

## Influence of vegetation and seasonal flow patterns on parafluvial nitrogen retention in a 7<sup>th</sup>-order river

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**Abstract.** We examined whether presence of vegetation and seasonal changes in flow affected N chemistry and denitrification rates within sandbars of a 7<sup>th</sup>-order sandy alluvial river (Wisconsin River, USA). We addressed these questions with a broad-scale approach of measuring parafluvial water chemistry and denitrification rates in multiple sandbars distributed along a 15-km river reach during summer 2004 and 2005. After recession of spring flooding, parafluvial chemistry in unvegetated bars was characterized by moderate dissolved O<sub>2</sub> (DO) and elevated NO<sub>3</sub><sup>-</sup>-N concentrations (>3.5 mg N/L), whereas vegetated bars tended to be hypoxic (<2 mg/L DO) and depleted in NO<sub>3</sub><sup>-</sup>-N (0.2 mg N/L) relative to unvegetated bars and surface water (0.47 mg N/L). As flow declined over the summer, NO<sub>3</sub><sup>-</sup>-N also declined in both bar types, whereas SO<sub>4</sub><sup>2-</sup> was relatively constant in unvegetated bars but decreased in vegetated bars. Amendment experiments demonstrated that denitrification was limited primarily by NO<sub>3</sub><sup>-</sup>-N and secondarily by organic C in both bar types, but the strength of this limitation varied over time and was greater in vegetated bars, a result suggesting loss of denitrification capacity. Thus, spatial and temporal patterns of water chemistry and denitrification activity among multiple sandbars indicated that unvegetated bars shifted from N transformers/NO<sub>3</sub><sup>-</sup>-N sources early in the summer to N retainers/NO<sub>3</sub><sup>-</sup>-N sinks as discharge declined, whereas vegetated bars always supported anaerobic processes and probably shifted from NO<sub>3</sub><sup>-</sup>-N to SO<sub>4</sub><sup>2-</sup> sinks. We hypothesize that the contribution of vegetated islands to overall riverine N retention is small because establishment of vegetation reduces hydrologic linkages between bars and surface water. Modern changes in the flow regime of the Wisconsin River have increased establishment of riparian vegetation on exposed bars, a pattern suggesting that parafluvial N retention is being reduced while riverine N loading is increasing.

**Key words:** denitrification, flow modification, hydrologic exchange, hyporheic, parafluvial, nitrate, nitrification, organic carbon, riparian vegetation, sandbar, Wisconsin.

N processing in streams and rivers can be strongly influenced by the metabolically active sediments of the hyporheic and parafluvial zones (reviewed by Boulton et al. 1998, Dahm et al. 1998, Malard et al. 2002). Investigations of N cycling have focused predominantly on small streams because in-channel processes can be particularly significant with respect to the form and amount of N transported downstream (Alexander et al. 2000, Peterson et al. 2001) and because working in small systems is more practical than working in large systems. However, N retention in larger river channels also can have a significant effect on watershed exports (Seitzinger et al. 2002),

and this influence also might be affected by subsurface processes (Sjodin et al. 1997, Hinkle et al. 2001).

Parafluvial zones can be N transformers/NO<sub>3</sub><sup>-</sup>-N sources in situations in which the processes of mineralization and nitrification predominate, or N retainers/NO<sub>3</sub><sup>-</sup>-N sinks if biotic uptake or denitrification prevail (Jones and Holmes 1996, Malard et al. 2002). The balance in status between N source or sink has become an increasing focus of research because of progressive N enrichment in inland and marine environments (Puckett et al. 2008). Attributes affecting this balance include sediment composition (Claret et al. 1997), flow conditions (Stanley and Boulton 1995), season (Deforet et al. 2008), the magnitude of N loading (Cooke and White 1987, Van der Hoven et al. 2008), and the supply of labile organic C (Bernhardt and Likens 2002).

