

Statistics

Differences in the various nutrient fluxes, vegetation characteristics and site conditions were tested between the fens and floodplains in both areas using Tukey tests after one-way ANOVA. Data were log-transformed if they had a skewed distribution. A two-way ANOVA was used to assess the relative importance of Dutch/Belgian vs Polish sites, and fens vs floodplain for the measured values.

Results

Nutrient fluxes

Atmospheric deposition was assessed at 43 kg N and 0.15 kg-P.ha^{-1}.a^{-1} in the western European sites and at 5-10 kg N and 0.05 kg-P.ha^{-1}.a^{-1} in the Polish sites (Tables 2 and 3). Symbiotic N_2-fixation was only likely to be of any importance in the Dutch and Belgian fens where the percentage of legumes in the plant cover was significant.

Nutrient input by flooding was high in the Polish floodplains, particularly because of sediment deposition. Sedimentation was not measured in the western European floodplains.

Nutrient input by groundwater was especially large in the Polish fens, which is a combined effect of the strong seepage (271 mm.a^{-1}) and relatively high N-concentrations in some groundwater samples (0.13-1.47 mg.l^{-1} inorganic N). Leaching only removed substantial amounts of N in the Dutch floodplain.

Mean N-mineralization rates ranged between 4-133 kg-N.ha^{-1}.a^{-1} and were significantly higher in floodplains than in fens, and higher in western Europe than in Poland (Tables 2 and 4).

Table 2. Fluxes of N in fens and flood-plains (mean ± 1s.d. in kg.ha^{-1}.a^{-1}). N-balance is the sum of all external input and output fluxes. N-budget for the vegetation is the sum of external fluxes and mineralization but does not include output by hay. Figures for hay-making are based on an annual hay-making regime. Different characters indicate significant differences ($P < 0.05$; one-way ANOVA, Tukey).

Nitrogen	Dutch/Belgian Fen	Dutch Flood-plain	Polish Fen	Polish Flood-plain
Input fluxes				
Atmosph. Dep.	43	43	5-10	5-10
N_2-fixation	0-1.9	0-0.4	0	0-0.3
Groundwater	1.9±2.0a	1.0±0.4a	2.3 ±1.4a	0.1±0.0b
Flood dissolved	0.1±0.3b	11.4±4.3a	0.0±0.0b	3.3±1.9b
Flood sediment	0 b	?	0 b	31.3±16.5a
Subtotal In	46.9	55.8 + ?	9.8	42.5
Output fluxes				
Leaching	1.6±1.6b	5.2±7.2 a	0.4±0.1b	0.8± 0.8b
Hay-making	50.4±13.6b	128.6±25.1 a	28.6± 5.0c	102.5± 24.0a
Subtotal out	52.0	133.8	29.0	103.3
N-mineralization	19±22b	133±69a	4±6b	34±53b
N-balance	-5.1	> -78	–19.2	–60.8
N-budget	64.3	>183.6	13.4	75.7

Annual nutrient balances

For most wetland types annual N and P output fluxes exceeded total N- and P-input fluxes resulting in negative annual N- and P-balances. Only the N-balance in the Dutch/Belgian fens and the P-balance in the Polish fens were close to equilibrium. The net nutrient loss is especially large in the floodplains where the net export of N is ca. 60 - 80 kg.ha^{-1}.a^{-1} and the net P-output is 10 - 18 kg.ha^{-1}.a^{-1}. N output by hay harvesting seems to counterbalance N-enrichment in the Polish fens and floodplains and diminishes N-enrichment of the Dutch fens and floodplains.

Table 3. Fluxes of P in fens and flood-plains (mean ± 1SD in kg.ha^{-1}.a^{-1}). P-balances is the sum of all external input and output fluxes. P-balances are incomplete since we did not measure annual soil P-release. Figures for hay-making are based on an annual hay-making regime. Different characters indicate significant differences ($P < 0.05$; one-way ANOVA, Tukey).

