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Denitrification potential of a river floodplain during flooding with nitrate-rich water: grasslands versus reedbeds

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Abstract. Denitrification is a major mechanism for nitrogen removal from nitrogen-rich waters, but it requires oxygen-poor conditions. We assessed denitrification rates in nitrate-rich but also oxygen-rich river water during its stay in a floodplain. We measured diurnal oxygen fluctuations in floodwater along the river Rhine, and carried out an experiment to assess denitrification rates during day, evening and night. Denitrification in floodwater and flooded sediment were measured, comparing activity of periphyton and sediment from agricultural grasslands and reedbeds. Floodwater along the river Rhine was oxygen-saturated (> 10 mg O_2/L) during the day, but oxygen largely disappeared during the night (0.4–0.8 mg O_2/L). Independent of oxygen concentrations, denitrification in surface water alone hardly occurred. In flooded sediments, however, denitrification rates were much higher (1.1–1.5 mg N m^{-2} h^{-1}), particularly at dark and oxygen-poor conditions (nighttime). In the experimental jars, reedbed-periphyton bacteria achieved similar denitrification rates as bacteria in sediment, but overall periphyton denitrification was of minor importance when calculated per square meter. Apart from oxygen levels, maximum denitrification appeared to be regulated by nitrate diffusion from water into the sediment, as the maximum quantity of N denitrified in the sediment equalled the quantity of N lossed from the surface water. Assessed 24-hr denitrification rates in the flooded floodplains (c. 15 mg N m^{-2} d^{-1}) were similar in grasslands and reedbeds, and were rather low compared to rates in other floodplains.

Introduction

River embankment and agricultural development have eliminated most natural floodplain wetlands along rivers in Western Europe and North America (Haycock et al. 1993; Naiman and Décamps 1997; Keddy 2000). Both the reduced water quantity passing through floodplains, as well as a changed floodplain vegetation cover, may have reduced the rivers natural capacity to remove nutrients from the water (cf. Groffman et al. 1991; Pinay et al. 1994; Naiman and Decamps 1997; Sjodin 1997; Olde Venterink et al. 2003), and hence may have contributed to eutrophication of rivers and coastal marine waters (cf. Howarth et al. 1996). Factors affecting nutrient removal from large rivers are not well known (Alexander et al. 2000).

Denitrification is considered as a major mechanism for nutrient removal from nitrogen-enriched waters (Hill 1979; Howard-Williams 1985; Seitzinger 1988; Johnston 1991; Sjodin et al. 1997; Mitsch et al. 2001; Vymazal 2001). High denitrification rates are achieved in constructed wetlands where site conditions are optimized for the benefit of waste water treatment (Vymazal 2001). Waste water is generally oxygen-poor and ammonium-rich; large amounts of nitrogen can be removed from the water through coupled nitrification-denitrification (Patrick and Reddy 1976; Eriksson and Weisner 1999; Vymazal 2001). In contrast, river water is often oxygen-rich and nitrogen is mainly present as nitrate, particularly in the densely populated areas of Western Europe and North America (Caraco and Cole 1994; Sjodin et al. 1997). Because oxygen inhibits denitrification (Tiedje 1988), denitrification may only occur if the water becomes oxygen-poor. Microbial respiration may create such low oxygen concentrations in standing water, particularly during the night (Kersting and Kouwenhoven 1989; Cronk and Mitsch 1994; McMahon et al. 1995; Schreijer et al. 2000).

Studies in which denitrification in floodplains of large rivers was measured, mostly focused on denitrification rates in soil or sediment (Spink et al. 1998; Pinay et al. 1993, 1995; Verhoeven et al. 2001). During flooding, however, nitrogen may also be removed from the river by denitrification of nitrate from the floodwater. Denitrification of floodwater nitrate may be performed by free-living denitrifying bacteria in the water, by bacteria in the flooded sediment, or by bacteria in periphyton attached to submerged plants (Weisner et al. 1994; Eriksson and Weisner 1999; S. Toet, personal communication). Denitrification rates in flooded sediment and periphyton not only depend on the bacterial activity, but also on the rate of nitrate diffusion from the surface water into the sediment or periphyton (e.g., Christensen et al. 1990; Eriksson 2000). Differences between agricultural grasslands and natural floodplain wetlands are not to be expected for diffusion between water and sediment zone, but can be expected for diffusion between water and periphyton. Since the surface area for periphyton is much lower in agricultural grasslands than in natural floodplain types such as reedbeds, woodlands or ponds (i.e., reed stems, trees, macrophytes), it can be expected that periphyton denitrification per square meter is more important in the natural wetland types.

