Biogeochemistry **67:** 113–134, 2004.

Water table elevation controls on soil nitrogen cycling in riparian wetlands along a European climatic gradient

M. HEFTING[1,]*, J.C. CLÉMENT[2,8], D. DOWRICK[3], A.C. COSANDEY[4], S. BERNAL[5], C. CIMPIAN[6], A. TATUR[7], T.P. BURT[3] and G. PINAY[2,9]
[1]*Department of Geobiology, Utrecht University, PO Box 80084 3508 TB Utrecht, The Netherlands;* [2]*UMR 6553 ECOBIO Université de Rennes I, Avenue du Général Leclerc, F-35042 Rennes, France;* [3]*Department of Geography, University of Durham, Durham DH1 3LE, United Kingdom;* [4]*IATE-Pedology, Rural Engineering Department Swiss Federal Institute of Technology, 1015 Lausanne, Switzerland;* [5]*Departament d'Ecologia, Fac. Biologia, Avgda. Diagonal 645, 08028 Barcelona, Spain;* [6]*Department of Systems Ecology and Management of Natural Capital, University of Bucharest, 91-95 Splaine Independentei Avenue, 5, Bucharest, Romania;* [7]*Instytut Ekologii PAN, Konopnickiedj 1, Dziekanow Lesny 05-092 Lomianki, Poland;* [8]*Current addresses: Department of Ecology, Evolution and Natural Resources, Cook College, Rutgers University, New Brunswick, NJ 0890, USA;* [9]*CEFE CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France;* **Author for correspondence (e-mail: M.M.Hefting@bio.uu.nl; phone: +31 302537441; fax: +31 302518366)*

Received 6 February 2003; accepted in revised form 14 April 2003

Key words: Ammonification, Denitrification, Hydromorphic conditions, Nitrification, Riparian zone

Abstract. Riparian zones have long been considered as nitrate sinks in landscapes. Yet, riparian zones are also known to be very productive ecosystems with a high rate of nitrogen cycling. A key factor regulating processes in the N cycle in these zones is groundwater table fluctuation, which controls aerobic/anaerobic conditions in the soil. Nitrification and denitrification, key processes regulating plant productivity and nitrogen buffering capacities are strictly aerobic and anaerobic processes, respectively. In this study we compared the effects of these factors on the nitrogen cycling in riparian zones under different climatic conditions and N loading at the European scale. No significant differences in nitrification and denitrification rates were found either between climatic regions or between vegetation types. On the other hand, water table elevation turned out to be the prime determinant of the N dynamics and its end product. Three consistent water table thresholds were identified. In sites where the water table level is within −10 cm of the soil surface, ammonification is the main process and ammonium accumulates in the topsoils. Average water tables between −10 and −30 cm favour denitrification and therefore reduce the nitrogen availability in soils. In drier sites, that is, water table level below −30 cm, nitrate accumulates as a result of high net nitrification. At these latter sites, denitrification only occurs in fine textured soils probably triggered by rainfall events. Such a threshold could be used to provide a proxy to translate the consequences of stream flow regime change to nitrogen cycling in riparian zones and consequently, to potential changes in nitrogen mitigation.

Abbreviations: CH – Switzerland; F – France; NL – The Netherlands; NM – process not measured; PL – Poland; R – Romania; S – Spain; SMP – sum of the rates of the main N cycling microbial processes; UK – England

Introduction

Riparian zones are important components of stream ecosystems since they are intimately linked to the functioning of the stream itself (Hynes 1983; Naiman and Décamps 1997). Due to their position between upland and aquatic systems, riparian zones contribute to the control of energy, nutrients and organic matter fluxes both in longitudinal (Schlosser and Karr 1981; Pinay et al. 2000) and lateral directions (Peterjohn and Correll 1984; Haycock et al. 1997). Riparian zones are often nutrient-rich systems with a high productivity and rapid nutrient cycling. (Mitsch and Ewel 1979; Brinson et al. 1981, 1984; Mitsch and Rust 1984). The extent of riparian zones and their high productivity is also largely controlled by the timing and duration of flooding and low flow events (Salo et al. 1986; Gregory et al. 1991; Nilsson and Svedmark 2002). Odum et al. (1979) hypothesized in their subsidy-stress model that plant productivity in wetlands will be highest when periodic flooding of short duration occurs because of subsidies of nutrients and water; long-lasting floods will cause physiological stress to the plants, while complete lack of flooding will limit production due to the lack of nutrient inputs. However, in recent studies this adaptation of the theory of intermediary perturbation has been questioned. For instance, in a field study Megonigal et al. (1997) did not find any significant difference in above-ground production between moderately wet and dry sites. They hypothesized that periodically dry and flooded conditions require additional morphological and physiological trade-offs such that trees cannot tolerate both drought and flooding. Moreover, when considering multiple indices, that is, below-ground biomass, litter fall and current annual increment of woody biomass, Clawson et al. (2001) found that the wettest sites had the greatest net primary productivity due to the woody biomass increment. This is consistent with previous studies where they found that biomass allocation was strongly influenced by flooding gradient with significantly higher above-ground production compared to below-ground under flooded conditions (Day and Megonigal 1993). However, apart from the study of Burke et al. (1999), which related the lowest net primary production observed to the low nutrient availability in the wet transition zone, most of these studies have mainly focused on the importance of oxygen stress for plants as the primarily driver of plant productivity in such fluctuating environments. Biogeochemical processes, especially those related to nitrogen and phosphorus, are sensitive to redox conditions of the soil, and differences in nutrient availability as a result of these moisture-driven redox conditions may also be a key factor for plant production. In riparian zones subject to considerable N loading from the adjacent upland fields, the redox conditions of the soil determine the nutrient removal capacity of the riparian zones by controlling plant uptake and the dominant biogeochemical processes (Cirmo and McDonnell, 1997).

Redox conditions in wetland soils are strongly influenced by water table fluctuations. Spatial and temporal changes in the occurrence of oxic and anoxic conditions have drastic effects on the rates of ammonification, nitrification and denitrification (Reddy et al. 1980; Patrick 1982; Reddy et al. 1989; Hill 1996; Hedin et al. 1998; Clément et al. 2002). Ammonification of organic nitrogen can be realized both under aerobic and anaerobic conditions but the nitrification process, which requires the presence of free oxygen, can only occur in aerated soils or sediments. As a consequence, under permanently anaerobic conditions the organic nitrogen mineralization process results in the accumulation of ammonium. Other processes involved in nitrogen cycling, such as nitrogen dissimilation or denitrification, are strictly anaerobic. Therefore, the end products of nitrogen cycling available for plants in wetlands are controled by soil moisture. Soil temperature also has a significant influence on the rate of nitrogen cycling processes with relationships more or less according to the Arrhenius equation (Maag and Vinther, 1996).

Soil moisture and temperature might both be affected by global climate change (Shaver et al. 2000; Georgakakos and Smith 2001). Indeed, water table level and its dynamics may be altered both from upslope by land use/land cover change and from below by river discharge changes as a result of climate change (Nilsson and Berggren 2000; Nijssen et al. 2001; Burt et al. 2002; Pinay et al. 2002). At the same time, temperature is expected to rise as a result of an increase in the concentration of atmospheric carbon dioxide (IPCC 1996). For instance in Europe, scenarios of change in the hydrological regime forecast an overall increase of the inter-annual variability of runoff, together with an increase of the average annual runoff in northern Europe and a decrease in the south (Arnell 1999). Additionally, the timing and duration of high and low flow events might shift, especially in the eastern part of the continent. Moreover, higher temperatures would enhance mineralization of organic matter (Rustad et al. 2001) increasing the amount of nutrients in inorganic form (Freeman et al. 1994). Combined with increased runoff from upland fields in northern Europe, this may result in higher nutrient loading of riparian zones in agricultural environments. Ultimately, these changes will affect the rates of nitrogen cycling in riparian wetlands and their plant productivity.

