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Rapid nitrate loss and denitrification in a temperate river floodplain

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Abstract. Nitrogen (N) pollution is a problem in many large temperate zone rivers, and N retention in river channels is often small in these systems. To determine the potential for floodplains to act as N sinks during overbank flooding, we combined monitoring, denitrification assays, and experimental nitrate (NO_3^--N) additions to determine how the amount and form of N changed during flooding and the processes responsible for these changes in the Wisconsin River floodplain (USA). Spring flooding increased N concentrations in the floodplain to levels equal to the river. As discharge declined and connectivity between the river and floodplain was disrupted, total dissolved N decreased over 75% from 1.41 mg l^{-1}, equivalent to source water in the Wisconsin River on 14 April 2001, to 0.34 mg l^{-1} on 22 April 2001. Simultaneously NO_3^--N was attenuated almost 100% from 1.09 to <0.002 mg l^{-1}. Unamended sediment denitrification rates were moderate (0–483 μg m^{-2} h^{-1}) and seasonally variable, and activity was limited by the availability of NO_3^--N on all dates. Two experimental NO_3^--N pulse additions to floodplain water bodies confirmed rapid NO_3^--N depletion. Over 80% of the observed NO_3^--N decline was caused by hydrologic export for addition #1 but only 22% in addition #2. During the second addition, a significant fraction ($>60\%$) of NO_3^--N mass loss was not attributable to hydrologic losses or conversion to other forms of N, suggesting that denitrification was likely responsible for most of the NO_3^--N disappearance. Floodplain capacity to decrease the dominant fraction of river borne N within days of inundation demonstrates that the Wisconsin River floodplain was an active N sink, that denitrification often drives N losses, and that enhancing connections between rivers and their floodplains may enhance overall retention and reduce N exports from large basins.

Introduction

Dramatic changes in the global nitrogen (N) cycle and conspicuous regional effects of these alterations such as coastal hypoxia have emphasized the need to understand basic processes governing transformation and retention of N as it moves through drainage basins (Vitousek et al. 1997; Mosier et al. 2002). To date, most aquatic research has focused on the role of small (and often relatively pristine) headwater streams in nutrient processing (Haggard et al. 2001). Yet despite the greater percent retention and cumulative length of small (1st–4th) order streams, the mass of N removed per meter of reach is greatest in large order (6th–9th) rivers, and total N retained within an entire drainage network appears to be equally divided between small and large channels (Seitzinger et al. 2002). Because loads are funneled through a limited number of large channels, even modest increases in retention by these downstream reaches have the potential to reduce riverine N exports substantially. Reconnecting floodplains and channels may be one such means of increasing the retention capacity of large river reaches. Unfortunately, while it is generally assumed that floodplains are effective N sinks, few studies have quantified the amount of riverine N retained by these environments or the rates of biogeochemical processes responsible for retention during flooding in nutrient-rich north temperate rivers. Indeed, only a handful of studies (e.g., Brunet et al. 1994; Knowlton and Jones 1997; Tockner et al. 1999) have even documented changes in surface water chemistry over the course of flooding in this type of river system.

Floodplains in tropical (Hamilton and Lewis 1987; Kern et al. 1996; Esteves et al. 2001) and lowland southeastern U.S. rivers (Brinson et al. 1983; Lindau et al. 1994; DeLaune et al. 1996) are capable of retaining N during flooding, so it may be reasonable to assume that this capacity is widespread in world rivers. However, extrapolation to human-dominated rivers in temperate zones may be precarious (Olde Venterink et al. 2003b). Nutrient concentrations are often considerably higher and the vast majority of temperate-zone floodplain rivers have experienced substantial changes in land use, vegetation, overall size, and hydrology (Haycock et al. 1993; Malanson 1993; Dynesius and Nilsson 1994; Sparks et al.1998), with unknown consequences for N retention.

During floods, riverine N arrives on the floodplain in some combination of organic N, NH_4^+-N, and NO_3^--N, and several possible biogeochemical processes can affect each of these fractions. Among all possible transformations, denitrification is of particular interest in N-rich rivers because it results in the permanent removal of N from the system. For floodplains to be effective N sinks, denitrification must occur rapidly and be a dominant process during floods. To evaluate the potential for a large-river floodplain to act as an N sink during flooding, we asked: how does the form and amount of N change in floodplain water bodies during a flood pulse, and what are the processes that drive N concentration changes in the floodplain? These questions were addressed by (1) documenting N changes during spring flooding, (2) conducting experimental NO_3^--N additions to quantify rates of N loss in floodplain water bodies, and (3) assessing the potential for denitrification to explain losses of NO_3^--N observed in natural and experimental NO_3^--N pulses.

Methods

Site description

The Wisconsin River is a 7th order tributary of the Mississippi River. The watershed supports a diversity of agriculture that is responsible for non-point nutrient inputs. Unlike many Midwestern U.S. rivers, large amounts of the river's floodplain remain intact and maintain some degree of hydrologic connectivity to the main channel in the lower half of the riverway (Freeman et al. 2003). We conducted our study at the Leopold Memorial Reserve (LMR), a floodplain area in the south-central section of the river approximately 178 km from the confluence with the Mississippi River (43°34′ N, 89°39′ W) (Figure 1). The LMR has historical significance as the setting for *A Sand County Almanac* (Leopold 1949), which inspires the 'restoration ethic' used to manage this area. With the Wisconsin River as the northern boundary, the LMR is approximately 3.2 km long and 1.6 km wide. The floodplain has typical ridge and swale topography (Liegel 1988) dominated by marshes, deciduous forests, and backwater channels scattered across the floodplain that often retain water throughout the year. Floodplain soils and sediments are dominated by sand and sandy loam of glacial origin that have been