The objectives of this study were: (i) to determine whether denitrification takes place in floodplains during flooding with nitrate-rich but also oxygen-rich river water; (ii) to assess the importance of denitrifying bacteria in water, sediment and periphyton for such denitrification; (iii) to compare denitrification rates between flooded agricultural grasslands and reedbeds. We measured diurnal oxygen fluctuations in floodwater along the river Rhine, and subsequently we carried out an experiment to assess denitrification rates during day and night, in flooded agricultural grasslands and reedbeds.

Methods

Diurnal fluctuations in oxygen concentration were measured in water of the river Waal and of its flooded floodplain near Gorinchem (5°00′ E–51°50′ N). The Waal is the main distributary of the river Rhine in The Netherlands. Oxygen concentration and saturation were measured by means of an oxygen-electrode (OXI 340, WTW) on 26 April 2001 at 4 p.m. and on 27 April at 6 a.m., at the same spots. These times were assumed to approximate diel maximum and minimum oxygen concentrations, respectively (cf. Kersten and Kouwenhoven 1998; Schreijer et al. 2000).

Subsequently, a laboratory experiment was carried out to assess denitrification rates in floodwater of the river Waal. Various treatments were established to determine differences in denitrification rates in floodwater between: (i) river water only, water + sediment, water + periphyton, and water + sediment + periphyton, (ii) light and oxygen conditions during the day, the evening and the night, (iii) agricultural grasslands and reedbeds. The experiment was carried out with 1-L gas-tight jars in a climate room at 16 °C, which approximated the river water temperature at the moment of water and soil collection (16 May 2001). All treatments were carried out with five replicate jars, resulting in a total of 120 incubated jars. Denitrification was determined by the acetylene-blockage method. This method makes use of acetylene inhibiting the final step in denitrification: the reduction of nitrous oxide to nitrogen gas. The rate of denitrification is assessed by measuring nitrous oxide production, in the presence of acetylene Yoshinari and Knowles (1976).

All 120 jars were filled with 540 mL water of the river Waal and 60 mL acetylene saturated water of the same river (acetylene content 10% v/v). Saturation was achieved by bubbling with acetylene for 10 minutes. For the water treatment nothing else was added to the water. The effect of sediment on denitrification was determined by inserting a top-soil core (depth 5-cm, diameter 5-cm) including the surface biofilm into the jar. Cores were collected in recently flooded agricultural grasslands and reedbeds along the river Waal, near Gorinchem. In agricultural grasslands, cores were carefully collected with the grass (*Lolium perenne* and other species) shoots attached to the soil. In the lab, grass and soil were separated. The soil was used for the sediment treatment, the grass shoots—and attached periphyton—were used for the periphyton treatment. Periphytic denitrification in reedbeds was assessed by adding six basal parts of reed (*Phragmites australis*) shoots to the jars (following S. Toet, personal communication). Only the submerged parts (c. 30 cm long) covered with periphyton (epiphytic biofilm containing bacteria and algae) were added, after they were carefully cut in pieces. Floating of grass or reed shoots in the jars was prevented using iron frames.

Day, evening and night conditions were simulated by incubating the jars at various combinations of light (700 lux) and dark, as well as oxygen-rich (100% saturated) and oxygen-poor conditions. To simulate oxygen-poor conditions (night treatment), the 540 mL water in the jars were flushed with N_2 until oxygen concentrations were below 1 mg/L (N_2 flushing preceded addition of sediment or periphyton). Additionally, headspaces of the jars of the night treatment were flushed with N_2 for

Table 1. Diurnal fluctuations in oxygen concentrations in the river Rhine and in river water that has entered its floodplain. Mean (S.E.) values of three replicate sites are shown.

	O_2 concentration (mg/L)		O_2 saturation (%)	
	day	night	day	night
river	11.1 ± 0.2	10.3 ± 0.1	103 ± 1	93 ± 1
reedbed 1	15.7 ± 1.8	0.4 ± 0.0	145 ± 10	3 ± 0
reedbed 2	18.5 ± 0.3	0.5 ± 0.0	169 ± 1	5 ± 0
woodland	14.4 ± 0.9	0.8 ± 0.1	138 ± 6	6 ± 1

day = 26 April 2001 at 4 p.m.; night = 27 April 2001 at 6 a.m.

a minute, before the jars were closed. All jars were placed on a shaker to create a gentle water movement in the jars.