Phosphorus	Dutch/Belgian Fen	Dutch Flood-plain	Polish Fen	Polish Flood-plain
Input fluxes				
Atmospheric deposition	0.15	0.15	0.05	0.05
Groundwater	0.12±0.08 a	0.16±0.32 a	0.17± 0.06 a	0.01±0.00 b
Flood dissolved	0 b	0.70±0.40 a	0 b	0.94±0.70 a
Flood sediment	0 b	?	0 b	6.46±4.07 a
Subtotal In	0.27	1.01 + ?	0.22	7.46
Output fluxes				
Leaching	0.08±0.09 ab	0.01±0.00 b	0.02± 0.01 b	0.17± 0.10 a
Hay-making	5.7±1.9 b	18.8±3.3 a	1.4±0.2 c	17.9±4.6 a
Subtotal out	5.78	18.81	1.42	18.07
Soil P-release	?	?	?	?
P-balance	-5.51	> -17.8	-1.2	-10.6

Table 4. Relative importance of western Europe (The Netherlands/Belgium) vs Poland (country) and fens vs flood-plain (wetland type) for differences in nutrient fluxes and other variables. *F*-values and significance of two-way ANOVA (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

	Country	Wetland type	Country × Wetland type
N ground water input	8.9**	95.3***	73.2***
N input from flooding (dissolved matter)	21.4***	66.6***	20.0***
N output by leaching	17.9***	8.3**	1.3
N output by hay-making	26.3***	212.1***	4.2*
net N mineralization	11.1**	18.3***	5.6*
P groundwater input	11.4**	41.6***	24.6***
P input from flooding (dissolved matter)	0.4	25.4***	0.5
P output by leaching	4.5*	3.0	20.5***
P output by hay-making	64.5***	448.7***	53.2***
Standing crop vascular plants	23.5***	395.6***	17.7***
Standing crop bryophytes	12.3**	26.2***	11.6**
Water level flood	13.5**	66.2***	19.5***
Water level summer	149.7***	61.6***	19.4***
Organic matter	121.8***	2.5	0.1
Bulk density	56.0***	11.1**	5.8*
Soil N-pool	0.3	3.9	0.1
Soil P-pool	3.7	1.4	2.0
Soil ALA-extr. P-pool	24.4***	1.3	0.7

Annual N-budgets for the vegetation

The N-budgets, which can be considered as annual N-availability for plants, are larger in floodplains than in fens in both areas. They are also higher in the Dutch and Belgian sites than in the Polish sites, for both wetland types (Table 2). Atmospheric deposition and mineralization are the two important N-sources. Deposition is the major N-source in the fens, whereas both deposition and mineralization are important in the floodplains. Both N-fluxes are larger in the Dutch/Belgian sites than in the Polish sites (Table 2).

Discussion

In the present study we evaluate the importance of various fluxes of N and P for some fen and floodplain ecosystems in The Netherlands, Belgium and Poland. The objective of this evaluation, and especially the comparison between quite undisturbed sites in Poland with disturbed sites in The Netherlands and Belgium, was to determine if historical increases in N- and P-fluxes had occurred in the western European sites. We note that our data only allow limited generalization, since we only have studied a few sites and have faced differences in temporal resolution and timing of sampling between the areas studied. To avoid speculation we will restrict our conclusions and discussion to a number of apparent differences and obvious patterns.

Nutrient limitation

Assessing N- and P-fluxes is particularly relevant if N and/or P are limiting factors for plant growth. In previous studies the type of nutrient limitation was assessed in some of our sites by means of fertilization experiments (Wassen et al. 1998; Olde Venterink et al. 2001a; Boeye et al. 1997; van Duren et al. 1997), and in all sites by means of N:P ratios in the above-ground vegetation (Wassen et al. 1995; Olde Venterink et al. 2002a). The Dutch and Belgian fens and floodplains appeared to be mainly N-limited, with possibly co-limitation by potassium in some sites (Olde Venterink et al. 2001a; Boeye et al. 1997; van Duren et al. 1997). Fertilization experiments in 1992 showed that one of the Polish fens was N-limited, whereas a floodplain site appeared not to be limited by nutrients (Wassen et al. 1998). However, N:P ratios in above-ground plant material harvested in 1990 and in 2003 indicated that the Polish fens appeared to be P-limited (Wassen et al. 1995; El-Kahloun 2004). Hence, both N and P are potentially growth limiting in the fens and/or floodplains we have investigated. Therefore, understanding eutrophication in these wetlands requires insight in the contribution of various nutrient fluxes to the annual balances and budgets of both N and P.