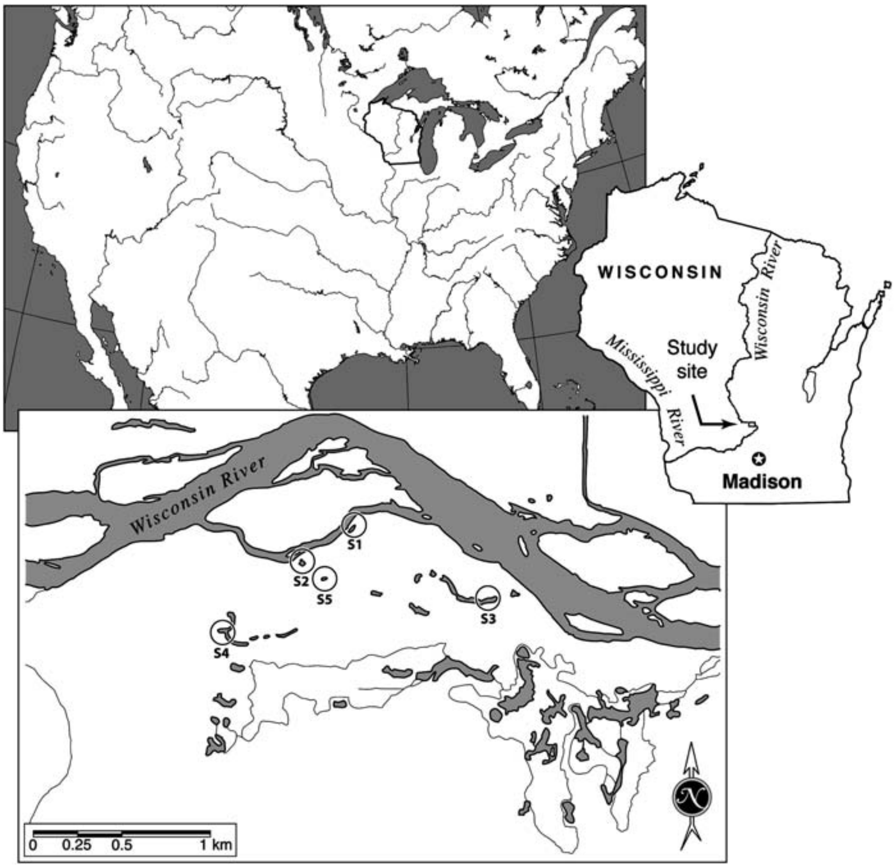

Figure 1. Location of floodplain study sites in the Leopold Memorial Reserve and the Wisconsin River in Wisconsin, USA.

subsequently reworked by fluvial processes (Liegel 1982) and have high porosity and hydraulic conductivity (Hunt 1987).

Floods in this region are typical in the spring and fall due to seasonal rains, snowmelt, and reservoir operation. Short-term releases from upstream reservoirs often cause rapid but brief (1 day) increases in river stage, whereas snowmelt and precipitation-driven floods can persist for several days. Average discharge in the spring is 360 and 120 $m^3 s^{-1}$ in the fall. Fluctuations in hydraulic potential of the shallow groundwater table occur daily, and can produce rapid movement of surface water and shallow groundwater through sediments (Hunt 1987; Pfeiffer 2001).

Four sites (S1–S4) were chosen for flood monitoring in 2001 (Figure 1) and two sites were used for experimental N additions (S2 and S5) in 2002. Each site had a surface area of at least 5 m long × 15 m wide prior to flooding. These sites did not have extensive macrophyte or macro-algae beds and had sediment bottoms. Water bodies varied in position between 10–40 (S1, S2) and 150–500 m (S3, S4) from the main channel of the Wisconsin River. All sites inundated and connected to the river during spring 2001 and 2002 floods, then became isolated as water levels decreased. Samples from the river channel were taken from the south bank between S1 and S2.

Flooding and flood chemistry

We collected water samples prior to, during, and following flooding to document changes in the form and amount of N in the floodplain as a result of overbank inundation. Discharge data were acquired from USGS gauging station #505404000 (USGS 2003) at Wisconsin Dells, ca. 10 km upstream from the LMR. Hydrologic status (connected to or isolated from the river) of each site was recorded on all sample dates. Sampling of the main channel of the Wisconsin River began on 24 March 2001 and S1 and S2 sampling began prior to flooding on 9 April 2001. Sites S3 and S4 were added at the peak of the flood on 14 April 2001 and all sites were sampled at weekly or bi-weekly intervals until 12 June. Mid-day dissolved oxygen (DO) was measured in the field using a YSI Model 85 DO meter at a depth of 0.1 m. Samples for nutrient analyses were collected in 1-l high-density polyethylene amber bottles and transported to the laboratory on ice. All samples were filtered through two stacked glass fiber filters with nominal pore sizes of 1.0 and 0.7 μm. The filtrate was frozen for later analysis. The pre-ashed and pre-weighed 1.0 μm filters were dried and weighed to determine total suspended solids (TSS) then ashed to determine particulate organic matter (POM) concentration.

Samples were analyzed to determine total dissolved nitrogen (TDN) using persulfate oxidation (Valderrama 1981) followed by colorimetric analysis of NO_3^--N. NO_3^- and NO_2^- as N (hereafter referred to as NO_3^--N) was determined by cadmium–copper reduction (Wood et al. 1967), ammonium nitrogen (NH_4^+-N) by the salicylate–hypochlorite method (Bower and

Holm-Hanson 1980), and soluble reactive phosphorus (SRP) by the phosphomolybdate blue technique (Eaton et al. 1995). Colorimetric measurements for all analyses were made on a Beckman DU 640 spectrophotometer. Dissolved organic nitrogen (DON) was determined as the difference between TDN and the sum of NO_3^--N and NH_4^+-N. Water chemistry results at each site were tested for normality, then differences between floodplain and river sites were evaluated using ANOVA (site × date) and Tukey's individual pairwise comparisons on individual days.

Sediment denitrification

We measured rates of sediment denitrification at sites S1–S4 to assess the potential for this process to remove nitrate from surface waters and to identify limits on denitrification activity during floodplain inundation. Bioassays were conducted on 23 April 2001, 14 June 2001, and 8 June 2002 using the acetylene blockage technique modified for sediments (Tiedje et al. 1989; Holmes et al. 1996). Sediment cores were 10–15 cm in depth by 6.5 cm in diameter in 2001 and 4.7 cm in diameter in 2002. Four pairs of replicate samples in 2001 and three replicate pairs in 2002 were randomly selected at each site. Pairs consisted of cores collected immediately adjacent to one another (within 10 cm), and each core was divided in half (longitudinally) to generate four samples per coring location. Sediments were put into plastic bags, sealed, put on ice, and immediately transported to the laboratory. The top 5 cm of the surface sediment was transferred to a 250-ml jar fitted with a gas-tight lid with a gas sampling-septum. To determine whether denitrification was limited by nitrate and/or organic carbon, samples from each coring location were amended with 100 ml of water from their respective water body plus either 3300 mg l^{-1} C as glucose amendment (C), 200 mg l^{-1} N as KNO_3 (N), or a combination of nitrate and glucose (CN). Control (O) samples received unamended site water. Each jar was filled with the appropriate solution to submerge sediments completely, injected with 10% by volume acetylene, and gently agitated to ensure adequate acetylene distribution. We attempted to maintain soil structure and simulate field conditions as closely as possible, and thus, did not bubble nitrogen gas to remove oxygen. Initial gas samples were extracted from the sample's head space and injected into 5-ml Vacutainer vials. Jars were then incubated in the dark between 3–4 h very near (± 3 °C) the temperature at the sediment–water interface at the time of sample collection (10 °C on 23 April 2001, 20 °C on 14 June 2001, and 15 °C on 8 June 2002). Final headspace samples were injected into Vacutainers and stored at room temperature until analysis. Headspace volume was measured in all samples following incubation. N_2O was determined on a Varian Model 3800 gas chromatograph using a HayeSep R column with electron capture detector. Gas concentrations were corrected for headspace and water volume using Bunsen's coefficient (Groffman et al. 1999) at the temperature of incubation. Denitrification was expressed as an areal an rate based on half of the surface area of the corer used to collect sediments since individual cores were divided for assays (16.6 cm^2 in 2001, 8.7 cm^2 in 2002). Values were (ln $[x+1]$) transformed to normalize variance, then differences among sites, dates, and amendment treatments were evaluated using a three-way ANOVA followed by Tukey's *post-hoc* test with alpha = 0.05.