Both 30 minutes and 330 minutes after closing the jars, N_2O concentrations were measured in the headspaces of the jars by means of a photo-acoustic multi-gas monitor (Innova Airtech Instruments). N_2O production was calculated for the period between measurements, correcting for N_2O equilibrium between water and gas using the Bunsen coefficient (S. Toet, personal communication). Differences in denitrification between treatments were tested by means of 4-way ANOVA. Denitrification rates were calculated per square meter with a flooding depth of 30-cm; i.e., this depth corresponded with the amount of water in the jars compared to the surface of the soil core (19.6 cm^2). For periphyton in reedbeds, denitrification per square meter was calculated using the average area that the 6 reed stems (a jar contained 6 stems) covered in the field. The reedbed contained on average 315 reed stems per m^2, so the 6 stems in the jars corresponded to an area of 190 cm^2. As the reed stems were 30-cm long, the calculations corresponded to a flood depth of 30-cm.

As a control, oxygen concentrations were measured at the start and at the end of the experiment, and water samples were taken to determine the decrease in nitrate concentration. Nitrate concentrations were measured by means of UV-VIS photospectrometry (Lambda 20, Perkin Elmer).

Results

Water of the river Waal was close to 100% oxygen saturation, both during day and night (Table 1). In contrast, oxygen concentrations in floodwater in adjacent floodplains were over-saturated during the day (140–170%), but dropped drastically during the night (3–6%) (Table 1).

Denitrification rates were very low in the water treatments; whether oxygen concentrations were high or low made no difference (Figure 1). Denitrification was clearly higher in the ’flooded sediment’ treatments than in the treatments without sediment (Figure 1; Table 2). It made no difference whether sediment was derived from a reedbed or from an agricultural grassland (cf. interaction floodplain type ×

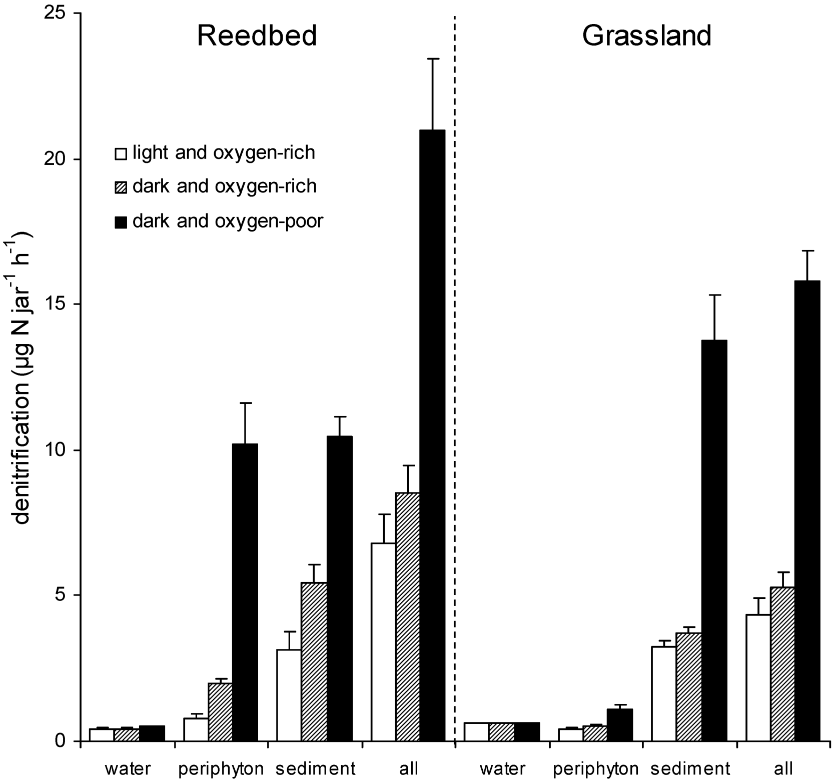

Figure 1. Denitrification rates in river water above flooded grasslands and reedbeds, performed by bacteria in water, in sediment and in periphyton. Diurnal changes in site conditions were simulated by different combinations of light and oxygen concentrations during incubation. Denitrification was measured as N_2O production after acetylene addition. Error bars represent standard errors of five replicates. Statistics are shown in Table 2.

sediment; Table 2). Denitrification rates were also clearly higher in the dark oxygen-poor treatment, than in the two oxygen-rich treatments (Figure 1; Table 2). Note, however, that denitrification clearly took place (i.e., rates > 0) in some of the oxygen-rich treatments (Figure 1).