The significance of external fluxes

Nutrient fluxes from external sources were of different importance for the N-balance than for the P-balance.

They were more or less negligible for P, except for P-input by sedimentation during floods. For the N-balance two external nutrient fluxes were important: atmospheric deposition and sedimentation.

In the Dutch and Belgian fens, N-deposition of 43 $kg.ha^{-1}.a^{-1}$ made up 92% of the annual N-input (and 66% of the annual N-budget for the vegetation). N-deposition in this region is estimated to be 30-70 $kg\text{-}N.ha^{-1}.a^{-1}$ (Erisman & Bobbink 1997); which has increased from 5-20 $kg\text{-}N.ha^{-1}.a^{-1}$ before the 1950s (Erisman & Draaijers 1995). From a historical point of view, N-input from atmospheric deposition has probably increased N-availability for plants, and may have caused eutrophication in N-limited ecosystems in western Europe (Bobbink et al. 1998). Atmospheric N-deposition in eastern Poland is lower at <10 $kg.ha^{-1}.a^{-1}$ (see also Holland et al. 1999), but nevertheless makes up 77% of the annual N-input in the fens.

In the Polish floodplain, sediment deposition from flooding is another important input flux of N and P. Although in the Dutch floodplains of the present study, the input of N and P through sediment deposition was not measured, Olde Venterink et al. (2006) showed that the input of deposited particulate matter (organic as well as mineral) in Dutch floodplains along the rivers Waal and IJssel amounted to 25-144 $kg\text{-}N.ha^{-1}.a^{-1}$ and 12-61 $kg\text{-}P.ha^{-1}.a^{-1}$. Sediment deposition is recognized as a significant source of phosphorus in floodplains along rivers and streams (Vought et al. 1994).

Contributions of nutrient input and output by groundwater flow to nutrient availability were negligible, except for the Polish fens. The present study shows that the large flux of groundwater slightly enriched with N (inorganic N = 0.13-1.47 $mg\text{-}N.l^{-1}$) into this fen may have been responsible for N-enrichment. Drexler & Bedford (2002) also showed predominant N-loading of a small groundwater discharge fen via groundwater flow from a farm field. That study, as well as our results, contradicts with the general observation that N in groundwater descending from agricultural land disappears by denitrification before reaching the root zone in groundwater discharge areas (Lowrance et al. 1983; Hill 1996; Hoffmann 1998; Pieterse et al. 2005).

Considerable amounts of N and P are removed from our sites by mowing and removal of the vegetation near the peak of the growing season. In the studied western European ecosystems hay-making occurs annually. In Poland hay was collected once in one to two years in the floodplain, depending on the wetness of the summer, and has been abandoned for ca. 15 years in the fen. If hay-making was carried out annually in the Polish fen P-export by hay harvesting would still be lower in Poland than in The Netherlands or Belgium (Table 3) because of lower biomass and lower P-concentrations in the biomass. Net N-export would be higher in the Polish fens than in the western European ones. This suggests that annual hay harvesting would direct a trend towards P-limitation in the Dutch/Belgian fens and towards N-limitation in the Polish fen. Since endangered plant species of western European wetlands appear to persist better at low productive P-limited conditions than at N-limited conditions (Olde Venterink et al. 2003a; Wassen et al. 2005), annual hay-making appears to be an essential management measure for species conservation in western European fens. For the Polish fen abandonment of regular mowing implies that both the N- as well as the P-balance will be positive, which means nutrient enrichment. Since this effect increases with increasing nutrient input from external sources, in absolute terms N and P enrichment will be larger for the floodplains than for the fens, although even a relatively small N enrichment from deposition may already have large effects in the fens because of the very low annual N-budget (Table 2).