In this context, our objective was to determine in a pan-European study called NICOLAS (*Ni*trogen *Co*ntrol in Agricultural *La*ndscape*s*), if there was a threshold of water table level above which the redox conditions shift from aerobic to anaerobic conditions in riparian zones and whether this threshold was consistent in a wide range of climatic conditions and for different vegetation types. Indeed, the determination of such a threshold could be used to provide a proxy to translate the consequences of stream flow regime change to nitrogen cycling in riparian zones and, consequently, to potential changes in nitrogen mitigation. The hypothesis to be tested was whether the water table level in riparian zones is a good predictor of the relative importance of net ammonification, *in situ* denitrification and net nitrification, irrespective of climatic conditions or vegetation cover.

The study was conducted in 13 riparian sites with a vegetation cover of either forest or meadow along a climatic gradient in west and central Europe. The main processes involved in the nitrogen cycle, that is, ammonification,

Table 1. Main characteristics of the study areas (after Pinay and Burt 2000).

Country	France	United Kingdom	Netherlands	Spain	Poland	Romania	Switzerland
Geographic factors							
Catchment name	Vieux-Viel	Skerne	Twente	Fuirosos	Jorka	Glavacioc	Montricher
Discharge area (km^2)	10	8	0.15	16.80	65	26	8
Latitude	48°3′N	54°4′N	51°5′N	41°4′N	53°4′N	45°5′N	46°4′N
Longitude	1°3′W	1°2′W	5°0′W	2°3′W	21°3′W	23°4′W	6°3′W
Altitude (m)	20	100	64	80	150	200	650
Climatic variables							
Mean annual temperature (°C)	11.6	9	9.5	17	6.8	10.3	7
Maximum montly temperature (°C)	25	20	13	29	23	22	19
Minimum montly temperature (°C)	−2.6	1	5.6	3	−4.4	−2.7	1
Annual precipitation (mm)	880	800	761	885	580	600	1100
Maximum monthly precipitation (mm)	164	68	136	210	120	80	120
Minimum monthly precipitation (mm)	12	42	16	10	10	30	65
Mean annual soil temperature (°C)	14.4	9.9	8.5	13.7	9.8	11.1	13.7
Land use							
% Agriculture	70	80	80	20	46	70	80
Fertilization rate ($kg\,N\,ha^{-1}$)	200	20–50	270	80	60–120	60	100
Water quality							
Stream nitrate ($mg\,N\,L^{-1}$)	4.6	4.0	5–10	< 1.00	2.2	?	6.2
Groundwater nitrate (input) ($mg\,N\,L^{-1}$)	15	1	35	11	0.9	0.4	7

Table 1. (continued)

Country	France	United Kingdom	Netherlands	Spain	Poland	Romania	Switzerland
Maximum annual N loading ($g\,N\,m^{-2}\,year^{-1}$)	84	311	627	7	1.1	0.52	27
Geological substratum	Schist	Morenic sand	Glacial moraine	Granite	Sandy clay	Loess	Glacial deposit
Soil Type	Silty clay loam, mixed, isomesic, typic haplaquoll	Stagnoluvic gley soil mesic, typic albaqualfs	Sandy loam, mixed, mesic, entisol, fluvent Or mesic, histosol, hemist	Sandy soil sandy clay, mixed, isomesic, typic xerochrepts	Loamy sand , mixed leached brown soils	Silty clay mixed, luvihemist	Loamy clay, mixed, hemic, histosol Terric
Vegetation cover (main species)							
Meadow site	*Holcus lanatus* *Dactylis glomerata* *Juncus effusus*	*Lolium perenne* *Poa trivialis* *Trifolium repens*	*Glyceria* maxima *Urtica dioica*	*No meadow site*	*No meadow site*	*Lolium perenne* *Trifolium repens*	*Poa trivialis* *Ranunculus* sp. *Lolium multiflorum*
Wooded site	*Salix alba*	*Acer* sp.	*Alnus glutinosa*	*Platanus* × *Acerifolia*	*Alnus glutinosa*	*Populus nigra*	*Alnus glutinosa*
	Phalaris arundinacea	*Fagus sylvatica*	*Urtica dioica*	*Alnus glutinosa*	*Padus avium*	*Crateagus* sp.	*Fraxinus excelsior*
	Quercus sp.	*Lolium perenne*	*Sambucus nigra*	*Rubus ulmifolius*	*Quercus robur*	*Carex riparia*	*Prunus padus*

nitrification and *in situ* denitrification were measured seasonally and related to the average water table level.

Site descriptions

The study sites were located in seven European countries fairly evenly distributed along a climatic gradient (Table 1), with widely different conditions represented by Mediterranean (i.e., Spain), continental (i.e., Poland and Romania), and Atlantic (i.e., France and United Kingdom) climates. The study sites were chosen in order to obtain a wide spectrum of conditions to test hypotheses regarding the importance of the groundwater table versus the soil temperature on soil N cycling processes. Indeed, climatic parameters varied among sites and exhibited major differences in temperature and precipitation (Table 1). For instance, mean annual air temperature ranged from 6.8 °C in Poland to 17 °C in Spain. Mean annual soil temperature ranged from 8.5 °C in the Netherlands to 14.4 °C in France. Mean annual precipitation ranged from 580 mm in Poland to 1100 mm in Switzerland, and seasonal rainfall patterns varied widely between countries (Table 1). The riparian zones were selected along lower-order streams (1–4).

In each region, a wooded riparian site and a wet meadow riparian site was selected except in Spain and Poland, where only forested riparian zones were available at the sites. The vegetation of each site has been documented and was characterized by typical wetland trees and herbaceous species in the wooded and grassed riparian sites, respectively (Pinay and Burt 2001, Table 1).

Lateral N loading rates by subsurface flow (input fluxes) were highly variable ranging from $0.52\,g\,N\,m^{-2}\,year^{-1}$ in the forested site in Romania to over $600\,g\,N\,m^{-2}\,year^{-1}$ in the forested site in the Netherlands and England (Table 1, Sabater et al. 2003).

Methods

Water table elevation

At each site we followed the same experimental design to monitor groundwater table movements and nutrient fluxes (Burt et al. 2002; Sabater et al. 2003). Basically, three transects of four piezometers were installed across an elevation gradient from near the river edge towards the non-flooded upland bordering the agricultural field. Water table elevation was measured at least once a month for at least 1 year. At several sites water table level was continuously recorded with a data logger (Campbell CR10, Logan UT, USA). By convention, water table level is expressed in centimetres below the soil surface. Positive values refer to situations where the water table is above the soil surface while negative values refer to situations where it is below the soil surface.