Although periphyton addition increased denitrification in the reedbed treatments substantially (Figure 1), the effect of periphyton was only marginal when it was calculated per square meter (Figure 2). The latter was due to a relatively low in situ density of reed stems compared to our experimental conditions. The interaction term between sediment and periphyton, although weakly significant, only explained 0.6% of the variation in denitrification (Table 2), indicating that denitrification processes in sediment-water and periphyton-water contact areas were largely independent from each other.

Overall, denitrification reached maximal rates of c. 1.0–1.6 mg N m^{-2} h^{-1}, in oxygen-poor 'flooded sediment' treatments (Figure 2). If nitrate in the water was

Table 2. Analysis of variance of the effect of floodplain type (reedbed vs. grassland), day/night (differences in light and oxygen content of the floodwater), periphyton and sediment on denitrification rates in the jars.

effect	df	F	*P*	%V
floodplain type	1	22.0	***	2.0
day/night	2	147.5	***	26.6
periphyton	1	65.4	***	5.9
sediment	1	399.6	***	36.0
floodplain type x day/night	2	3.1	ns	0.6
floodplain type x periphyton	1	33.1	***	3.0
floodplain type x sediment	1	0.1	ns	0.0
day/night x periphyton	2	17.2	***	3.1
day/night x sediment	2	56.9	***	10.3
periphyton x sediment	1	6.1	*	0.6
floodplain type x day/night x periphyton	2	12.1	***	2.2
floodplain type x day/night x sediment	2	5.9	**	1.1
floodplain type x periphyton x sediment	1	0.1	ns	0.0
day/night x periphyton x sediment	2	0.2	ns	0.0
floodplain type x day/night x periphyton x sediment	2	0.4	ns	0.1

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant; %V = explained variance (sum of squares/corrected total sum of squares; in%)

the sole source for denitrification, these maximum rates should have led to a decrease in nitrate concentrations in the water with c. 0.2 mg N/L. Indeed, at the end of the experiment nitrate concentrations in the water were 0.2–0.3 mg N/L lower in the with-sediment treatments and combined treatments than in the water-only treatments (Table 3; not determined for the reedbed treatments). At the end of the experiment, the oxygen concentration in water of the water treatments was still 10 mg/L, but it had dropped in the other treatments; e.g., to 4 mg/L in the dark reedbed-periphyton treatment (Table 4). Oxygen concentrations in the N_2-flushed jars were 0.8–1.1 mg/L. Daily denitrification rates in flooded floodplains were estimated at c. 15 mg N m^{-2} d^{-1}, in both reedbeds and grasslands (Figure 3).

Discussion

In many wetland ecosystems, denitrification is largely regulated by nitrification rates (Patrick and Reddy 1976; Seitzinger 1988, 1994; Eriksson and Weisner 1999; Vymazal 2001; Olde Venterink et al. 2002). Floodplain wetlands of many large rivers in Western Europe and North America, however, form a distinct exception because of the regular external nitrate supply through flooding. Since the river water is not only nitrate-rich but also oxygen-rich, denitrification in flooded floodplains will only occur if oxygen concentrations will drop to sufficiently low levels. Reviewing three other studies, Seitzinger (1988) concluded that an oxygen concentra-