Nutrient addition experiments

An experimental approach was used to determine N removal capacity and quantify the contributions of different pathways of N change in floodplain water bodies. To simulate a pulse of nitrate introduced by a flood and to separate the effects of hydrologic and biogeochemical processes, two floodplain water bodies were amended with a solution of concentrated $NaNO_3$ and NaCl by spraying the solution evenly over the water surface. Addition #1 and #2 began on 19 June 2002 and 8 August 2002, respectively. Both additions started within 2 weeks of minor flooding. Grab samples were taken prior to and immediately following amendment using the methods described above, then with an ISCO auto-sampler at 3-h intervals for addition #1, and 2-h intervals with two auto-samplers (for field replication) during addition #2 to provide fine scale temporal resolution of chemical and biological changes. The auto-samplers were packed with ice during sampling and samples were transported back to the laboratory daily for processing as described above. Samples were analyzed for Cl^- and NO_3^--N using a Dionex DX-500 ion chromatograph. Chlorophyll-*a* (chl *a*) samples were collected on a 0.7 μm glass fiber filters, frozen, extracted with methanol, then measured on Turner TD-700 fluorometer (Eaton et al. 1995). Particulate nitrogen (PN) was calculated by difference between unfiltered total nitrogen (TN) measured by persulfate oxidation and TDN. All other chemical analyses are described earlier.

Water surface area was determined by measuring cross sectional width every 2–5 m of water body length and length along a single perpendicular transect. Effective volumes were determined using the known mass of Cl^- added and the average initial concentration of each water body. An exponential decay model was used to describe NO_3^--N concentration changes with respect to the conserved ion (Cl^-) over time to determine the nitrate removal rate and to account for effects of groundwater dilution. To estimate the contribution of different transformations to the fate of the added NO_3^--N, we constructed mass balances for each addition using the following equation:

$$\Delta NO_3^- \text{-N} = \Delta PN + \Delta NH_4^+ \text{-N} + \Delta DON + NO_3^- \text{-N}_{\text{dilution}} + x\text{N}, \qquad (1)$$

where ΔN for all N fractions represents the change in the mass of each fraction, NO_3^--N_{dilution} equals the loss of NO_3^--N based on the disappearance of the Cl^- tracer which indicates the physical exchange of surface water with subsurface water and not necessarily removal from the floodplain, and xN denotes the mass of N that could not be attributed to hydrologic losses or conversions to other N forms. Conversion of NO_3^--N to other forms of N was evaluated by linear regressions of Cl^--weighted NO_3-N *versus* Cl^--weighted NH_4^+-N, DON, and PN.

Results

Flooding and flood chemistry

Nitrogen in floodplain water bodies responded directly to the arrival of river flood waters (Figure 2). On 6 April 2001, Wisconsin River discharge was below flood stage and all sites were disconnected from the main channel. River stage increased ~2.5 m on 9 April 2001, and connected all floodplain water bodies to the river. During this connected phase, TDN at all sites was similar to the main river channel ($F = 1.34$, $df = 10$, ANOVA $p = 0.316$; Figure 2). Discharge subsequently decreased, disconnecting all sites from the main channel by 22 April 2001. During this second phase, mean TDN at all floodplain sites decreased over 75%, from an average concentration of 1.41 mg l^{-1} (sd = 0.29 mg l^{-1}) on 14 April 2001 to 0.34 mg l^{-1} (sd = 0.049 mg l^{-1}) on 22 April 2001 such that TDN concentrations in the floodplain sites were significantly lower than the main channel ($F = 139.5$, $df = 12$, ANOVA $p < 0.001$).

NO_3^--N was the primary nitrogen species in flood waters at all sites and represented 72–82% of TDN during peak flow, thus it followed a similar pattern to that of TDN in response to flooding (Figure 2). Between connected and disconnected phases, average floodplain NO_3^--N decreased from 1.09 mg l^{-1} (sd = 0.242) to < 0.002 mg l^{-1} (sd = 0.002) on 22 April, and was significantly less than riverine NO_3^--N ($F = 3.2 \times 10^5$ $df = 12$, ANOVA $p < 0.001$).

Small discharge increases occurred over the next 3 weeks (Figure 2), occasionally resulting in brief overbank flows. These pulses were associated with moderate increases in TDN and/or increases in the fraction of N present as nitrate at the two sites closest to the river channel (S1 and S2; Figure 2). For example, on 6 May, discharge increased to 447 m^3 s^{-1} and re-connected sites S1 and S2, but not S3 and S4, to the main channel. TDN in S1 and S2 increased and did not differ from the main river channel, whereas TDN showed no change at S3 and S4 and remained significantly different from the river ($F = 7.87$, $df = 19$, ANOVA $p = 0.001$). By the next sampling date (18 May), TDN concentrations were once again lower than in the river at S1 and S2 following hydrologic separation from the river.

Flooding had no apparent effect on NH_4^+-N or DON (Figure 2). NH_4^+-N was variable and typically low (< 0.10 mg l^{-1}) at all sites, with little discernable pattern across sites or over time. During the flood pulse, DON concentration varied between sites and sampling dates. The proportion of TDN as