Islands and bars are hallmark features of undisturbed riverine landscapes (Gurnell and Petts 2002),

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and are often defined as a river's parafluvial zone (Lewis et al. 2007). Islands and bars vary with respect to their long-term physical stability. Colonization of exposed sediments (bars) by plants stabilizes these structures through root growth and increased channel roughness, which in turn promotes further sediment trapping (Gurnell et al. 2001). Trapping of sediments and plant development eventually transform bars into islands. Individual islands can persist for decades (Kollmann et al. 1999) to centuries or even millennia (Collins and Knox 2003). In contrast, unvegetated bars typically are transient features that might persist for only 1 to a few years (Trush et al. 2000, Zanoni et al. 2008). Because islands often originate from bars, bars and islands can be viewed as endpoints along a biogeomorphic successional continuum (Gilvear and Willby 2005). Alternatively, establishment of vegetation creates a positive feedback system between plants and sediments, so several investigators recognize vegetated and unvegetated geomorphic forms as alternate states in fluvial systems (Corenblit et al. 2007, Heffernan 2008).

The establishment of vegetation on bare exposed sediments can lead to a number of physical changes, including accelerated vertical accretion, sediment fining, and organic matter accumulation (Gurnell et al. 2001, Gilvear and Willby 2005). In turn, these physical changes are likely to alter local hydraulic characteristics and the supply of  $O_2$  or organic C to interstitial environments (Heffernan et al. 2008). Thus, the shift to a vegetated state might facilitate denitrification (N retention/ $NO_3^-$ -N sink) directly by providing C from litter or leachates (Schade et al. 2001, Deforet et al. 2008), or indirectly by promoting sediment anoxia caused by reduced hydrologic exchange or increased respiration (Heffernan et al. 2008). Low interstitial  $NO_3^-$ -N and dissolved  $O_2$  (DO) concentrations in vegetated stream reaches (Heffernan et al. 2008) support this prediction of islands as N retainers/N sinks. However, in contrast to these observations, Deforet et al. (2008) did not observe differences in parafluvial N concentrations among bars that differed with respect to vegetative cover. Instead, the greatest changes in interstitial chemistry were attributed to seasonal dynamics, with bars shifting from N sinks in summer to N sources in autumn as discharge increased. This result suggests an alternative hypothesis: that flow conditions, rather than vegetation, determine parafluvial source/sink status through changes in surface–subsurface exchange and hydrologic residence within sediments (Clilverd et al. 2008).

The goal of our study was to determine the  $NO_3^-$ -N sink/source status of parafluvial sediments in a sandy

7<sup>th</sup>-order river (Wisconsin River, USA) and how this status is affected by river discharge and presence of vegetation. We addressed this goal by asking the following questions: 1) Do parafluvial zone water chemistry and denitrification rates differ between vegetated and unvegetated bars in the Wisconsin River? 2) How do parafluvial denitrification rates and water chemistry vary as a function of seasonal flow patterns in these 2 patch types?

### Site Description

The Wisconsin River is a 7<sup>th</sup>-order sandy, braided alluvial channel river that flows ~700 km southwest through Wisconsin before joining the Mississippi River (Fig. 1). Annual discharge typically peaks in April then decreases steadily through the summer, but summer flooding is not unusual. High flows occurred in April in both study years (2004 and 2005). However, larger floods also occurred in May and June 2004, and average daily flows were consistently higher during the 1<sup>st</sup> study year than in the 2<sup>nd</sup> study year (Fig. 2). The maximum flow reached during the 2004 flood was 1147  $m^3/s$ , ~2× the maximum flow of 592  $m^3/s$  reached in 2005. Flow declined over the sampling season in both years, and was lower overall in 2005 than in 2004.