Soil processes

At each of the 13 study sites, three replicate soil samples were taken four times a year from three different locations corresponding to a transect from the near-stream strip to the upland-riparian wetland interface. These transects corresponded to a gradient of soil moisture conditions. Sample locations were named after their position along the transect, that is, stream strip, intermediate strip and field strip. Soil analysis focused on the upper 20 cm which corresponds to the most active zone in a biological sense (Clément et al. 2002; Pinay et al. 2002). *In situ* denitrification rates were measured using an intact core incubation method with acetylene inhibition (Yoshinari and Knowles 1976; Ryden 1987). Intact soil cores were inserted in gas-tight jars. At the start of the incubation, jars were amended with acetone-free acetylene to bring soil atmosphere concentration to 10 kPa (10% V/V) acetylene and 90 kPa air. Samples were incubated at field temperature, and denitrification rates were calculated as the rate of nitrous oxide (N_2O) accumulation in the head space between 1 and 4 h. Gas samples were analysed directly via gas chromatography (GC Varian 3300) equipped with an electron capture detector (ECD ^{63}Ni) and Porapak Q columns (2 m long packed columns).

Net nitrogen mineralization was calculated from measured changes in the mineral-N content of largely undisturbed soil isolated inside polyethylene bags allowing air to pass through but preventing leaching (Eno 1960; Pastor et al. 1987; Binkley and Hart 1989). After 1 month of incubation in the field, nitrogen content in the incubated bags was compared to the soil nitrogen content at the beginning of the incubation. Net nitrification and net ammonification were estimated from measured changes in NO_3–N and NH_4–N content, respectively.

Soil analysis

Before and after incubation, 20 g of fresh soil were extracted with 100 ml of either 0.2 M K_2SO_4 or 0.4 M KCl, for 1 h. The extracts were filtered and analysed for NH_4–N and NO_3–N and dissolved N organic using an auto analyser (Technicon 1977). Nitrate was analysed by the Griess-Ilosvay colorimetric method (Keeney and Nelson 1982) after reduction by percolation on a copperized cadmium column. NH_4^+ was measured following the colorimetric Indophenol Blue Method (Keeney and Nelson 1982). Dissolved N organic was measured on the extract by oxidation to NO_3^- with potassium persulphate at 120 °C, and analysed by the above-mentioned procedure for nitrate. Soil moisture content was determined gravimetrically after drying approximately 20 g of fresh soil at 105 °C for at least 48 h. The Pipette Sampling Method was used to determine soil grain-sizes (Day 1965). Soil samples were pre-treated with hydrogen peroxide and hydrochloric acid and dispersed in a sodium hexametaphosphate solution.

Data analysis

Statistical procedures were performed using SPSS 8.0 for Windows (SPSS, Chicago, Illinois, USA). Variables were analysed using ANOVA and Tukey's Post Hoc tests. Data were tested for homogeneity of variance; denitrification rates were log-transformed prior to statistical analysis to meet these requirements.

Water table levels were averaged over 4 weeks preceding the process measurements to relate to the measured soil N cycling processes. Thresholds were identified with trial and error using the adjusted regression coefficient and r^2 of the linear regressions between ammonification, denitrification and nitrification versus the sum of soil N cycling process rates as decision criteria. The data set for groundwater levels was separated into three groups of process rates with maximum differences between the slopes and r^2 and values closest to one; values closest to the 1:1 relationship between the process rates and the sum of all main N cycling rates indicated that the process was the dominant N cycling processes under these conditions.

Results

There was a significant seasonal pattern in water table elevation at each of the 13 sites. However, the amplitude of the water table fluctuations varied widely within and between sites depending on the local topographic and geomorphic context (Table 2). Therefore, there were no significant relationships between geographical location of the site, that is, latitude and longitude, and the average water table level. In most cases, the water table remained closer to the soil surface in the near-stream and intermediate strips than in the near-field strips. Overall, the forested sites in England and Spain had lower water tables than the other sites. At each site, water table variations followed a seasonal pattern but at the European scale it was not related to average monthly temperature or precipitation (Burt et al. 2002).

Nitrogen cycling process rates did not show any significant differences between the forested and the wet meadow sites (Table 3). However, significant seasonal patterns in process rates were found at the different study sites (Table 3). On the other hand, no patterns were detected that related to climatic differences, expressed as latitude (Figure 1(A–C)). Similarly, no significant trends could be found between climatic parameters such as average annual soil temperature or precipitation and the annual rates of N cycling processes (Figure 1 (D–I)). A significantly higher average net nitrification rate was measured at the Spanish site (0.9 mg N kg^{-1} dry soil day^{-1}), whilst the highest average denitrification rates (0.6–0.9 N mg kg^{-1} dry soil day^{-1}) were measured in the Netherlands, France and Switzerland (Figure 2). No significant positive relation was found between N cycling process rates and annual N loading rates or extractable inorganic nitrogen (Figure 3). For further details on this aspect see the data analysis by Cosandey et al. (2002).

Table 2. Number of days in which the groundwater table is within the specified groundwater table class, specified for each strip along the piezometer transects. GWT classes are in cm. Italic site information is from a forested site in Poland with an abundant herbaceous undergrowth.

GWT class I > −10 cm, −10 cm > II > −30 cm, III > −30 cm	France			United Kingdom			Netherlands			Spain			Poland			Romania			Switzerland		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Meadow site																					
Stream strip	273	16	76	47	60	258	269	96	0				*365*	*0*	*0*	0	221	144			
Intermediate strip	215	12	138	107	94	164	258	107	0				*243*	*122*	*0*	125	85	155	34	210	121
Field strip	0	138	227	0	47	318	0	67	298				*0*	*96*	*269*	79	113	173	0	230	135
Forested site																					
Stream strip	133	108	124	0	0	365	337	28	0	0	0	365	128	159	78	174	146	45	48	237	79
Intermediate strip	0	208	157	0	28	337	222	124	19	0	0	365	96	151	118	80	213	72			
Field strip	0	162	203	0	75	290	0	168	197	0	0	365	0	0	365	0	57	308			

Table 3. Results from a three-way ANOVA with differences between the study sites, vegetation cover and season.

Process	Ammonification			Denitrification			Nitrification		
	df	*F*	*P*	df	*F*	*p*	df	*F*	*p*
Study site	5	15.238	0.000	5	43.160	0.000	5	11.443	0.000
Vegetation type	1	2.588	0.109	1	2.038	0.155	1	0.440	0.508
Season	3	4.797	0.003	3	3.392	0.019	3	4.195	0.000
Site × vegetation	3	1.908	0.129	3	2.580	0.054	3	2.553	0.056
Site × season	15	4.054	0.000	15	3.196	0.000	15	3.183	0.000
Vegetation × season	3	0.722	0.540	3	0.916	0.434	3	0.862	0.461
Site × vegetation × season	9	1.653	0.100	9	3.684	0.000	9	1.457	0.164

At most sites net ammonification rates were significantly lower than nitrification and denitrification rates (Wilcoxon rank test $p < 0.0001$). Highest average net ammonification rates measured at the Dutch sites were in the same order of magnitude as nitrification and denitrification ($0.3\,mg\,N\,kg^{-1}$ dry soil day^{-1}).

Global analysis of the data set, that is, collating results from all sites, resulted in a significant relationship ($r^2 = 0.908$, $p < 0.001$) between net ammonification and total mineralization rate in the riparian top-soils when groundwater levels were above -10 cm (Figure 4(A)). Ammonium was the main end product of the N mineralization under these waterlogged conditions. Below this -10 cm groundwater level threshold, no relationship was found between net ammonification and total mineralized N in topsoil. However, when groundwater table was below -10 cm we measured a significant relationship ($r^2 = 0.917$, $p < 0.001$) between net nitrification and total N mineralization (Figure 4(B)), with nitrate as the predominant end product of N mineralization.