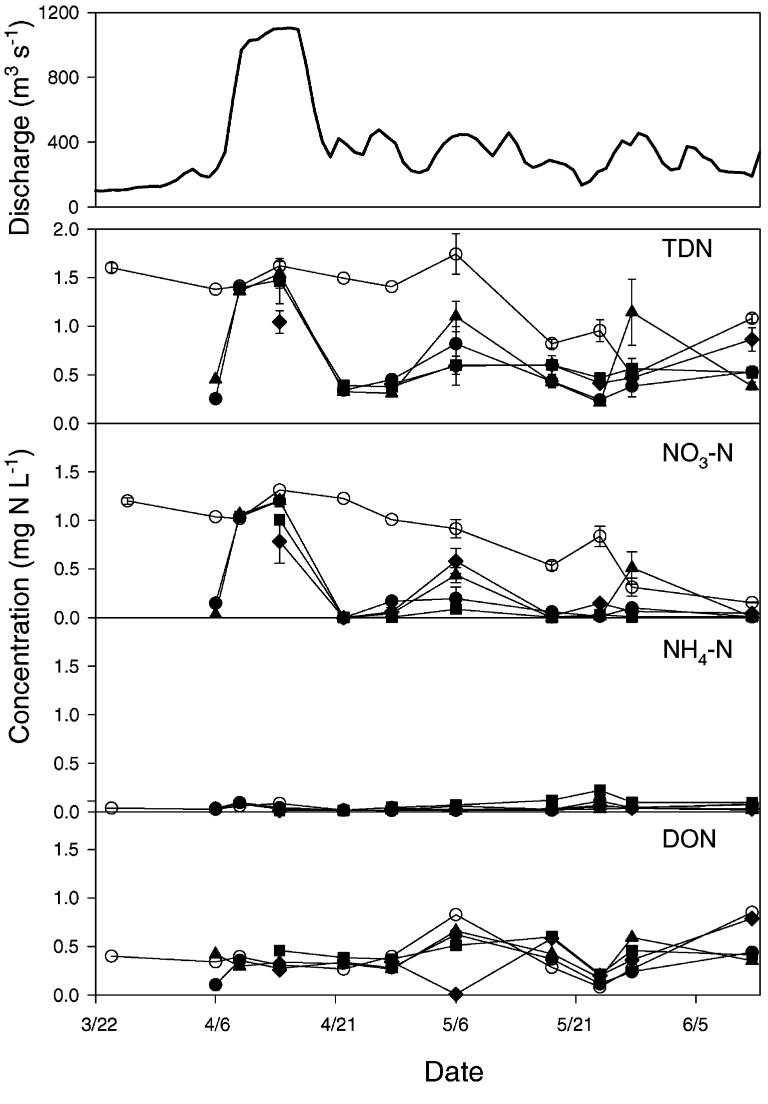

Figure 2. Changes in discharge, total dissolved nitrogen (TDN), NO_3^--N, NH_4^+-N, and dissolved organic N (DON) during spring flooding in the Wisconsin River. Values are means ± 1 standard error. Open symbols (○) represent concentrations in the river channel; ●, ▲, ■ and ◆ symbolize sites S1, S2, S3, and S4, respectively.

DON fluctuated greatly from 0 to 95%, and percent DON was negatively correlated with TDN concentration ($R = 0.71$, $p < 0.0001$). SRP concentrations were relatively constant throughout the flood pulse and remained below 0.05 mg l^{-1} on most sampling dates (Table 1). In general, inorganic N was very high relative to SRP. Molar N:P ratios were above 16:1 (Table 1) in river

Table 1. Total suspended solids (TSS), particulate organic matter (POM), soluble reactive phosphorus (SRP), molar N:P ratio, and dissolved oxygen (O_2) in the main river channel and four floodplain sites (S1–S4) during spring flooding in 2001.

	River	S1	S2	S3	S4
TSS					
9-Apr-01	0.062	0.045	0.061	–	–
14-Apr-01	0.028	0.029	0.028	0.026	0.024
22-Apr-01	0.028	0.076	0.035	0.040	0.050
28-Apr-01	0.019	0.039	0.068	0.166	0.026
6-May-01	0.037	0.026	0.027	0.022	0.026
18-May-01	0.034	0.055	0.127	0.027	0.071
24-May-01	0.030	0.025	0.025	0.027	0.052
28-May-01	0.029	0.024	0.038	0.037	0.088
12-Jun-01	0.044	0.036	0.040	0.028	0.028
POM					
9-Apr-01	0.007	0.005	0.012	–	–
14-Apr-01	0.008	0.008	0.004	0.007	0.014
22-Apr-01	0.011	0.021	0.012	0.016	0.016
28-Apr-01	0.011	0.018	0.023	0.095	0.021
6-May-01	0.011	0.011	0.009	0.007	0.009
18-May-01	0.009	0.017	0.050	0.008	0.035
24-May-01	0.005	0.005	0.004	0.007	0.021
28-May-01	0.004	0.005	0.006	0.016	0.047
12-Jun-01	0.009	0.014	0.015	0.007	0.009
SRP					
6-Apr-01	0.021	0.015	0.009		
9-Apr-01	0.015	0.019	0.021		
14-Apr-01	0.028	0.028	0.029	0.018	0.008
22-Apr-01	0.014	0.011	0.012	0.020	
28-Apr-01	0.012	0.009	0.008	0.009	0.005
6-May-01	0.010	0.015	0.011	0.020	0.003
18-May-01	0.010	0.078	0.067	0.031	0.104
24-May-01	0.012	0.054	0.011	0.048	0.008
28-May-01	0.017	0.024	0.016	0.053	0.005
12-Jun-01	0.043	0.011	0.011	0.035	0.010
Molar N:P					
6-Apr-01	111.2	26.8	16.5		
9-Apr-01	161.3	135.1	124.1		
14-Apr-01	110.9	95.6	94.8	129.3	274.7
22-Apr-01	196.6	3.5	3.1	2.0	
28-Apr-01	194.3	54.1	18.8	13.2	36.3
6-May-01	197.0	48.2	83.9	21.3	421.0
18-May-01	129.9	2.6	0.3	9.1	2.8
24-May-01	159.0	13.2	7.6	11.7	62.2
28-May-01	47.3	12.9	77.6	4.4	56.2
12-Jun-01	12.0	20.3	22.6	6.9	17.1
O_2					
9-Apr-01	–	–	–	–	–
14-Apr-01	14.00	10.70	15.50	6.40	5.50

Table 1. (Continued)

	River	S1	S2	S3	S4
22-Apr-01	–	7.00	5.30	6.00	6.10
28-Apr-01	–	7.02	4.90	4.80	1.72
6-May-01	9.68	4.95	6.03	2.43	4.39
18-May-01	9.32	2.20	2.91	1.78	1.14
24-May-01	8.46	3.58	2.69	1.54	2.91
28-May-01	9.04	4.72	9.33	3.22	2.58
12-Jun-01	8.43	2.15	2.91	4.97	2.91

All values are mg l^{-1}. Underlined values for floodplain sites indicate connectivity with the river.

and floodplain sites throughout the study on most dates, although depletion of N and moderate increases in SRP during the end of May and June were associated with lower N:P ratios.

TSS and POM showed little variation during flooding (Table 1). DO in the main channel was typically higher than in the floodplain, and floodplain sites underwent a gradual directional change toward increasing subsaturation. Nevertheless, mid-day DO was greater than 2 mg l^{-1} on most sampling dates (Table 1).