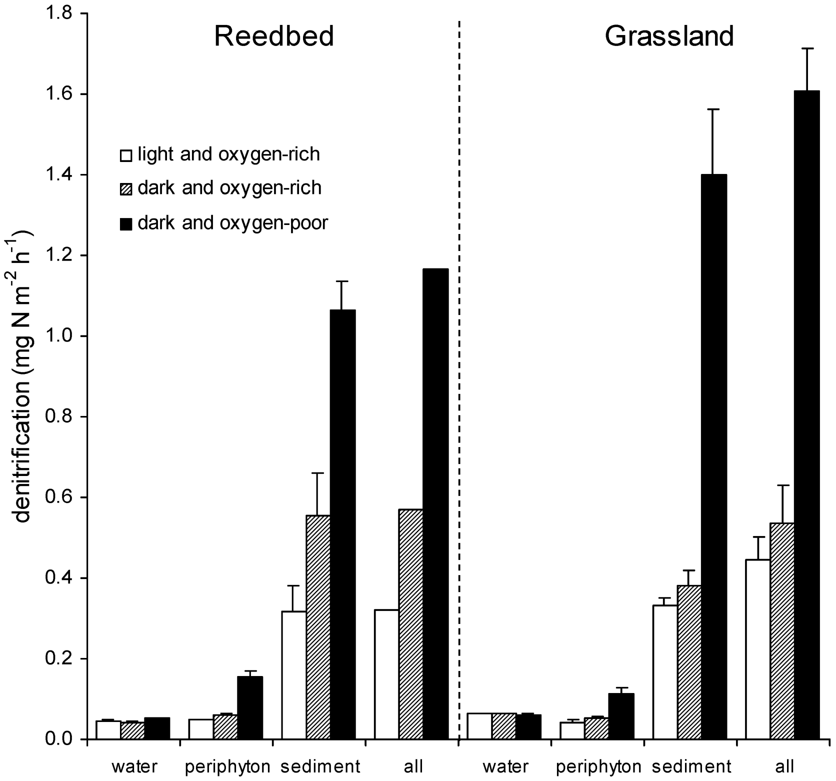

Figure 2. Denitrification rates in river water upon the various treatments as shown in Figure 1, but now calculated per square meter, with a flooding depth of 30 cm. Standard error could not be determined for the combined treatment in reedbeds, because true surface areas were unequal for sediment and periphyton.

Table 3. Nitrate concentrations (mg NO_3-N/L) in water at the end of the denitrification experiment. Only jars of the grassland treatments are included. Sediment addition decreased nitrate concentrations significantly ($P < 0.001$; 3-way ANOVA).

treatment	water	water + periphyton	water + sediment	all
light	2.22 ± 0.06	2.21 ± 0.05	2.19 ± 0.07	2.05 ± 0.06
dark	2.20 ± 0.12	2.06 ± 0.20	1.95 ± 0.13	1.86 ± 0.05
dark / N_2-flushed	2.25 ± 0.01	2.13 ± 0.08	2.00 ± 0.05	1.89 ± 0.02

tion of approximately 0.2 mg/L or less is required for denitrification in water or sediment. Studies on biofilms showed that denitrification started below oxygen concentrations of 0.3–0.6 mg/L (Nielsen et al. 1990; Dalsgaard and Revsbech 1992). Our field measurements demonstrated that oxygen concentrations in floodwater along large nitrate-rich rivers may drop to such levels (0.4–0.8 mg/L) during

Table 4. Average (± S.E.) oxygen concentrations in water after 5,5 hours incubation at the various treatments described in Figure 1. The oxygen concentration are shown in mg O_2/L. Oxygen concentration at the start of the incubation was c.10 mg/L.

	reedbed			grassland		
	light	dark	dark N_2-flushed	light	dark	dark N_2-flushed
water	10.0 ± 0.1	9.7 ± 0.1	1.1 ± 0.2	10.6 ± 0.1	10.4 ± 0.0	1.1 ± 0.1
periphyton	7.0 ± 0.3	4.7 ± 0.4	0.8 ± 0.0	9.6 ± 0.2	8.4 ± 0.3	0.9 ± 0.0
sediment	9.3 ± 0.2	9.0 ± 0.0	1.1 ± 0.1	9.1 ± 0.1	9.1 ± 0.1	0.8 ± 0.0
all	6.1 ± 0.4	4.1 ± 0.0	0.8 ± 0.0	8.5 ± 0.1	6.7 ± 0.4	0.8 ± 0.0