Relationships between the sum of the rates of the main N cycling microbial processes (SMP) in the top 20 cm of the riparian soils were correlated with each of the processes, that is, net ammonification, net nitrification and denitrification, in order to evaluate their respective contribution under different groundwater conditions (Figure 5). When water table level was above -10 cm, a significant positive relationship occurred between ammonification and SMP (Figure 5(A)) and between denitrification and SMP (Figure 5(B)). Net nitrification was negligible at all SMP values (Figure 5(C)). When the water table level was located between -10 and -30 cm, net ammonification rates were no longer significant (Figure 5(D)) but denitrification exhibited a highly significant positive relationship with SMP (Figure 5(E)) with a regression slope close to 1. Net nitrification rates were measurable but low at all values of SMP (Figure 5(F)). Where water table levels were below -30 cm ammonification was again very low (Figure 5(G)) but high rates of nitrification were measured (Figure 5(I)), representing the highest proportion of the microbial processes of N

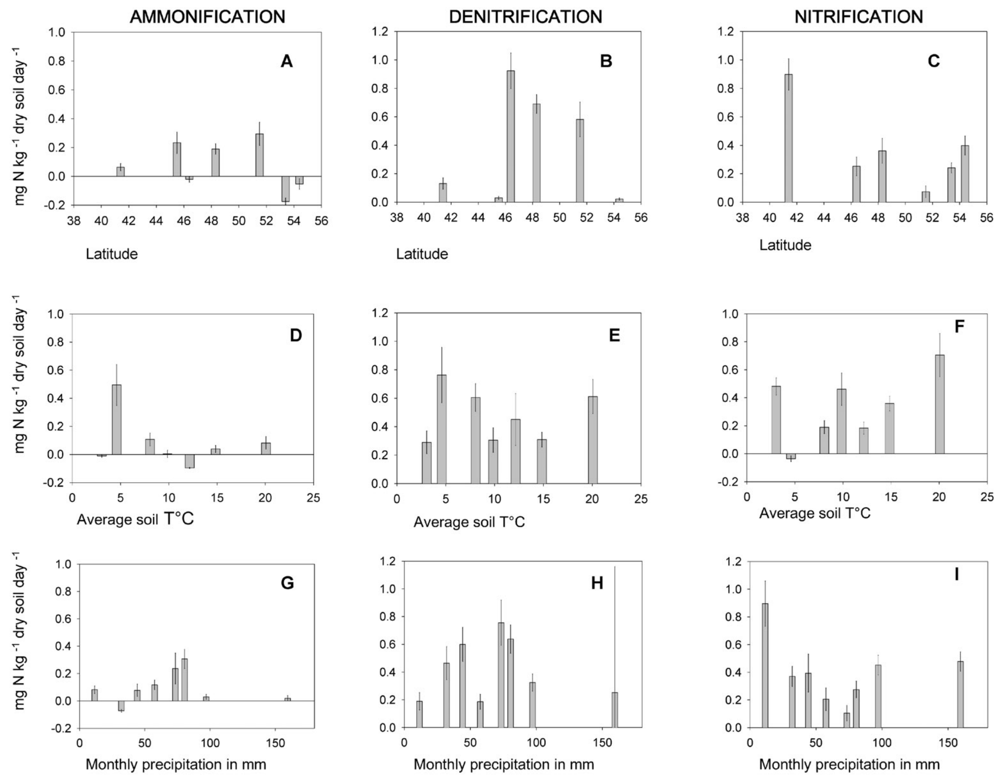

Figure 1. Climatic influence (latitude, average soil temperature and average monthly precipitation) on soil N cycling processes in the topsoil (0–20 cm). Values for soil temperature and monthly precipitation are values measured in the month prior to the process rate measurements. Means and standard errors of process rates are given ($n > 10$).

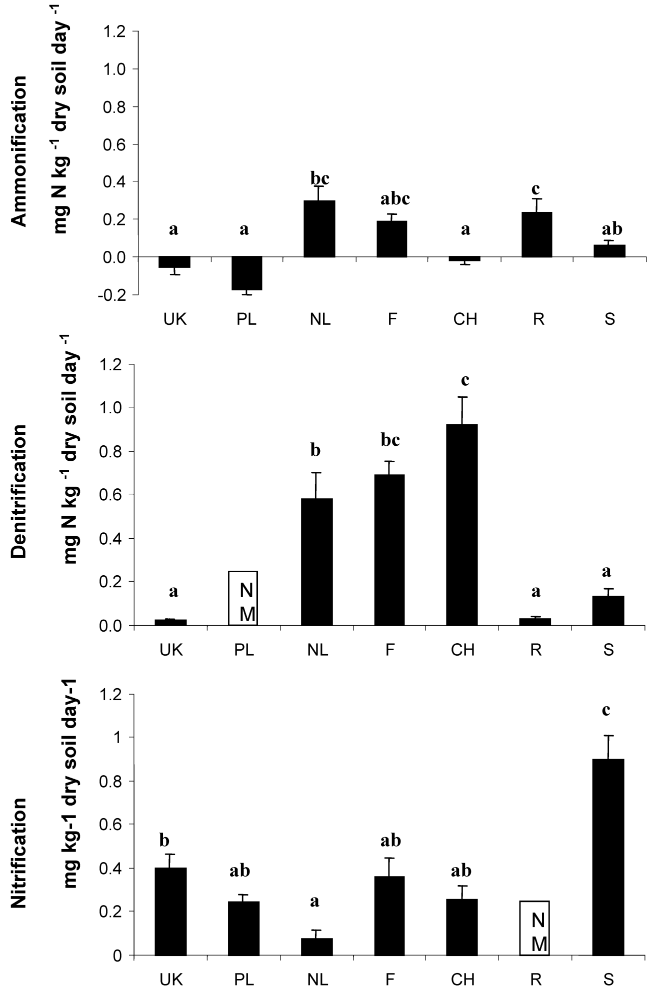

Figure 2. Nitrification, denitrification and ammonification in riparian top soils (0–20 cm) (NM process not measured). Means and standard errors of process rates are given ($n > 30$) Study sites in England (UK), Poland (PL), The Netherlands (NL), France (F), Switzerland (CH), Romania (R) and Spain (S). Letters (a, b, ab, c) indicate significant differences (Tukey's *a posteriori* test).

cycling measured ($r^2 = 0.77$, $p < 0.001$). There was still some denitrification activity, even when the groundwater table level was below −30 cm (Figure 5(H)). On closer inspection, these higher denitrification rates were measured in soil with high silt + clay content (Figure 6(A)). This relationship between soil grain size and denitrification did not exist when the groundwater table level was above −30 cm (Figure 6(B)).