Sediment denitrification

Sediment denitrification rates changed over time and in response to nutrient amendments. The ANOVA showed a three-way interaction ($p < 0.05$) between date, site, and treatment (Table 2). The interaction in part resulted from the C-amended assay on 14 June 2001 in S1 which had no detectable activity and unamended assays which did generate measurable N_2O, causing a significant difference ($p = 0.026$). Because the difference between unamended and

Table 2. Degrees of freedom (*df*), *F*-statistic, and significance for 3-way analysis of variance for denitrification in different floodplain water bodies (site) on three separate dates.

Source	*df*	*F*	*p*
Date	2	114.84	***
Site	3	7.88	***
Treatment	3	95.14	***
Date*site	6	3.09	**
Site*treatment	9	1.93	NS
Date*treatment	6	1.99	NS
Date*site*treatment	18	1.99	*
Error	126		
Total	173		

Treatment refers to amendments added to sediments (carbon, nitrogen, both in combination, or neither; see text for details).

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS, not significant.

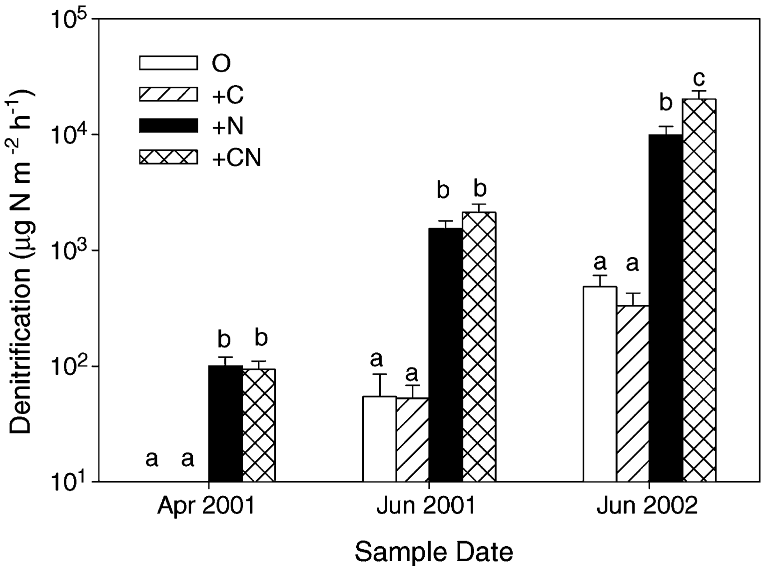

Figure 3. Sediment denitrification rates in floodplain water bodies amended with surface water alone (O) or river water plus NO_3^- (+N), organic C (+C), or C and N (+CN) in 2001 and 2002. Values are means ±1 standard error. Letters indicate significant differences (Tukey's pairwise comparisons $p < 0.05$) for treatment effects within each date. Note log scale of the y-axis.

C-amended sediments was not significantly different for any other combinations of dates and sites, we disregarded the three-way interaction. Significant differences in denitrification rates occurred between dates, indicating that rates were not the same over time. There was no interaction between sites and treatments, thus all sites responded in a similar fashion to the different experimental treatments ($p > 0.05$). Consequently, results are presented as denitrification per treatment averaged across all sites for each date (Figure 3). Values ranged from undetectable (O and +C treatments in April 2001) to >10,000 μg N m^{-2} h^{-1} for some +N and +CN samples during June 2001 and 2002. All treatments that included N (+CN and +N) were significantly greater than non-N treatments (O and +C) on all dates (Tukey's $p < 0.05$), indicating that denitrification was always N-limited. Similarly, sample date significantly affected denitrification, with highest rates occurring for samples collected in June 2002.

Nutrient additions

Nitrate added to floodplain water bodies was depleted rapidly during both amendment experiments. In nitrate addition #1, both Cl^- and NO_3^--N decreased approximately 70% within the first 2 h (Figure 4), indicating

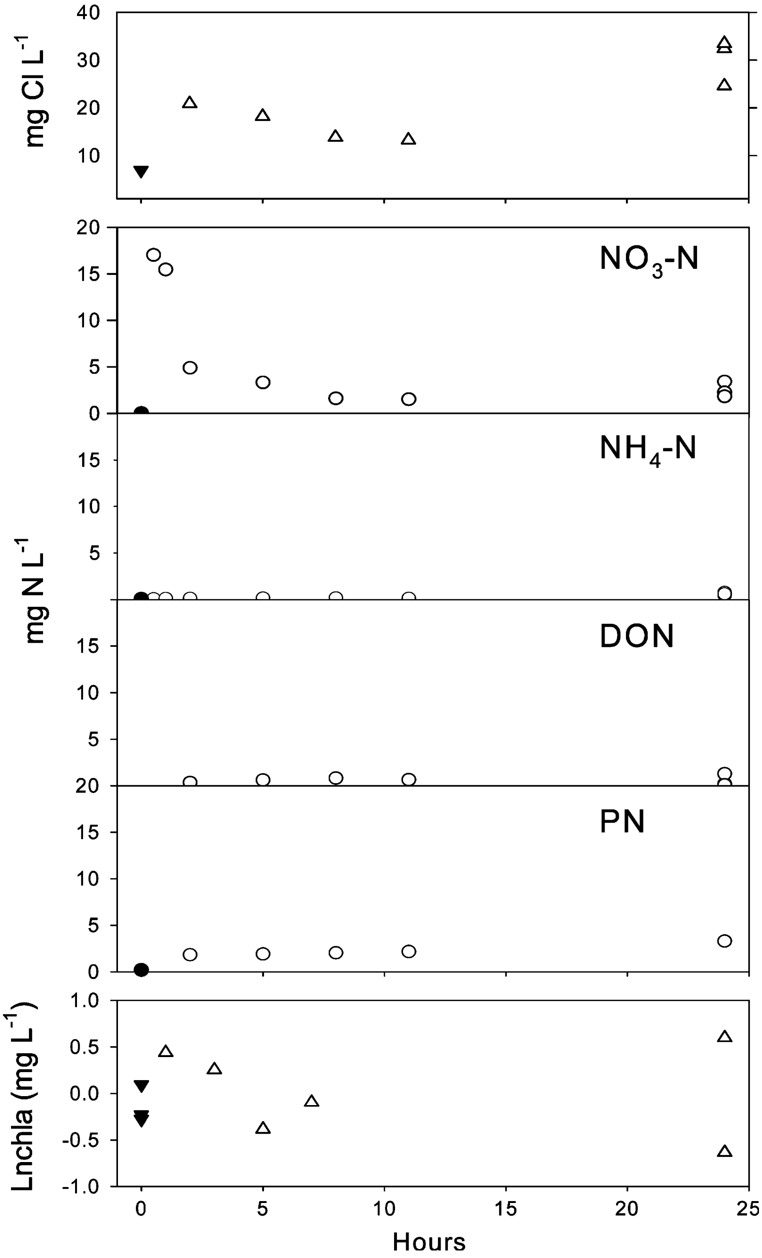

Figure 4. Changes in chloride (Cl^-), NO_3^--N, NH_4^+-N, DON, PN, and chl *a* before (solid symbols) and after (open symbols) a pulse addition of NO_3^--N plus a conservative ion tracer (Cl^-) on 19 June 2002.