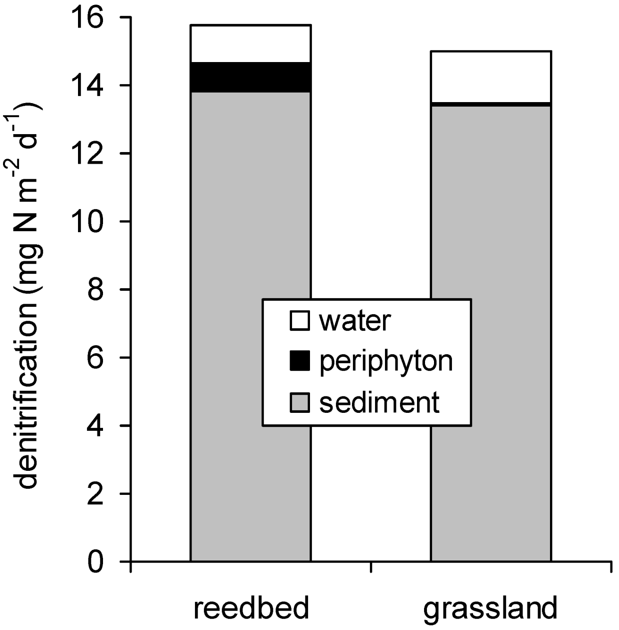

Figure 3. Estimated daily denitrification rates in floodwater in agricultural grasslands and reedbeds. Daily rates were calculated from rates in Figure 1; assuming 6 hours light and oxygen-rich, 12 hours dark and oxygen-rich, and 6 hours dark and oxygen-poor per day. A flood depth of 30-cm was assumed. Water = water treatment; Periphyon = periphyton treatment minus water treatment; Sediment = sediment treatment minus water treatment.

the night, and the lab-experiment showed that denitrification will indeed take place at these oxygen concentrations (0.8 mg/L or less).

In agreement with other studies (Seitzinger 1988; S. Toet, personal communication), we found that the denitrification rate in flooded sediment was much higher than in surface water without sediment. We have no direct evidence from denitrification measurements in the sediment, but the decreased nitrate concentrations in the water (Table 3) indicated that the denitrified-N in the flooded sediment was derived from the water. Christensen et al. (1990) also demonstrated that diffusion of nitrate from the overlying water into the sediment was the major nitrate source for denitrification in a Danish nitrate-rich stream. In contrast, Seitzinger (1988; 1994), mentioned that nitrate diffusing from the overlying water into the sediment was not the major source for denitrification, but nitrate produced in the sediment; i.e., she found that the rates of denitrification exceeded by far the rates of nitrate diffusion from an overlying aerobic water column into sediment. In our experiment, the maximum quantity of N denitrified in the sediment equalled the quantity of N lossed from the surface water. These equal amounts not only seem to suggest that the nitrate was derived from the water, but also that the maximum denitrification rate may even be regulated by the rate of nitrate diffusion from water into the sediment.

Nitrate in the floodwater as the major source for denitrification, may also explain why we did not observe large differences in denitrification rates between sediments from agricultural grasslands and reedbeds. Moreover, the soil/sediment cores were collected before the grasslands were fertilized, and nitrate from fertilization in previous years had probably been consumed by bacteria and plants before the time of sampling.

Periphyton denitrification in our nitrate-rich water was less important than in ammonium-rich water where the coupling of nitrification in periphyton with denitrification in sediment may result in relatively high denitrification rates (Eriksson and Weisner 1996; Eriksson 2000). Although reedbed-periphyton bacteria in our experimental jars were able to achieve similar denitrification rates as bacteria in sediment, denitrification rates of periphyton attached to reed stems were of minor importance compared to rates in sediment when calculated per square meter floodplain. The surface area for periphyton had to be about ten times larger than in our reedbeds to meet the denitrification rates in flooded sediment. Such surface areas for peripfyton may perhaps be reached in other types of floodplain wetlands; e.g., ponds with well-developed submerged macrophytes (cf. Eriksson and Weisner 1996; 1997).

We assessed the overall denitrification rates in our flooded grasslands and reedbeds at c. 15 mg N m^{-2} d^{-1}. Assuming 50 days of flooding per year (at our experimental conditions) would yield an annual denitrification rate of about 8 kg N ha^{-1} y^{-1}. Although this rough assessment is likely an overestimation (e.g., the 16 °C in the experiment was higher than the annual average temperature since flooding mainly occurs in winter and spring), it indicates that the denitrification rates in our flooded floodplains were in the same order of magnitude as the ’normal’ rate of denitrification rates in wetland soils (0–10 kg N ha^{-1} y^{-1}) according to Bowden (1987). The 8 kg N ha^{-1} y^{-1} is also comparable to the lower range of soil-denitrification rates reported for a number of floodplains in Europe and North America (Groffman et al. 1991; Spink et al. 1998; Verhoeven et al. 2001; Olde Venterink et al. 2002). However, much higher denitrification rates have been reported for other floodplain soils (> 50–100 kg N ha^{-1} y^{-1}; Pinay et al. 1993; 1995; Seitzinger 1994).

Upscaling of our assessed ’maximum’ denitrification rate to the entire floodplain area of the river Rhine in The Netherlands resulted in a negligible N-retention through denitrification (< 1% of annual N load of the River Rhine; Van der Lee et al. 2003). This negligible N-retention in the Dutch branches of the River Rhine was confirmed by water quality measurements during downstrean transport (Olde Venterink et al. 2003). The very low N-retention in the deep and fast-flowing River Rhine may be explained by a very low contact-time between river-nitrate and sediment (cf. Howart et al. 1996; Seitzinger et al. 2002). In other rivers, nitrogen retention can be clearly higher (e.g., Sjodin et al. 1997; Mitsch et al. 2001; Seitzinger et al. 2002).