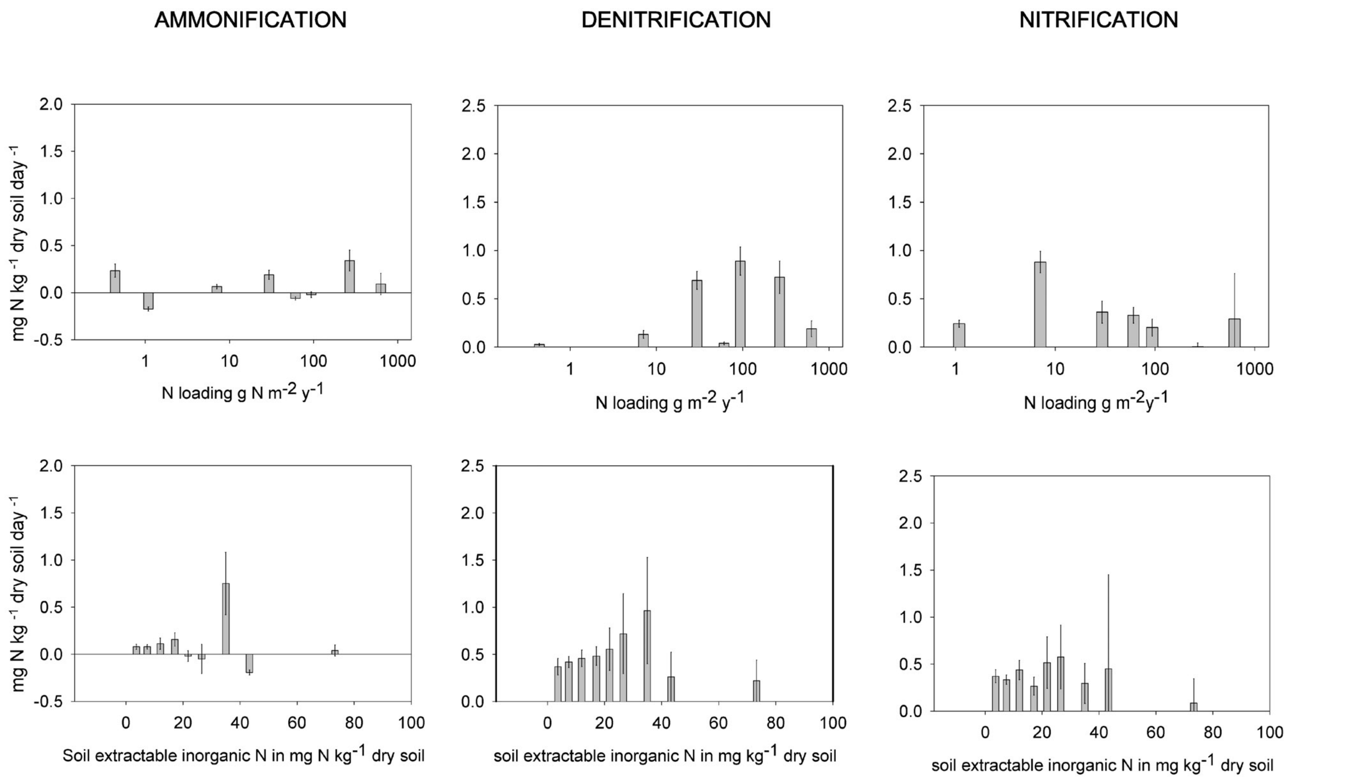

Figure 3. Influence of N loading and N availability on the soil N cycling processes in the topsoil (0–20 cm). Means and standard errors of process rates are given ($n > 10$).

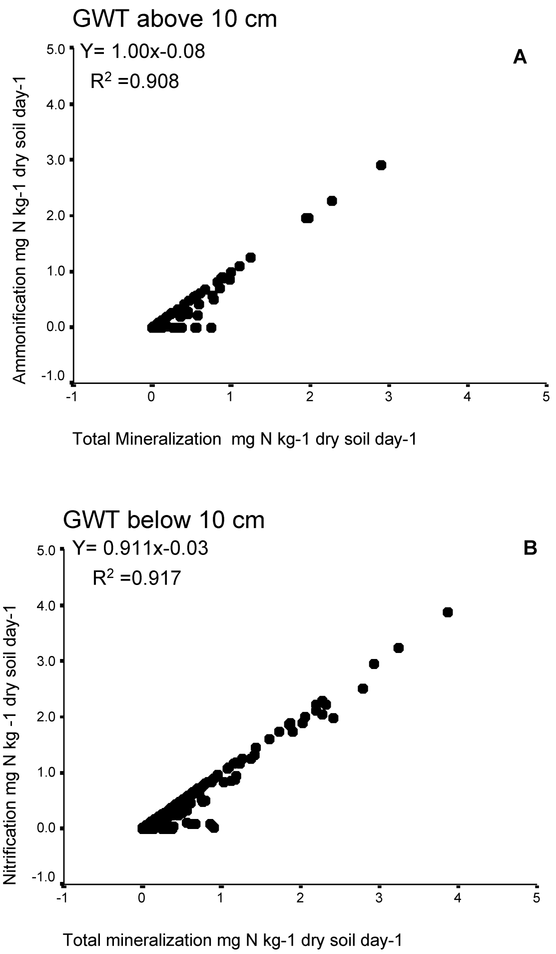

Figure 4. Relationship between ammonification and nitrification versus the total N mineralization in top-soils (0–20 cm) separated by groundwaterlevel at a threshold value of 10 cm below the soil surface ($63 < n < 249$)

Discussion

Results from this pan-European study confirmed the key role of the groundwater table level in soil N cycling processes in riparian zones. This direct control over the rates of soil N cycling processes overrides other key factors often mentioned in the literature such as soil texture (Groffman and Tiedje 1989; Pinay et al. 1995), soil type (De Klein and Van Logtestijn 1994), geomorphic context (Pinay et al. 2000; Johnston et al. 2001), climatic conditions (Groffmann et al. 1987; Tiedje 1988), N input (Hanson et al. 1994; Verchot et al. 1997) or vegetation cover (Daniels and Gilliam 1996; Groffman et al. 1996).

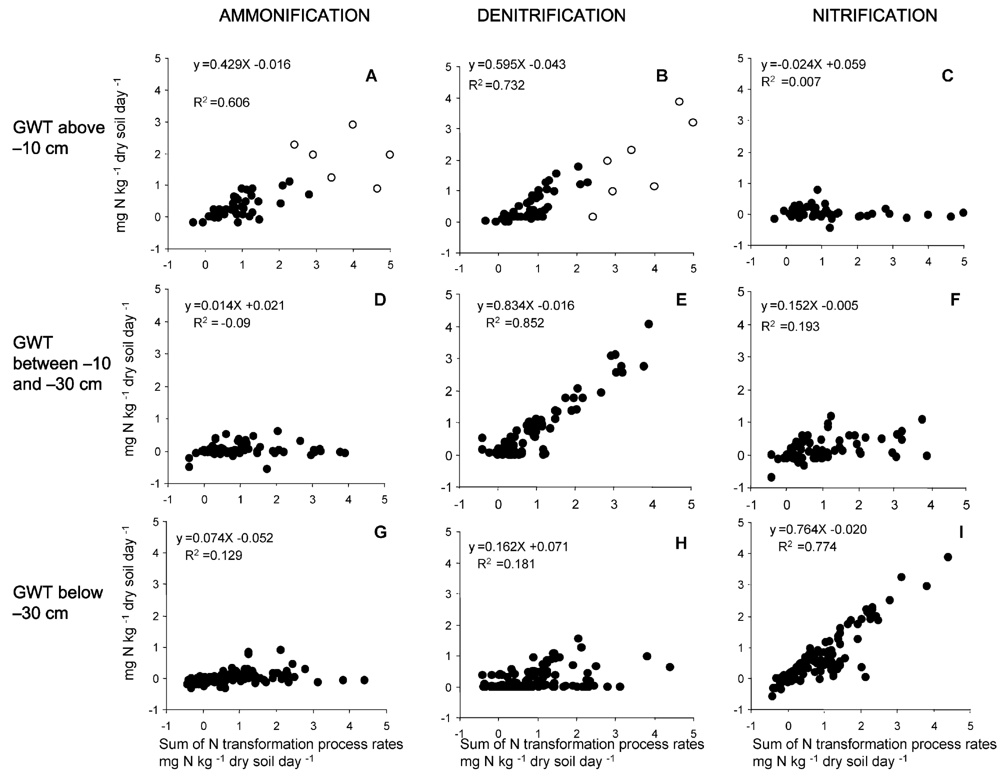

Figure 5. Relationship between ammonification, denitrification and nitrification versus the sum of N transformation processes in top 20 cm, separated for three groundwater classes based on thresholds calculated from r^2 values ($50 < n < 169$). Open symbols indicate specific sampling spots in the Dutch riparian zones with a high allochtonous nitrate input upto the stream.