substantial groundwater dilution of both solutes. Nonetheless, NO_3^--N decreased exponentially relative to the conserved ion ($k = 0.055$, $R^2 = 0.90$, $p < 0.001$, where k is the NO_3^--N loss coefficient in units of h^{-1}; Table 3), thus biotic processes also contributed to the NO_3^--N decline. The final samples were taken from shallow puddles because depth decreased from a maximum depth of 0.45 to 0.10 m overnight, and there was a slight increase in both Cl^- and NO_3^--N owing to evapoconcentration. NH_4^+-N, DON, and PN all increased following the addition (Figure 4), although the increase in DON was not significant over 24 h (Table 3). SRP (not shown) and chl *a* (Figure 4) did not change over time, except for an increase in chl *a* in the final sample collection. However, this aberration could have been due to benthic sediments getting stirred up in shallow pools.

In addition #2, nearly 100% of the added NO_3^--N was attenuated within 4 days. Unlike addition #1, Cl^- remained approximately constant for ~100 h following the initial amendment (Figure 5). NO_3^--N concentration decreased exponentially relative to the conserved ion ($k = 0.024$, $R^2 = 0.85$, $p < 0.001$; Table 3), while NH_4^+-N and DON both increased and PN decreased in a linear fashion after the addition (Table 3, Figure 5). As with nitrate during addition #1, neither SRP (not shown) nor chl *a* (Figure 5) increased in the several hours following the addition.

Mass balance calculations indicate different processes responsible for disappearance of the added nitrate for each addition. Because of the dramatic shrinkage in surface water extent and possible difficulties during final sample collection (see above), the calculation for addition #1 was restricted to the initial 11 h following amendment. For this addition, groundwater dilution

Table 3. Regression results for Cl-normalized N concentrations *versus* time for experimental N additions.

	Equation	R^2	p
Addition #1			
NO_3^--N	$y = 0.24e^{-0.055x}$	0.90	***
	$y = 0.26e^{-0.082x}$	0.96	**
NH_4^+-N	$y = 0.0007x + 0.0024$	0.90	**
	$y = 0.0008x + 0.0022$	0.69	*
DON			NS
	$y = 0.004X + 0.0127$	0.71	=0.15
PN			NS
	$y = 0.009X + 0.067$	0.96	*
Addition #2			
NO_3^--N	$y = 2.98^{-0.024x}$	0.87	***
NH_4^+-N	$y = 0.0005x - 0.020$	0.65	***
DON	$y = 0.0005x - 0.021$	0.36	***
PN	$y = -0.0003x + 0.063$	0.20	***

For addition #1, the top value represents regression results for the entire 24 h period; the second line reports results for the initial 11 h of the addition used in the mass balance calculations.
*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS, not significant.

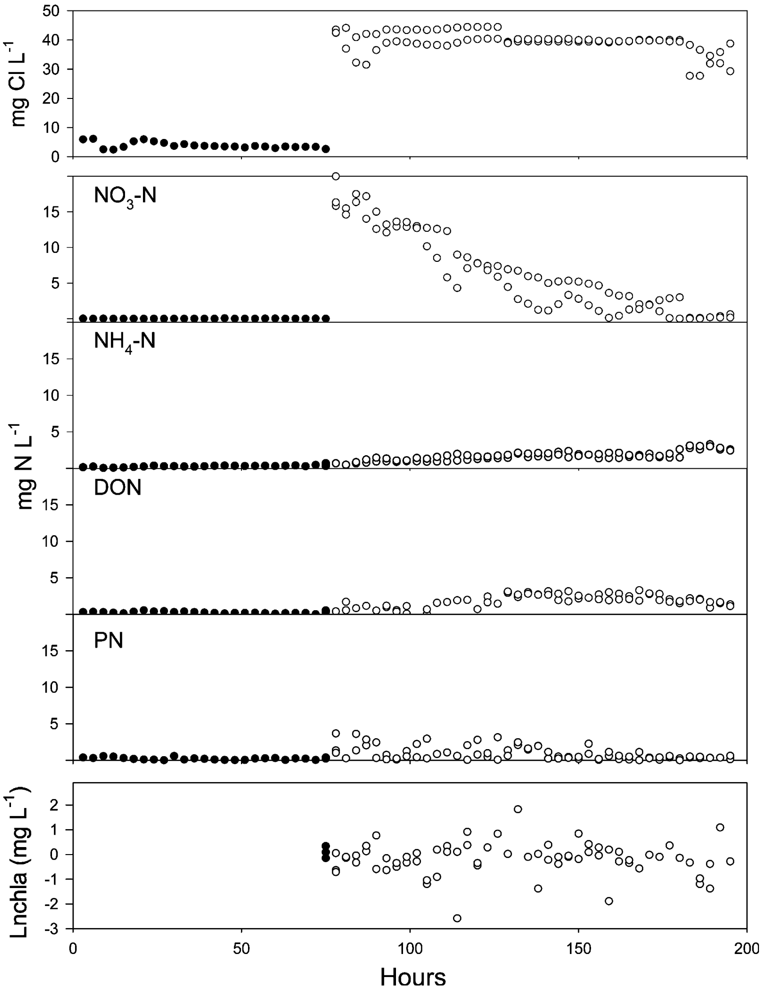

Figure 5. Changes in chloride (Cl^-), NO_3^--N, NH_4^+-N, DON, PN, and chl *a* before (solid symbols) and after (open symbols) a pulse addition of NO_3^--N plus a conservative ion tracer (Cl^-) on 8 August 2002.

represented the major pathway of NO_3^--N decline, accounting for 81% of the observed loss. Eleven percent of the NO_3^--N mass loss could be attributed to conversion to PN, DON, and NH_4^+-N, leaving 7.9% of the total unaccounted for (i.e., the *x*N pool).

For addition #2, hydrology played a minor role as dilution was responsible for only 22% of the NO_3^--N loss (Table 4). Conversion to DON and NH_4^+-N together accounted for 17% of the observed decline, and biotic uptake in the water column (conversion to PN) was assumed to be zero because PN stocks actually decreased after N addition. Consequently, unaccounted N (*x*N) represented over 60% of the total N reduction.

Table 4. Mass balance for experimental NO_3^--N additions to floodplain water bodies in the Wisconsin River floodplain in June (Addition #1) and August 2002 (Addition #2).