We sampled vegetated and unvegetated sandbars in the Wisconsin River along a 15-km reach between Lone Rock and Arena, Wisconsin (Fig. 1) in 2004 and 2005. The study reach was in the Lower Wisconsin State Riverway, downstream from the last of 27 dams in one of the longest stretches of free-flowing river in the US (Hale et al. 2008). Concentrations of dissolved organic C (DOC) are relatively high (range 5.66–13.37 mg C/L), but DOC quality is low (Popp 2005). N concentrations are relatively low for a Midwestern river in an agriculturally dominated landscape (summertime total N range is typically 1.0–1.5 mg/L), but  $NO_3^-$ -N has been increasing steadily in the river over at least the past 30 y, from an annual average of 0.3–0.4 mg/L in 1974–1975 to 0.6 mg/L in 2004–2005 (Turner et al. 2008).

### Methods

Rather than detailed sampling within a small number of bars or transects, we adopted a broad-scale approach and sampled multiple unvegetated and vegetated bars across the 15-km study reach. Well-defined longitudinal flow paths are often prominent within sandbars (Holmes et al. 1994), but we were unable to identify any such discrete pathways during our initial pilot sampling. Furthermore, we were unable measure hydraulic head in unvegetated

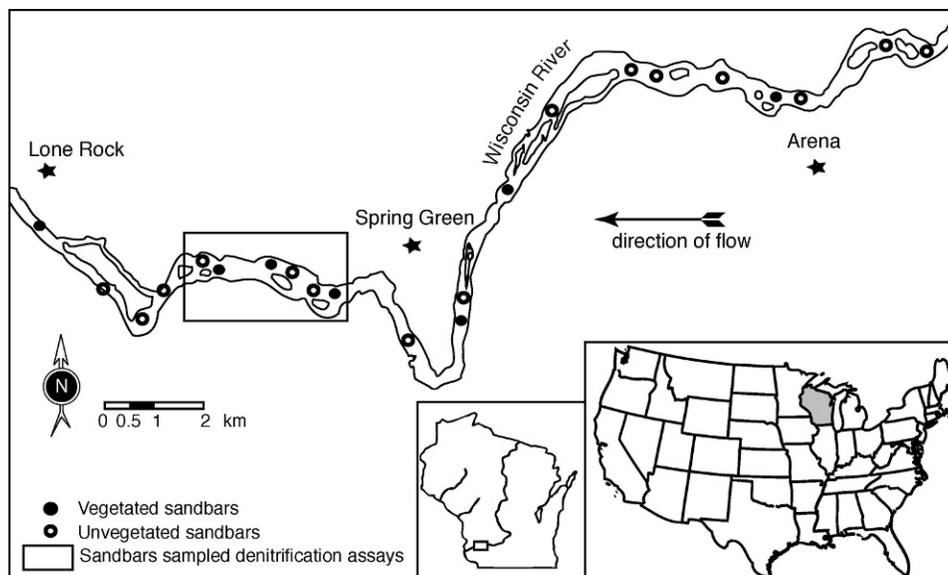


FIG. 1. Location of the Wisconsin River study reach, Wisconsin, USA. Inset maps show the location of Wisconsin within the US and the location of the sampling reach on the Wisconsin River within the state. A rectangle in the center of the reach map encloses the 6 sandbars sampled for denitrification assays.

bars because flow during slug tests was too rapid. These results, combined with the difficulty of installing many wells in vegetated bars to locate flow paths, suggested that a focus on comparing sandbars was more prudent. However, variation within bars caused by differences in flow paths, variation in sediment composition (resulting from both formation and deposition), and location within the channel (Holmes

et al. 1994, Claret et al. 1997) are likely. This variation is unaccounted for in our sampling design, but we used a mixed model to account for unexplained variation among wells within a bar.