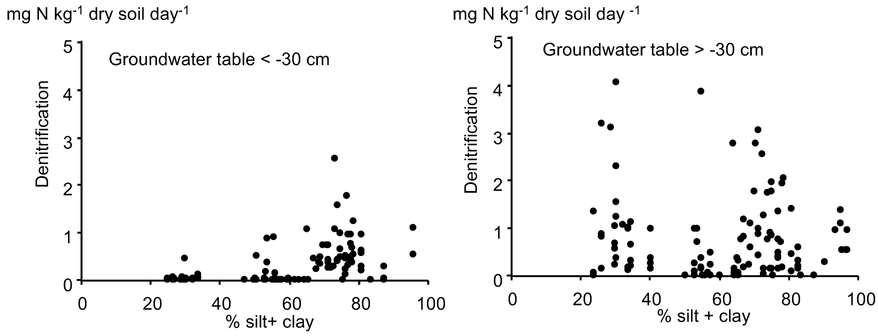

Figure 6. Denitrification rates in riparian top-soils (0–20 cm) as a function of the silt and clay content, separated for wet and dry sites using the groundwater table threshold value of −30 cm ($62 < n < 249$).

It is already well known that waterlogging limits oxygen diffusion by filling the soil pore space and, in turn, that it triggers anoxic conditions (Ponnamperuma 1972). Therefore, soil flooding or drainage type are often used as a proxy to determine the redox conditions, and denitrification potential, or to identify riparian sinks for nitrate in watersheds (Gold et al. 2001; Rosenblatt et al. 2001). In this European study, we found different water table level thresholds, that is, −10 and −30 cm, which characterized the predominance of different microbial N cycling processes in the soils. Denitrification activity occurred at all groundwater table levels; even in soils with groundwater levels below −30 cm (Figure 5). However, the rates varied widely, and the results provided evidence that the limiting factors of denitrification were directly related to the water table level.

When the water table was within −10 cm of the soil surface, the major end product of N mineralization was ammonium (Figure 5(A)). Net nitrification was insignificant (Figure 5(C)) because of the shortage of free oxygen in the soil. Even though it might occur in aerobic spots, the nitrate end product will have been denitrified. Therefore, under these conditions nitrification can be considered as the rate-limiting step for the denitrification process (Davidson and Swank 1986; Van Oorschot et al. 2000). The very high denitrification rates measured at the Dutch sites occurred because of an extremely high allochtonous nitrate input from the adjacent upland fields so that there was a high nitrate availability even in the saturated near-stream strip (Figure 5(B)). The high ammonification rates found at the Dutch sites under these reduced conditions (Figure 5(A)) may have partly been caused by microbial dissimilatory reduction of NO_3^- to NH_4^+ (Howard-Williams and Downes 1993).

When water table levels were between −10 and −30 cm from the soil surface we measured the highest rates of denitrification. Under these conditions, aerobic and anaerobic hot spots co-exist in the soil profile allowing both nitrification and denitrification to occur (McClain et al. 2003). The nitrification activity was demonstrated indirectly by the lack of net ammonification

(Figure 5(D)), which revealed that most ammonium being released was further nitrified. However, net nitrification was still limited (Figure 5(F)) since its nitrate end product was denitrified as soon as it was formed (Figure 5(E)). Therefore water table fluctuations within the upper soil horizons, that is, circa -10 to -30 cm, allows the co-existence of both nitrification and denitrification microbial processes in close proximity, which results in a large removal of nitrogen from the riparian soils via denitrification (average values range from 0.62 to 1.04 mg N kg^{-1} dry soil day^{-1}).

In drier sites or periods, that is, when water table levels were below -30 cm, the end product of N mineralization was nitrate (Figure 5(I)). At such sites denitrification can only occur in fine-textured soils and is probably triggered by short-term events such as rainfall or flash floods that generate partial anaerobiosis in these fine-textured soils. This significant relation between soil texture and denitrification activity in floodplain soils has been observed elsewhere (e.g., Groffman and Tiedje 1989). For instance Pinay et al. (2000) found a threshold value of 65% silt and clay above which significant denitrification rates were found. In our study no such clear threshold value could be observed, although the highest denitrification rates under these dry conditions occurred in sites with a silt and clay content above 70% (Figure 6(B)).

According to Burt et al. (2002), water table movement is regulated by upslope hydrology in steep (headwater) riparian zones and by the adjacent stream level in flat floodplains. Under natural conditions the hydrological regime of riparian wetlands often entails large seasonal fluctuations in water table elevation (Naiman et al. 2002; Nilsson and Svedmark 2002). Our results show that water level variations can enhance nutrient losses by denitrification in wet riparian zones leading to a decrease of N availability. In riparian zones with low N loading rates this will lead to a decrease of plant production compared to permanently wetter or drier sites. This result is consistent with previous studies by Clawson et al. (2001) who found the highest primary productivity in the wettest zones and Burke et al. (1999) who related the lowest net primary production in the intermittently flooded zone to nutrient deficiency.

In riparian zones subjected to considerable N enrichment, increased water level variations will enhance the nitrogen removal efficiency. Indeed, several studies have demonstrated that alternating aerobic and anaerobic conditions affect soil microbial activity (Mamilov and Dilly 2002), enhancing organic matter mineralization and nitrogen loss through denitrification (Reddy and Patrick 1975; Groffman and Tiedje 1988). In a recent study (Clément et al. 2002) found that the potential denitrifying community of the upper soil horizons of riparian zones did not vary significantly between the near-stream strip and the non-flooded upland bordering the agricultural field, despite the large seasonal groundwater table fluctuations. This large and ubiquitous potential denitrification activity even in drier sites reveals that any change in the hydrological regime might affect the denitrification activity in riparian soils. Scenarios of climate change on the hydrological regime forecast an increase of the inter-annual variability of runoff (Arnell 1999).

Therefore, water table level and its dynamics can be altered both from the upslope by land use/land cover change influencing the runoff response and from the changes in river discharge.

Although it is difficult to forecast all the consequences of climate change on N cycling in riparian ecosystems, the prevalent role of water table dynamics in N cycling provides some basis for predictions of possible changes. Indeed, an increase in runoff variability will result in larger fluctuations in water table level and consequently larger fluctuations in soil redox conditions, which in turn will stimulate N removal by denitrification. Moreover, enhanced temperatures may increase rates of N mineralization (Rustad et al. 2001), nitrification and denitrification (Maag et al. 1997). In northern Europe, Arnell (1999) expect an increase in average annual runoff, which may result in an increased nutrient loading of riparian zones. Thus, in terms of water quality enhancement riparian buffer zones in the north are expected to become even more effective under the new climatic conditions. In southern Europe, however, drier soil conditions as a result of climatic change, are expected to compensate the effects of temperature increase on mineralization and N removal by denitrification (Leiros et al. 1999; IPCC 2001). Furthermore, the total area of wetlands is expected to decrease in the south, which could reach the point that their nutrient amendment function would become insignificant from the catchment perspective.