We did not assess denitrification. Denitrification rates in the root zone of freshwater wetlands are usually in the range of 0-10 $kg\text{-}N.ha^{-1}.a^{-1}$ (Bowden 1987; Hefting et al. 2003). In two unfertilized fen meadows soil denitrification was 17 $kg\text{-}N.ha^{-1}.a^{-1}$ (Berendse et al. 1994). Denitrification as measured in the Polish fens and floodplains by Verhoeven et al. (1996b) was 0.6 and 0.4 $kg.ha^{-1}$ for a six week summer period. Olde Venterink et al. (2003b, 2006) estimated mean denitrification rates for floodplains along the Dutch rivers Waal and IJssel at 1 - 32 $kg.ha^{-1}.a^{-1}$. It is important to note that denitrification rates can also be much higher (> 50-100 $kg\text{-}N.ha^{-1}.a^{-1}$) when nitrate availabilities are high in floodplains (Pinay et al. 1995; Seitzinger 1994), in areas with inlet of nitrate rich water (Davidsson & Leonardson 1998), or in drained wetlands (Davidsson et al. 2002).

N-mineralization

Net N-mineralization was lower in fens than in floodplains, and lower in the Polish sites than in the Dutch/Belgian sites, which in both cases corresponds with soil wetness; i.e. lowest mineralization at the wettest sites (Table 1). The importance of mineralization for the N-budget for plants agrees well with other studies in meadows (Grootjans et al. 1985; 1986; Berendse et al. 1994; Olff et al. 1994; Olde Venterink et al. 2002a) and fens (Koerselman & Verhoeven 1992). The relative importance of N-mineralization also demonstrates that drainage, which is clearly larger in western Europe than in Poland, 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; Olde Venterink et al. 2002b). The value we measured in the Polish floodplain (34 kg-N.ha^{-1}.a^{-1}) was lower than the values we measured along a transect through another floodplain site along the river Biebrza in the summer of 1990 (5 - 50 kg N/ha/6 weeks; Wassen et al. 2003). Koerselman & Verhoeven (1992) report N-release rates of 67-320 kg-N.ha^{-1}.a^{-1} and van Wirdum (1991) of 28-170 kg-N.ha^{-1}.a^{-1} for Dutch fens and Hoffmann (1998) measured 90 kg-N.ha^{-1}.a^{-1} in Danish wet meadows.

Conclusions and recommendations with reference to the limitations of the study

Above-ground biomass of vascular plants, and the amount of N in it was much higher in the highly productive floodplains than in the lower productivity fens. The amount of N in the above-ground biomass in the western European fens and floodplains was ca. 78% and 70%, respectively, of the assessed N-budget. For Polish fens and floodplains this was 213% and 135% respectively. These percentages imply that overall N availability appeared to be assessed fairly well in our Dutch and Belgian sites, but are clearly underestimated in the Polish sites. The underestimated N availability in the Polish sites may be due to underestimation of N-mineralization. An important source for underestimating net N-mineralization is the loss of N through denitrification from the incubated soil. This is an artefact of the soil incubation method: in the incubated soil core ammonium and nitrate accumulate whereas in the field they are taken up by plants. As a result the nitrate in the incubated soil is available for denitrification. This N loss is especially high in wet soil cores (Olde Venterink et al. 2002b), and may therefore be higher in the constantly wet Polish fens than in Dutch and Belgian fens which are slightly drained in summer (cf. Table 1).