The timing of sandbar sampling in both years was done in response to recession of flooding. Sampling dates were intended to capture early, middle, and late post-flood periods. As discharge declined in 2004, we selected 15 sandbars ( $n = 8$  unvegetated,  $n = 7$  vegetated) to sample. Sandbars were  $\geq 25$  m long and 5 m wide, in contact with the main channel flow,  $\geq 10$  m from another sampled bar, and oriented such that they appeared unlikely to become attached to the river bank during lower flow. Both sandbars (vegetated and unvegetated) and larger, permanent islands were present in the channel. We focused on vegetated bars rather than islands to ensure similar sizes and a common origin of both bar types (in addition to plant colonization of bars, islands can form by channel avulsions that cleave off sections of floodplains; Leopold et al. 1964). Vegetated sandbars as defined in our study are similar to pioneer islands described by Edwards et al. (1999) and were distinguished from islands by the presence of predominantly sandy soil, frequent inundation, and the absence of a mature forest canopy. Dense shrub ground cover consisted of sandbar willow (*Salix exigua*) and Missouri willow (*Salix eriocephala*), and a few sapling or adult silver maples (*Acer saccharinum*) were present on each vegetated sandbar. Vegetated sandbars capture sediment, and most rise 1 to 2 m above the typical river

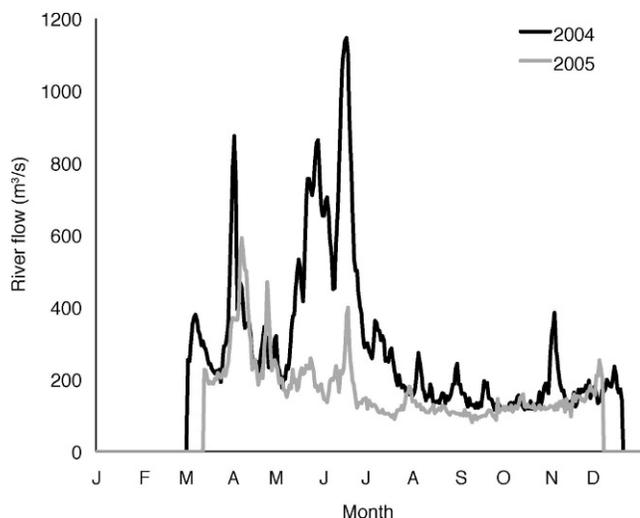


FIG. 2. Wisconsin River discharge in 2004 and 2005 at US Geological Survey gauging station 055407000 in Muscoda, Wisconsin. Sampling dates were in July, August, and September in 2004 and in June, July, and August in 2005.

water level. They are submerged during large floods (such as the 2004 flood) and are relatively permanent in the channel. Unvegetated bars are typically <0.5 m above the river height at low flow and are often submerged during high flows and floods. Unvegetated bars are more ephemeral than vegetated bars and often move downstream or disappear completely after floods.

Sampling of parafluvial water and sediment began in July 2004 when discharge declined to a point that a sufficient number of bars were exposed and could be safely identified and sampled ( $\sim 280 \text{ m}^3/\text{s}$ ). Because of the size of the river, we accessed bars by boat and visited them over a 3 to 5 d period. Vegetated and unvegetated bars were intermixed along the channel, so we sampled a similar number of each bar type on each day. We took samples again in August and September 2004. We derived discharge data from US Geological Survey gauging station 055407000 in Muscoda, Wisconsin,  $\sim 10 \text{ km}$  downstream from the end of the sampling reach.

In 2005, we resampled the 7 vegetated sandbars and 6 of the 8 unvegetated bars (the remaining 2 from 2004 were absent in 2005), and sampled 7 additional sandbars that were present because discharge was lower than in 2004. In 2005, we sampled in June, July, and August because of the lower discharge and earlier spring flood recession.

We collected interstitial water from three 3.5-m-long polyvinyl chloride (PVC) wells slotted at the bottom 20 cm and installed to the water-table depth in each sandbar ( $\sim 3 \text{ m}$  in vegetated bars and  $\sim 0.5 \text{ m}$  in unvegetated bars). We installed slotted wells along a longitudinal transect running down the center of the bar at 1, 11, and 21 m from the farthest upstream edge of the bar. We were unable to identify discrete flowpaths, but the intent of this design was to collect water that probably had both brief (1 m) and more prolonged (11, 21 m) residence times in the bar. Prior to sampling, we measured depth to water with an electronic water level meter (Solinst Model 101, Solinst Canada Ltd., Georgetown, Ontario). We then cleared wells of standing water with a peristaltic pump and allowed them to refill before sampling. We collected fresh interstitial water in 125-mL acid-washed polyethylene bottles. In 2005, we also collected separate samples in 60-mL acid-washed amber glass bottles for measurement of DOC from a subset of 3 vegetated and 3 unvegetated bars. We also collected a single grab sample of river water just upstream of each bar on all dates. We put all samples on ice for transport to the laboratory where we filtered them through a  $0.45\text{-}\mu\text{m}$  cellulose acetate filter and stored them frozen until analysis.