	Addition #1		Addition #2	
	g	%	g	%
Total NO_3^--N added	224.0		169.8	
Total decrease in NO_3^--N	205.3	91.6	165.9	97.7
Dilution	166.5	81.1	36.2	21.8
PN change	13.4	6.5	–	0.0
DON change	6.9	3.4	14.8	8.9
NH_4^+-N change	2.3	1.1	13.9	8.4
Unaccounted N (xN)	16.2	7.9	101.0	60.9

See text for details regarding specific calculations. For each pathway of N loss, % values represent the percent of the total NO_3^--N decrease (rather than the percent of total NO_3^--N added) attributable to that conversion.

Discussion

These data reveal a distinct temporal pattern of N cycling and a substantial capacity for NO_3^--N removal from surface water during flood recession in the Wisconsin River floodplain. As discharge increases in the river, N-rich flood water moves out onto the floodplain and displaces the relatively small volume of N-poor surface water. As the flood recedes, riverine water pools in depressional areas across the floodplain and localized processes assert control over N, causing a dramatic and rapid decrease in NO_3^--N concentration without concomitant increases in other forms of N. Once surface water on the floodplain becomes disconnected, these low-lying areas are capable of depleting large quantities of N, as we observed nearly complete removal of NO_3^--N from isolated water bodies by both natural flooding and experimental pulse additions.

The basic pattern of increasing N during flooding followed by decreasing concentrations as hydrologic connectivity between the river and floodplain is lost has also been observed in the Rhine and Danube floodplains of Europe, and the Missouri River floodplain in the U.S. (Van den Brink et al. 1994; Knowlton and Jones 1997; Tockner et al. 1999). The Wisconsin River floodplain attenuated NO_3^--N concentration to below-detectable limits in less than 6 days following isolation from the main channel. In contrast, a month was required for NO_3^--N concentration to fall to pre-flood levels in the Danube River (Hein et al. 1999) and in experimental NO_3^--N additions of inundated floodplain soils in a bottomland hardwood wetland in the southeastern U.S. (DeLaune et al. 1996). Several factors can influence the speed with which N concentrations decline during flood recession or intentional N additions, including water depth, sediment organic matter content (DeLaune et al. 1996; Brettar et al. 2002), initial NO_3^--N concentration (García-Ruiz et al. 1998) and time of year (Brunet and Astin 2000). With a limited number of sites available for comparison, it is not clear what physical factors foster the rapid *versus* slow N removal among rivers, suggesting an important question for future research.

Depletion of floodwater nitrate in temperate rivers is typically attributed to either planktonic uptake (e.g., Knowlton and Jones 1997; Hein et al. 1999) or denitrification (e.g., DeLaune et al. 1996; Olde Venterink et al. 2003a). NO_3^--N far exceeds concentrations of SRP and N:P ratios were relatively high, indicating that nutrient uptake by phytoplankton alone was not likely to be sufficient for the extreme decrease in NO_3^--N concentration. Further, low and unchanging TSS and POM concentrations during spring flooding are consistent with limited phytoplankton development. We did not measure benthic uptake or monitor benthic algal biomass, largely because aquatic macrophytes and algal mats were not seen at either site during the additions, and both sites were shaded by the surrounding floodplain forest. However, we cannot discount benthic assimilation as an additional possible NO_3^--N sink. Nonetheless, we predict that the combination of relatively brief flood pulses (days to weeks) and presence of a forest canopy are likely to reduce the contribution of autotrophic uptake in the Wisconsin River floodplain, and losses of N from surface waters are more likely dominated by denitrification.

Denitrification is often assumed to be the dominant process driving N reduction during floodplain inundation as these environments provide an opportunity for extensive contact between N-rich flood water from the river and often oxygen depleted organic matter-rich soils. We observed 5 orders of magnitude variation in sediment denitrification, from undetectable rates for unamended samples in April to $>10{,}000\ \mu g\ m^{-2}\ h^{-1}$ for some C- and N-amended sediments collected in June. Average rates for +N and +CN treatments (mean = 4821) were very similar to values reported for Amazon floodplain soils (mean = 4946; Kern et al. 1996), and slightly higher than flooded sediments in the Rhine River floodplain ($\sim 1600\ \mu g\ m^{-2}\ h^{-1}$; Olde Venterink et al. 2003a) (note that both studies also used acetylene block methods). Seasonal differences were clearly apparent, suggesting that timing of floods can affect the contribution of denitrification to N loss. However, low or undetectable rates for spring (April) sediments saturated with overlying floodwater only (i.e., no N or C added) may have resulted from the fact that NO_3^--N had already been depleted from the overlying water column when samples were collected. Amendments of nitrate to these same samples significantly increased denitrification rates, demonstrating active N-removal potential of these sediments despite cool spring temperatures. Because denitrification was consistently N-limited in floodplain water bodies, the arrival of NO_3^--N in floodwaters is likely to be processed rapidly regardless of flood timing.

Field NO_3^--N addition experiments provided another approach for assessing N depletion and the relative importance of different pathways of N loss. These pathways include hydrologic export, conversion to NH_4^+-N via dissimilatory nitrate reduction to ammonium (DNRA), biotic uptake (conversion to PN and later to DON), and denitrification. While NO_3^--N stocks were rapidly depleted in both additions, the major pathways of loss differed among the experiments. During addition #1, more than 80% of the observed N loss was attributable to hydrologic export, but represented only 22% of the losses during addition #2. The significance of hydrologic export for processing of added (or floodwater) NO_3^--N is unclear; however, we predict that N carried into sediment and soil layers may be subject to additional processing. Vertical movement of water can enhance NO_3^--N removal (McMahon and Bohlke 1996; Baker and Vervier 2004), and groundwater in the Wisconsin River floodplain is typically N-poor shortly after flooding (Hunt 1987; Forshay 2003). While nitrate in deeper groundwater originating in upland areas often experiences minimal processing (Philips et al. 1993; Bohlke and Denver 1995; Pinay et al. 1998; Burt et al. 1999), we suggest that movement of surface floodwaters through the vegetated soil layer and into the shallow groundwater environment is likely to lose most of its nitrate load via uptake or, more likely, denitrification. If this is the case, then loss of nitrate to groundwater provides an additional opportunity for removal of river-derived N during floods.

Conversion of added NO_3^--N to NH_4^+-N, PN, and DON accounted for a relatively small fraction of observed NO_3^--N losses in both experiments. While NH_4^+-N did not increase during spring flooding, it did show modest increases during both N addition experiments. In these latter situations, NH_4^+-N production is likely due to a combination of processes including DNRA and mineralization. However, even if all the observed NH_4^+-N production was the result of DNRA, this transformation could account for only $\sim$10% of the observed NO_3^--N loss, similar to estimates for a freshwater wetland (Bowden 1986). Microbial communities capable of DNRA are favored over denitrifiers in sediments with continuous anoxia and high organic matter content (Tiedje 1988). Given the characteristic cycles of wetting and drying, areas of consistently anoxic sediments are often limited in floodplains (Robertson et al. 1999), thus we suspect that DNRA is relegated to a minor role in the floodplain N cycle of temperate zone rivers. With respect to biotic assimilation, N addition experiments suggest a minor role ($<10\%$) for planktonic uptake.