Although we missed some potentially important fluxes (e.g. denitrification, sediment deposition in some of the sites) in our assessment and we are dealing with processes which are largely variable in time we may still draw some conclusions. Without annual hay-harvesting our Dutch and Belgian fens and floodplains would be enriched with N. As a result of the lower atmospheric N deposition, and probably lower N-mineralization rates, hay-harvesting does not have to be carried out annually to prevent N-enrichment in the Polish fen, but abandoning hay-making totally will lead to N-enrichment (fens and floodplains) and P-enrichment (floodplains) in the Polish sites. The lower mineralization rates are probably the result of wetter conditions in the studied Polish ecosystems. Hence, water management aiming at preventing unwanted drainage in nature reserves seems to be of equal importance for maintaining balanced nutrient budgets as the traditional practice of hay-harvesting. Returning to the primary aim of our paper; we conclude that increases in N fluxes in western European fens and floodplains have been caused by enhanced atmospheric N deposition and drainage in nature reserves. Hence, the comparison with the Polish sites supported the conclusions drawn from the previous study along productivity gradients in The Netherlands and Belgium (Olde Venterink et al. 2002a). In addition to the findings of Olde Venterink et al. (2002a) the present study shows that in the Polish fens both the N-balance and the N-budget are considerably lower than in The Netherlands/ Belgium, mainly because of low atmospheric deposition. An increase of atmospheric deposition towards western European values in Poland would significantly alter the N-budget of both fens and floodplains. Further, the sedimentation data from the Polish floodplain suggest that in the Dutch/Belgian sites (in which sedimentation was not measured) the P-balance may have been significantly underestimated. The present study shows that even estimates of annual nutrient fluxes, can be of value for nature managers targeting at management of nutrient fluxes and availabilities as a measure to influence vegetation development and succession. In future research special attention should be paid to fluxes which contribute significantly to the budget and which may have a large spatial and temporal variability such as N and P input by floods, as well as denitrification. P turnover rates in the soil through mineralization and physico-chemical processes also deserve special attention since their contribution to the P-budget is largely unknown.

References

Batelaan, O. & Kuntohadi, T. 2002. Development and application of a groundwater model for the Upper Biebrza River basin. *Annals of Warsaw Agricultural University - SGGW, Land Reclamation* 33: 57- 69.

Berendse, F., Oomes, M.J.M., Altena, H.J. & de Visser, W. 1994. A comparative study of nitrogen flows in two similar meadows affected by different groundwater levels. *J. Appl. Ecol.* 31: 40-48.

Bobbink, R., Hornung, M. & Roelofs, J.G.M. 1998. The effect of air-borne nitrogen pollutant on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86: 717-738.

Boeye, D., Verhagen, B., Van Haesebroeck, V. & Verheyen, R.F. 1997. Nutrient limitation in species-rich lowland fens. *J. Veg. Sci.* 8: 415-424.

Bowden, W.B. 1987. The biogeochemistry of nitrogen in freshwater wetlands. *Biogeochem.* 4: 313-348.

Bridgham, S.D., Updegraff, K. & Pastor, J. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79: 1545-1561.

Davidsson, T.E. & Leonardson, L.G. 1998. Seasonal dynamics of denitrification activity in two water meadows.

Hydrobiologia 364: 189-198.

Davidsson, T.E., Trepel, M. & Schrautzer, J. 2002. Denitrification in drained and rewetted minerotrophic peat soils in Northern Germany (Pohnsdorfer Stauung). *J. Plant Nutr. Soil Sci.* 165:199-204.

Drexler, J.Z. & Bedford, B.L. 2002. Pathways of nutrient loading and impacts on plant diversity in a New York peatland. *Wetlands* 22: 263-281.

El-Kahloun, M. 2004. *Vegetation dynamics in P-limited rich fens*. Ph.D. Thesis, Universiteit Antwerpen, BE.

Elser, J.J. et al. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408: 578-580.

Erisman, J.W. & Bobbink, R. 1997. De ammoniakproblematiek; wetenschappelijke achtergronden. *Landschap* 14: 87-104.

Erisman, J.W. & Draaijers, G.P.J. 1995. *Atmospheric deposition in relation to acidification and eutrophication*. Elsevier Science, Amsterdam, NL.

Fojt, W. & Harding, M. 1995. Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. *J. Appl. Ecol.* 32: 561-577.

Grootjans, A.P., Schipper, P.C. & van der Windt, H.J. 1985. Influence of drainage on N-mineralization and vegetation response in wet meadows: I *Calthion palustris* stands. *Acta Oecol.* 6: 403-417.