Conclusions

In this study, three consistent water table thresholds were identified at very different riparian sites in terms of climate and N loading. When water table levels are within -10 cm of the soil surface, ammonification prevails and ammonium accumulates in the topsoil. Average groundwater tables between -10 and -30 cm favour denitrification and therefore reduce the nitrogen availability in soils. At sites with water table levels below -30 cm, nitrate is the main end product as a result of high net nitrification. At these latter sites, denitrification is triggered by rainfall events in fine-textured soils. These threshold values provide a proxy to evaluate the consequences of water level variations under human or natural changes on nitrogen processes and N availability in riparian wetlands.

Acknowledgements

The results reported here were collected as part of an European project on nitrate buffer zones, the NICOLAS (Nitrogen Control by landscape structures in agricultural environments) project. This was funded by the European commission DG XII (Scientific Advisor, H. Barth), grant number ENV4-CT97-0395.

References

Arnell N.W. 1999. The effect of climate change on hydrological regimes in Europe: a continental perspective. Global Environ. Chang. 9: 5–23.

Benke A.C., Chaubey I., Ward G.M. and Dunn E.L. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. Coastal Plain. Ecology 81 (10): 2730–2741.

Binkley D. and Hart S.C. 1989. The components of nitrogen availability; assessments in forest soils. Adv. in Soil Sci. 10: 57–112.

Brinson M.M., Bradshaw H.D. and Kane E.S. 1984. Nutrient assimilative capacity of an alluvial floodplain swamp. J. of Appl. Ecol. 21: 1041–1057.

Brinson M.M., Lugo A.E. and Brown S. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annu. Rev. Ecol. Syst. 12: 123–161.

Burke M.K., Lockaby B.G. and Conner W.H. 1999. Above-ground production and nutrient circulation along a flooding gradient in a South Carolina coastal plain forest. Can. J. Forest Res. 29: 1402–1418.

Burt T.P. 1997. The hydrological role of buffer zones within the drainage basin system. In: Haycock, N.E. Burt T.P., Goulding K.W.T. and Pinay G. (eds) Buffer Zones: Their Processes and Potential in Water Protection. Quest Environmental, pp. 21–32.

Burt T.P. and Haycock N.E. 1996. Linking floodplains to rivers. In: Anderson G.M., Walling D.E. and Bates P.D. (eds) Floodplain Processes. Wiley, pp. 461–492.

Burt T.P., Pinay G., Matheson F.E., Haycock N.E., Butturini A., Clément J.C., Danielescu S., Dowrick D.J., Hefting M.M., Hilbricht-Ilkowska A. and Maitre V. 2002. Water table fluctuations in the riparian zone: comparative results from a pan-European experiment. J. Hydrol. 265: 129–148.

Cirmo C.P. and McDonnell J.J. 1997. Linking the hydrologic and biogeochemical controls of nitrogen transport to near-stream zones of temperate-forested catchments: a review. J. Hydrol. 199: 88–120

Clawson R.G., Lockaby B.G. and Rummer B. 2001. Changes in production and nutrient cycling across a wetness gradient within a floodplain forest. Ecosystems 4: 126–138.

Clément J.C., Pinay G. and Marmonier P. 2002. Seasonal dynamics of denitrification along topohydrosequences in three different riparian wetlands. J. Environ. Qual. 31 (3): 1025–1037.

Cosandey A.C., Guenat C., Dowrick D.J., Pinay G., Bernal S., Cimpian C., Clément J.C., Hefting M.M., Kruk M. 2002. Controls of denitrification in European riparian soils. In: Denitrification in Riparian Soils: Patterns Controls and Influence on Water Quality. PhD Thesis Number 2518 (2001). EPFL Lausanne, Switzerland.

Daniels R.B. and Gilliam J.W. 1996. Sediment and chemical load reduction by grass and riparian filters. Soil Sci. Soc. Am. J. 60: 246–251.

Davidson E.A. and Swank W.T. 1986. Environmental parameters regulating gaseous nitrogen losses from two forested ecosystems via nitrification and denitrification. Appl. Environ. Microbio. 52: 1287–1292.

Day P.R. 1965. Particle fractionation and particle size analysis. In: Black C.A. (ed). Method of Soil Analysis. A Series. 9: 545–567.

Day F.P. and Megonigal J.P. 1993. The relationship between variable hydroperiod, production allocation, and below-ground organic turnover in forested wetlands. Wetlands 13: 115–121.

De Klein C.A.M. and Van Logtestijn R.S.P. 1994. Denitrification in the top soil of managed grasslands in the Netherlands in relation to soil type and fertilizer level. Plant Soil 163: 33–34.

Eno C. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Sci. Soc. of Am. J. 24: 277–279.

Freeman C., Gresswell R., Guasch H., Hudson J., Lock M.A., Reynolds B., Sabater F. and Sabater S. 1994. The role of drought in the impact of climatic change on the microbiota of peatland streams. Freshwater Biol. 32: 223–230.

Georgakakos K.P. and Smith D.E. 2001. Soil moisture tendencies into the next century for the conterminous United States. J. Geophys. Res. 106 (D21): 27361–27382.

Gillham R.W. 1984. The capillary fringe and its effect on water-table response. J. Hydrol. 67: 307–324.

Gold A.J., Groffman P.M., Addy K., Kellogg D.Q., Stolt M. and Rosenblatt A.E. 2001. Landscape attributes as controls on ground water nitrate removal capacity of riparian zones. J. Am. Water Resour. Assoc. 37 (6): 1457–1464.

Gregory S.V., Swanson F.J., McKee W.A. and Cummins K.W. 1991. An ecosystem perspective of riparian zones. BioScience 41 (8): 540–551.

Groffman P.M. and Tiedje J.M. 1988. Denitrification hysteresis during wetting and drying cycles in soil. Soil Sci. Soc. of Am. J. 52: 1626–1629.

Groffman P.M. and Tiedje J.M. 1989. Denitrification in north temperate forest soils: spatial and temporal patterns at the landscape and seasonal scales. Soil Biol. Biochem. 21 (5): 613–620.

Groffman P.M., Tiedje J.M., Robertson G.P. and Christensen S. 1987. Denitrification at different temporal and geographical scales; proximal and distal controls. In: Wilson J.R. (ed) Advances in Nitrogen Cycling in Agricultural Ecosystemspp. 174–192.

Groffman P.M., Hanson G.C., Kiviat E. and Stevens G. 1996. Variation in microbial biomass and activity in four different wetland types. Soil Sci. Soc. Am. J. 60: 622–629.

Hanson G.C., Groffman P.M. and Gold A.J. 1994. Denitrification in riparian wetlands receiving high and low nitrate inputs. J. Environ. Qual. 23: 917–922.

Haycock N.E., Burt T.P., Goulding K.W.T. and Pinay G. 1997. Buffer Zones: Their Processes and Potential in Water Protection. Quest Environmental, Harpenden, UK.

Hedin L.O., Vonfischer J.C., Ostrom N.E., Kennedy B.P., Brown M.G. and Robertson G.P. 1998. Thermodynamic constraints on nitrogen transformations and other biochemical processes at soil-stream interfaces. Ecology 79: 684–703.

Hill A.R. 1996. Nitrate removal in stream riparian zones. J. Environ. Qual. 25: 743–755.

Howard-Williams C. and Downes M.T. 1993. Nitrogen cycling in wetlands. In: Nitate Processes, Patterns and Management, Burt T.P., Heatwaite A.L., Trudgill S.T. (eds) Wiley and Sons: Chichester, UK, pp. 141–167.

Hynes H.B.N. 1983. Groundwater and stream ecology. Hydrobiologia 100: 93–99.