The final process affecting the mass of added NO_3^--N is denitrification. If we assume that all N not attributable to hydrologic export or conversion to other N fractions (i.e., the xN pool) was lost to denitrification, then this process was responsible for 8 and 61% of the total NO_3^--N loss in addition #1 and #2, respectively. These percentages translate to areal rates of 6 mg m^{-2} h^{-1} for addition #1 and 14 mg m^{-2} h^{-1} for addition #2, which are consistent with bioassay- estimated rates for $+$N and $+$CN treatments during June 2001 and 2002. Similar and substantially higher rates of denitrification estimated by mass balance and/or the open-channel N_2 method have been reported for N-enriched streams and rivers as well (Laursen and Seitzinger 2002; Pribyl et al. 2004). While we cannot definitively exclude the contribution of other processes (e.g., benthic uptake), these results strongly suggest high rates of *in situ* denitrification on the floodplain, and that denitrification is likely to play a significant role in reducing NO_3^--N if floodwaters are not rapidly lost to groundwater discharge.

Several potential sources of error intrinsic to this type of study need to be recognized. Field additions of nitrate were sprayed on the surface and may have underestimated denitrification and dilution because added N needed to diffuse to through the water column before these processes could influence the new N. However, these water bodies are small and easily mixed through wind-mixing, and replicate samples taken at different points in the pond showed little spatial variation in N concentrations. Further, because N began to decline within 2–6 h, this does not appear to be a significant source of error. Larger errors are likely attributable to processes that were not measured, including nitrification and benthic algal uptake. Failure to include nitrification potentially underestimates processes that remove NO_3^--N from the water column. However, nitrification occurs in oxygenated sediments, which are scarce during flooding (Lindau et al. 1994; Robertson et al. 1999) and (DeLaune et al. 1996) estimated that nitrification accounted for 10% or less of the total amount of NO_3^--N that was denitrified during floodplain inundation, again suggesting a minor role for this process. In contrast to nitrification, omission of benthic algal uptake creates a potential overestimation bias of denitrification in the mass balance calculations. As discussed previously, absence of conspicuous periphyton development, shading, high N:P ratios, and minimal phytoplankton uptake suggest that benthic N assimilation is likely a small sink for added NO_3^--N in these experiments.

The timing of our N addition experiments following flooding may enhance denitrification rates by allowing a build-up of the denitrifying microbial community. Unfortunately, such experimental procedures are simply not possible during peak flooding. Thus, these results highlight potential capacity for N removal rather than actual flood removal. Finally, experimental NO_3^--N additions enriched surface water to levels 10 × those of actual floods. Loading rates were made intentionally high so that pathways and limits of potential N loss could be clearly identified. While the Wisconsin River does not normally experience such extremes, N additions used here translated to 0.4–1 g N m^{-2} day^{-1} for a single day, well within the range of daily loadings for various river diversions and treatment wetlands (Lane et al. 2003).

Denitrification rates from addition experiments can be combined with information on flood magnitude, water chemistry, and inundation extent to estimate the potential N removal capacity of the Wisconsin River floodplain. A flood with a 2-year return interval (950 m^3 s^{-1}) inundates 400 ha of the floodplain for a 4-km section of the Wisconsin River that includes our study area (Gergel et al. 2002). If we assume a denitrification rate of 10 mg m^{-2} h^{-1} (the average rate estimated from the two N addition experiments), a floodwater concentration of 1.4 mg NO_3^--N l^{-1} (see Figure 2), and 100 ha of inundated floodplain per kilometer of river, then approximately 479 km would be required to deplete the entire load of floodwater N. The LMR study reach is 178 km upstream from the confluence of the Mississippi River (Freeman et al. 2003) so the estimated floodplain N reduction over this distance represents 37% of the NO_3^--N load entering the reach. Although multiple assumptions are built into this preliminary calculation and the magnitude of floodplain retention should be interpreted with great caution, it suggests the potential for the floodplain to alter N loads during flooding in the Wisconsin River. This estimate strongly contrasts the calculated retention of < 1–3% of the annual N load (Olde Venterink et al. 2003a; Van der Lee et al. 2004), and no detectable NO_3^--N retention during flooding (Olde Venterink et al. 2003b) in floodplain rivers in the Netherlands. However, these latter systems have undergone artificial floodplain narrowing and have higher discharge and greater N enrichment levels relative to the Wisconsin River, all of which conspire to minimize the floodplain's influence on net N retention. In contrast to these relatively channelized Dutch systems, a similar N reduction via denitrification of 34–45% occurred over a distance of only 18.5 km in the Platte River, Colorado because of extensive sediment–water contact that occurs in the coarse alluvial channel and banks (Sjodin et al. 1997; Pribyl et al. 2004).

Conclusion

This study emphasizes extremely rapid rates of N loss and high N removal capacity in the Wisconsin River floodplain following flooding. The processes responsible for rapid N removal from surface waters in the Wisconsin River floodplain appear to be dominated by denitrification and hydrologic export. Thus, N conveyed to the floodplain surface during high discharges has a brief residence time in this environment. If water persists on the floodplain for only a few days, its NO_3^--N load is likely lost to denitrification. The balance between hydrology and denitrification in conveying N off the floodplain surface depends on the nature of individual flood events, which in turn is strongly influenced by human manipulation of river stage. For water that seeps into floodplain soils, a key area for future research is to determine if its N load is removed as these fluxes move back toward the channel.

There are several implications of this work for floodplain-river management. Floodplain effectiveness as an N sink in human-dominated rivers is facilitated by the delivery of N in a form that is directly useable for denitrification (i.e., as nitrate; Caraco and Cole 1994; Perakis and Hedin 2002). This process appears to begin soon after the arrival of floodwaters and the absence of carbon limitation indicates that denitrification will proceed until NO_3^--N is depleted, given appropriate hydrological conditions. N addition experiments demonstrate the capacity to deplete repeated inputs of NO_3^--N. If N removal becomes a management goal, then pulsed flooding may be an effective means of managing water releases. Key questions that remain to be answered include understanding the fate of N in floodwaters that move into groundwater environments during flood recession, and determining the initiation and spatial distribution of denitrification activity during the ascending as well as descending limbs of floods. Nitrogen pollution is a growing regional problem that requires multifaceted solutions. Restoration and reconnection of large river floodplains may represent one of the few management opportunities to retain N that has moved from terrestrial sources and bypassed riparian filters and made its way into river channels.

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