Grootjans, A.P., Schipper, P.C. & van der Windt, H.J. 1986. Influence of drainage on N-mineralization and vegetation response in wet meadows: II *Cirsio-Molinietum* stands. *Acta Oecol.* 7: 3-14.

Güsewell, S. & Koerselman, W. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspect. Plant Ecol. Evol. Syst.* 5: 37-61.

Hefting, M.M., Bobbink, R. & de Caluwe, H. 2003. Nitrous oxide emissions and denitrification in chronically nitrate-loaded buffer zones. *J. Environ. Qual.* 21: 1194-1203.

Hill, A.R. 1996. Nitrate removal in riparian zones. *J. Environ. Qual.* 25: 743-755.

Hoffmann, C.C. 1998. *Nutrient retention in wet meadows and fens*. Ph.D. Dissertation. University of Copenhagen, Copenhagen, DK.

Holland, E.A., Dentener, F.J., Braswell, B.H. & Sulzman, J.M. 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46: 7-43.

Koerselman, W. & Verhoeven, J.T.A. 1992. Nutrient dynamics in mires of various trophic status: nutrient inputs and outputs and the internal nutrient cycle. In: Verhoeven, J.T.A. (ed.) *Fens and bogs in the Netherlands: vegetation, history, nutrient dynamics and conservation*, pp. 397-432. Kluwer Academic, Dordrecht, NL.

Koerselman, W., van Kerkhoven, M.B. & Verhoeven, J.T.A. 1993. Release of inorganic N, P and K in peat soils; effect of temperature, water chemistry and water level. *Biogeochem.* 20: 63-81.

Laine, J., Vasander, H. & Laiho, R. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *J. Appl. Ecol.* 32: 785-802.

Lowrance, R.R., Todd, R.L. & Asmussen, L.E.. 1983. Waterborne nutrient budgets for the riparian zone of an agricultural watershed. *Agric. Ecosys. Environ.* 10: 371-384.

Marrs, R.H. 1993. Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Adv. Ecol. Res.* 24: 241-300.

Mengel, K. 1982. Dynamics and availability of major nutrients in soils. *Adv. Soil Sci.* 2: 65-131.

Middelkoop, H. & Asselman, N.E.M. 1998. Spatial sedimentation of floodplain sedimentation at the event scale in the Rhine-Meuse Delta, The Netherlands. *Earth Surface Processes and Landforms* 23: 561-573.

Mioduszewski, W. & Querner, E.P. (eds.) 2002. *Hydrological system analysis in the valley of Biebrza River*. Wydawnictwo IMUZ, Falenty, PL.

Olde Venterink, H., van der Vliet, R.E. & Wassen, M.J. 2001a. Nutrient limitation along a productivity gradient in wet meadows. *Plant Soil* 234: 171-179.

Olde Venterink, H., Wassen, M.J., Belgers, J.D.M. & Verhoeven, J.T.A. 2001b. Control of environmental variables on species density in fens and meadows; importance of direct effects and effects through community biomass. *J. Ecol.* 89: 1033-1040.

Olde Venterink, H., Pieterse, N.M., Belgers, J.D.M., Wassen, M.J. & de Ruiter, P.C. 2002a. N, P and K budgets along nutrient availability-productivity gradients in wetlands. *Ecol. Appl.* 12: 1010-1026.

Olde Venterink, H., Davidsson, T.E., Kiehl, K. & Leonardson, L. 2002b. Impact of drying and rewetting on N, P and K dynamics in a wetland soil. *Plant Soil* 243: 119-130.

Olde Venterink, H., Wassen, M.J., Verkroost, A.W.M. & de Ruiter, P.C. 2003a. Species richness-productivity patterns differ between N-, P- and K-limited wetlands. *Ecology* 84: 2191-2199.

Olde Venterink, H., Hummelink, E. & van den Hoorn, M.W. 2003b. Denitrification potential of a river floodplain during flooding with nitrate-rich water: grassland versus reedbeds. *Biogeochem.* 65: 233-244.