Nowadays, natural floodplain wetlands are being rehabilitated along large European rivers, after centuries of deterioration. Similar denitrification rates in our simulated flooded agricultural grasslands and reedbeds, however, indicate that floodplain rehabilitation from grasslands into reedbeds may not increase N-retention through higher denitrification rates in the floodwater. Nevertheless, rehabiliation of floodplain wetlands may als serve as buffer strips reducing the amount of nitrate entering the river from polluted groundwater, and hence increasing N-retention in another way (e.g., Osborne and Kovacic 1993; Vought et al. 1994; Fennessy and Cronk 1997).

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References

Alexander R.B., Smith R.A. and Schwartz G.E. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. Nature 403: 758–761.

Bowden W.B. 1987. The biogeochemistry of nitrogen in freshwater wetlands. Biochem. 4: 313–348.

Caraco N.F. and Cole J.J. 1994. Human impact on nitrate export: an analysis using major world rivers. Ambio 28: 167–170.

Christensen P.B., Nielsen L.P., Sørensen J. and Revsbech N.P. 1990. Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism. Limnol. Oceanogr. 35: 640–651.

Cronk J.K. and Mitsch W.J. 1994. Aquatic metabolism in four newly constructed freshwater wetlands with different hydrologic inputs. Ecol. Engineer. 3: 449–468.

Dalsgaard T. and Revsbech N.P. 1992. Regulating factors in trickling filter biofilms as measured with the oxygen/nitrous oxide microsensor. FEMS Microbiol. Ecol. 101: 151–164.

Eriksson P.G. and Weisner S.E.B. 1996. Functional differences in epiphytic microbial communities in nutrient-rich freshwater ecosystems: an assay of denitrifying capacity. Freshwater Biol. 36: 555–562.

Eriksson P.G. and Weisner S.E.B. 1997. Nitrogen removal in a wastewater reservoir: the importance of denitrification by epiphytic biofilms on submerged vegetation. J. Environ. Qual. 26: 905–910.

Eriksson P.G. and Weisner S.E.B. 1999. An experimental study on effects of submerged macrophytes on nitrification and denitrification in ammonium-rich aquatic systems. Limnol. Oceanogr. 44: 1993–1999.

Eriksson P.G. 2000. Regulation of Epiphytic Nitrification and Denitrification in Macrophyte-Dominated Systems. PhD Thesis, Lund University, Lund.

Fennessy M.S. and Cronk J.K. 1997. The effectiveness and restoration potential of riparian ecotones for the management of nonpoint source pollution, particularly nitrate. Crit. Rev. Environ. Sci. Tech. 27: 285–317.

Groffman P.M., Axelrod E.A., Lemunyon J.L. and Sullivan W.M. 1991. Denitrification in grass and forest vegetated filter strips. J. Environ. Qual. 20: 671–674.

Haycock N.E., Pinay G. and Walker 1993. Nitrogen retention in river corridors; European perspectives. Ambio 22: 340–346.

Hill A. 1979. Denitrification in the nitrogen budget of a river ecosystem. Nature 281: 291–292.

Howard-Williams C. 1985. Cycling and retention of nitrogen and phosphorus in wetlands: a theoretical and applied perspective. Freshwater Biol. 15: 391–431.

Howarth R.W., Billen G., Swaney D., Townsend A., Jaworski N., lajtha K. et al. 1996. Regional nitrogen budgets and riverine N and P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. Biogeochem. 35: 75–139.

Johnston C.A. 1991. Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. Crit. Rev. Environ. Contr. 21: 491–565.

Keddy P.A. 2000. Wetland ecology, principles and conservation. Cambridge University Press, Cambridge.

Kersting K. and Kouwenhoven P. 1989. Annual and diel oxygen regime in two polder ditches. Hydrobiol. Bull. 23: 111–123.

McMahon P.B., Tindall J.A., Collins J.A., Lull K.J. and Nuttle J.R. 1995. Hydrologic and geochemical effects on oxygen uptake in bottom sediments of an effluent-dominated river. Water Resour. Res. 31: 2561–2569.