IPCC 1996. Climate change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, U.K.

IPCC 2001. Climate Change 2001: Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge, U.K.

Johnston C.A., Bridgham S.D. and Schubauer-Breigan J.P. 2001. Nutrient dynamics in relation to geomorphology of riverine wetlands. Soil Sci. Soc. of Am. J. 65 (2): 557–577.

Junk W.B., Bayley P.B. and Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. Fish. Aquat. Sci. 106: 110–127.

Keeney D.R. and Nelson D.W. 1982. Nitrogen-inorganic forms. In: Page A.L. (ed) Methods of Soil Analysis. ASA-SSSA Publisher. Agronomy Monograph 9: 643–698.

Leiros M.C., Trasar-Cepeda C., Seoane S. and Gil-Sotres F. 1999. Dependence of mineralization of soil organic matter on temperature and moisture. Soil Biol. Biochem. 31: 327–335.

Maag M. and Vinther F.P. 1996. Nitrous oxide emission by nitrification and denitrifcation in different soil types and at different soil moisture contents and temperatures. Applied Soil Ecology 4: 5–14.

Maag M., Malinovsky M. and Nielsen S.M. 1997. Kinetics and temperature dependence of potential denitrification in riparian soils. J Environ Qual 26: 215–223.

Mamilov A.S. and Dilly O.M. 2002. Soil microbial eco-physiology as affected by short-term variations in environmental conditions. Soil Biol. Biochem. 34: 1283–1290.

McClain M.E., Boyer E.W., Dent L., Gergel S.E., Grimm N.B., Groffman P.M., Hart S.C., Harvey J.W., Johnston C.A., Mayorga E., McDowell W.H. and Pinay G. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6: 301–312.

Megonigal J.P., Conner W.H., Kroeger S. and Sharitz R.R. 1997. Above-ground production in southeastern floodplain forests: a test of the subsidy-stress hypothesis. Ecology 78 (2): 370–384.

Mitsch W.J. and Ewel K.C. 1979. Comparative biomass and growth of cypress in Florida wetlands. Am. Midl. Nat. 101: 417–426.
Mitsch W.J. and Rust W.G. 1984. Tree growth response to flooding in a bottomland forest in northeastern Illinois. Forest Sci. 30: 499–510.
Naiman R.J. and Décamps H. 1997. The ecology of interfaces: riparian zones. Annu. Rev. Ecol. Syst. 28: 621–658.
Naiman R.J., Bunn S.E., Nilsson C., Petts G.E., Pinay G. and Thompson L.C. 2002. Legitimizing fluvial ecosystems as users of water: an overview. Environmental Management 30 (4): 455–467.
Nijssen B., O'Donnell G.M., Hamlet A.F. and Lettenmaier D.P. 2001. Hydrologic sensitivity of global rivers to climate change. Climatic Change 50: 143–175.
Nilsson C. and Berggren K. 2000. Alterations of riparian ecosystems caused by river regulation. Bioscience 50 (9): 783–792.
Nilsson C. and Svedmark M. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. Environ. Manag. 30 (4): 468–480.
Odum E.P., Finn J.T. and Franz E.H. 1979. Perturbation theory and the subsidy-stress gradient. Bioscience 29: 349–352.
Pastor J., Stillwell M.A. and Tilman D. 1987. Nitrogen mineralization and nitrification in four Minnesota old fields. Oecologia 71: 481–485.
Patrick W.J. 1982. Nitrogen transformations in submerged soils. Agronomy Monograph.
Peterjohn W.T. and Correll D.L. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. Ecology 65 (5): 1466–1475.
Pinay G. and Burt T.P. NICOLAS 2001. Nitrogen Control by Landscape Structures. Final report of the European research project 1997–2000 ENV4-CT97-0395. European commission DGXII.
Pinay G., Ruffinoni C. and Fabre A. 1995. Nitrogen cycling in two riparian forest soils under different geomorphic conditions. Biogeochemistry 4: 1–21.
Pinay G., Black V.J., Planty-Tabacchi A.M., Gumiero B. and Décamps H. 2000. Geomorphic control of denitrification in large river floodplain soils. Biogeochemistry 30 (9): 9–29.
Pinay G., Clément J.C. and Naiman R.J. 2002. Basic principles and ecological consequences of changing water regimes on nitrogen cycling in fluvial systems. Environ. Manag. 30 (14): 481–491.
Ponnamperuma F.N. 1972. The chemistry of submerged soils. Adv. in Agron. 24: 29–96.
Reddy K.R. and Patrick W.H. Jr. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. Soil Biol. Biochem. 7: 87–94.
Reddy K.R., Patrick W.H. Jr. and Philips R.E. 1980. Evaluation of selected processes controlling nitrogen loss in a flooded soil. Soil Sci. Soc. Am. J. 44 (6): 1241–1246.
Reddy K.R., Patrick W.H. and Lindau C.W. 1989. Nitrification-denitrification at the plant root-sediment interface in wetlands. Limnol. Oceanogr. 1004–1113.
Rosenblatt A.E., Gold A.J., Stolt M.H., Groffman P.M. and Kellogg D.Q. 2001. Identifying riparian sinks for watershed nitrate using soil surveys. J. Environ. Qual. 30: 1596–1604.
Rustad L.E., Campbell J.L., Marion G.M., Norby R.J., Mitchell M.J., Hartley A.E., Cornelissen J.H.C. and Gurevitch J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and above-ground plant growth to experimental ecosystem warming. Oecologia 126: 543–562.
Ryden J.C., Skinner J.H. and Nixon D.J. 1987. Soil core incubation system for the field measurement of denitrification using acetylene-inhibition. Soil Biol. Biochem. 19 (6): 753–757.
Sabater S., Butturini A., Clément J.C., Dowrick D., Hefting M.M., Maitre V., Pinay G., Postolache C., Rzepecki M. and Sabater F. 2003. Nitrogen removal by riparian buffers under various N loads along an European climatic gradient: patterns and factors of variation. Ecosystems 6: 20–30.
Salo J., Kalliola R., Häkkinen J., Mäkinen Y., Niemelä P., Puhakka M. and Coley P.B. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 332: 254–258.
Schlosser I.J. and Karr J.R. 1981. Riparian vegetation and channel morphology impact on spatial patterns of water quality in agricultural watersheds. Environ. Manag. 5 (3): 233–243.

Shaver G.R., Canadell J., Chapin F.S.I., Gurevitch J., Harte J., Greg H., Ineson P., Jonasson S., Melillo J., Pitelka L. and Rustad L. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. Bioscience 50: 871–882.

Technicon 1977. Nitrate and Nitrite in Water and Sea Water. Industrial Method 158–71 WIA. Tarrytown, New York, USA.

Tiedje J.M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium.In: Zehnder A.J.B. (ed) Biology of anaerobic microorganisms. pp. 179–244. New York.

Van Oorschot M., Van Gaalen N., Maltby E., Mockler N., Spink A. and Verhoeven J.T.A. 2000. Experimental manipulation of water levels in two French riverine grassland soils. Acta Oecol. 21: 49–62.

Verchot L.V., Franklin E.C. and Gilliam J.W. 1997. Nitrogen cycling in piedmont vegetated filter zones. 1. Surface soil processes. J. Environ. Qual. 26: 327–336.

Whiting P.J. and Pomeranets M. 1997. A numerical study of bank storage and its contribution to streamflow. J. Hydrol. 202: 121–136.

Yoshinari T. and Knowles R. 1976. Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. Biochem. Biophys. Res. Commun. 69 (3): 705–710.