Olde Venterink, H.., Vermaat, J.E., Pronk, M., Wiegman, F., van der Lee, G.E.M., van den Hoorn, M.W., Higler, M.(L.) W.G. & Verhoeven, J.T.A. 2006. Importance of sediment deposition and denitrification for nutrient retention in floodplain wetlands. *Appl. Veg. Sci.* 9: 163-174.

Olff, H., Berendse, F. & de Visser, W. 1994. Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application. *J. Ecol.* 82: 611-620.

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

Pieterse, N.M., Olde Venterink, H., Schot, P.P. & Verkroost, A.W.M. 2005. Is nutrient contamination of groundwater causing eutrophication of groundwater-fed meadows? *Landscape Ecol.* 20: 743-753.

Pinay, G., Ruffinoni, C. & Fabre, A. 1995. Nitrogen cycling in two riparian forest soils under different geomorphic conditions. *Biogeochemistry* 30: 9-29.

Rich, T.C.G. & Woodruff, E.R. 1996. Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: the BSBI monitoring scheme. *Biol. Conserv.* 75: 217-229.

Schaminée, J.H.J., Weeda, E.J. & Westhoff, V. 1995. *De*

Vegetatie van Nederland. II Wateren, Moerassen, Natte Heiden. Opulus Press, Uppsala, SE.

Schaminée, J.H.J., Stortelder, A.H.F. & Weeda, E.J. 1996. *De Vegetatie van Nederland. III Graslanden, Zomen, Droge Heiden*. Opulus Press, Uppsala, SE.

Scheffer, F. & Schachtschabel, P. 1989. *Lehrbuch der Bodenkunde*. Enke Verlag, Stuttgart, DE.

Schlesinger, W.H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, San Diego, CA, US.

Seitzinger, S.P. 1994. Linkages between organic matter mineralization and denitrification in eight riparian wetlands. *Biogeochemistry* 25: 19-39.

van der Hoek, D., van Mierlo, A.J.E.M. & van Groenendael, J.M. 2004. Nutrient limitation and nutrient-driven shifts in plant species composition in a species-rich fen meadow. *J. Veg. Sci*. 15: 387-394.

van Duren, I.C., Boeye, D. & Grootjans, A.P. 1997. Nutrient limitations in an extant and drained poor fen: implications for restoration. *Plant Ecol*. 133: 91-100.

van Wirdum, G. 1991. *Vegetation and hydrology of floating rich-fens*. Ph.D. Dissertation, University of Amsterdam, Amsterdam, NL.

Verhoeven, J.T.A., Koerselman, W. & Meuleman, A.F.M. 1996a. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends Ecol. Evol*. 11: 494-497.

Verhoeven, J.T.A., Keuter, A., van Logtestijn, R., van Kerkhoven, M.B. & Wassen, M.J. 1996b. Control of local nutrient dynamics in mires by regional and climatic factors: a comparison of Dutch and Polish sites. *J. Ecol*. 84: 647-656.

Vought, L.B.M, Dahl, J., Lauge Pederson, C. & Lacousière, J.O. 1994. Nutrient retention in riparian ecotones. *Ambio* 23: 342-348.

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

Wassen, M.J., Olde Venterink, H.G.M. & de Swart, E.O.A.M. 1995. Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *J. Veg. Sci*. 6: 5-16.

Wassen, M.J., van der Vliet, R.E. & Verhoeven, J.T.A. 1998. Nutrient limitation in the Biebrza fens and floodplain (Poland). *Acta Bot. Neerl*. 47: 241-253.

Wassen, M.J., Bleuten, W. & Bootsma, M.C. 2002. Biebrza as a geographical reference. *Ann. Warsaw Agricult. Univ*. 33: 27-47.

Wassen, M.J., Peeters, W.H.M. & Olde Venterink, H. 2003. Patterns in vegetation, hydrology, and nutrient availability in an undisturbed floodplain in Poland. *Plant Ecol*. 165: 27-43.

Wassen, M.J., Olde Venterink, H., Lapshina, E. & Tanneberger, F. 2005. Endangered plants persist under phosphorus limitation. *Nature* 437: 547-550.

Received 6 April 2005;
Accepted 12 January 2006;
Co-ordinating Editor: A. Grootjans.