Mitsch W.J., Day J.W., Gilliam J.W., Groffman P.M., Hey D.L., Randall G.W. et al. 2001. Reducing nitrogen loading to the Gulf of Mexico from the Mississippi River basin: strategies to counter a persistent ecological problem. Bioscience 51: 373–388.

Naiman R.J. and Décamps H. 1997. The ecology of interfaces: riparian zones. Ann. Rev. Ecol. Syst. 28: 621–658.

Nielsen L.P., Christensen P.B., Revsbech N.P. and Sørensen J. 1990. Denitrification and oxygen respiration in biofilms studied with a microsensor for nitrous oxide and oxygen. Microb. Ecol. 19: 63–72.

Olde Venterink H., Davidsson T., Kiehl K. and Leonardson 2002. Impact of drying and re-wetting on N, P and K dynamics in a wetland soil. Plant Soil 243: 119–130.

Olde Venterink H., Wiegman F., Van der Lee G.E.M. and Vermaat J.E. 2003. The role of active floodplains for nutrient retention in the river Rhine. J. Environ. Qual. (in press).

Osborne L.L. and Kovacic D.A. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. Fresh. Biol. 29: 243–258.

Patrick W.H. and Reddy K.R. 1976. Denitrification reactions in flooded soils and water bottoms: dependence on oxygen supply and ammonium diffusion. J. Environ. Qual. 4: 469–471.

Pinay G., Haycock N.E., Ruffinoni C. and Holmes R.M. 1994. The role of denitrification in nitrogen removal in river corridors. In: Mitsch W.J. (ed.), Global Wetlands: Old World and New. Elsevier, Dordrecht, pp. 107–117.

Pinay G., Roques L. and Fabre A. 1993. Spatial patterns of denitrification in a riparian forest. J. Appl. Ecol. 30: 581–591.

Pinay G., Ruffinoni C. and Fabre A. 1995. Nitrogen cycling in two riparian forest soils under different geomorhic conditions. Biogeochem. 30: 9–29.

Schreijer M., Kampf R., Verhoeven J.T.A. and Toet S. 2000. Nabehandeling van RWZI-effluent tot bruikbaar oppervlaktewater in een moerassysteem. Report Hoogheemraadschap van Uitwaterende Sluizen in Hollands. Noorderkwartier Utrecht University.

Seitzinger S.P. 1988. Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. Limnol. Oceanogr. 33: 702–724.

Seitzinger S.P. 1994. Linkages between organic matter mineralization and denitrification in eight riparian wetlands. Biogeochem. 25: 19–39.

Seitzinger S.P., Styles R.V., Boyer E.W., Alexander R.B., Billen G., Howarth R.W. et al. 2002. Nitrogen retention in rivers: Model development and application to wattersheds in the northeastern U.S.A. Biochem. 57/58: 199–237.

Sjodin A.L., Lewis W.M. Jr and Saunders J.F. III 1997. Denitrification as a component of the nitrogen budget for a large plains river. Biogeochem. 39: 327–342.

Spink A., Sparks R.E., Van Oorschot M. and Verhoeven J.T.A. 1998. Nutrient dynamics of large river floodplains. Regulated Rivers 14: 203–216.

Tiedje J.M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In: Zehnder A.J.B. (ed.), Biology of Anaerobic Microorganisms. John Wiley and Sons, New York.

Van der Lee G.E.M., Olde Venterink H. and Asselman N.E.M. 2003. Estimation of nutrient retention in floodplains of the Rhine distributaries in The Netherlands: upscaling the effect on river water quality. River Res. Appl. (in press).

Verhoeven J.T.A., Whigham D.F., Van Logtestijn R. and O'Neill J. 2001. A comparative study of nitrogen and phosphorus cycling in tidal and non-tidal riverine wetlands. Wetlands 21: 210–222.

Vought L.B.M., Dahl J., Lauge Pedersen C. and Lacousière J.O. 1994. Nutrient retention in riparian ecotones. Ambio 23: 342–348.

Vymazal J. 2001. Types of constructed wetlands for wastewater treatment; their potential for nutrient removal. In: Vymazal J. (ed.), Transformations of Nutrients in Natural and Constructed Wetlands. Backhuys Publishers, Leiden, pp. 1–93.

Weisner S.E.B., Eriksson P.G., Granéli W. and Leonardson L. 1994. Influence of macrophytes on nitrate removal in wetlands. Ambio 23: 363–366.

Yoshinari T. and Knowles R. 1976. Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. Biochem. Bioph. Res. Co. 69: 705–710.