$\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N were determined with a Technicon auto-analyzer (Seal Analytical, Mequon, Wisconsin) in 2004 and an Astoria-Pacific auto-analyzer (Astoria-Pacific International, Clackamas, Oregon) in 2005. Repeat analysis of standards and field samples demonstrated that results produced by the 2 analyzers were highly similar (slope = 0.96,  $r^2 = 0.98$  for  $\text{NO}_3^-$ -N; slope = 0.97,  $r^2 = 0.89$  for  $\text{NH}_4^+$ -N). We also quantified sulfate ( $\text{SO}_4^{2-}$ ) concentrations using a Dionex DX-500 ion chromatograph (Dionex Corporation, Sunnyvale, California) as an indicator of parafluvial redox status. We analyzed DOC on a Shimadzu TOC-V analyzer (Shimadzu Scientific Instruments, Columbia, Maryland).

We determined denitrification rates of parafluvial sediment for 3 unvegetated and 3 vegetated bars during August and September in 2004 and June, July, and August in 2005. We collected sediments just below the water table adjacent to wells with a bucket auger and transported them to the laboratory on ice. We sampled the same 6 sandbars for sediment each sampling period. These sandbars were the same as those sampled for DOC. At the time of sediment collection in June 2005, we measured DO in wells with an Orion DO probe (Thermo Fisher Scientific, Waltham, Massachusetts) before water samples were collected. Denitrification is an anaerobic process, but the measured DO concentrations required for this process to begin are unclear because microsite  $\text{O}_2$  status is difficult to predict from water measurements (Duff and Triska 1990). Denitrification can occur when measured DO rates are high (e.g., Holmes et al. 1996), but rates increase after thresholds of 2 to 3 mg DO/L in laboratory studies (van Kessel 1977). Thus, we used 2 mg/L DO as an hypoxia threshold to indicate times or places where anaerobic metabolism (including denitrification) was likely to predominate within the parafluvial environment.

We conducted sediment denitrification assays with the acetylene block technique (Groffman et al. 1999) within 24 h of field sampling. This method has a number of weaknesses (Groffman et al. 1999, 2006), but it is more robust than other methods in systems like the Wisconsin River that have high  $\text{NO}_3^-$ -N concentrations. The method provides a useful means of identifying limiting nutrients when used with amendments (Groffman et al. 2006). Our measures of denitrification might underestimate actual rates, but we assumed that methodological biases were similar among sites and dates, and thus, that the method was valid for assessing potential differences among bars and over time (Orr et al. 2007).

We subdivided each sample and amended subdivisions with 4 treatments to determine if organic C or

$\text{NO}_3^-$ -N limited denitrification activity. Treatments were: 1) water only amendment solution (control), 2) 0.05 mol/L dextrose amendment solution (+C), 3) 0.02 mol/L  $\text{KNO}_3$  amendment solution (+N), and 4) 0.02 mol/L  $\text{KNO}_3$  plus 0.05 mol/L dextrose amendment solution (+CN). For each treatment, we transferred 50 mL of sediment to a 150-mL glass bottle equipped with butyl rubber septa and then amended it with 40 mL of the amendment solution. Chloramphenicol (0.003 mol/L) was added to all amendment solutions to reduce microbial growth in response to nutrient additions (Smith and Tiedje 1979). Bottles were capped, purged with  $\text{N}_2$  to create anoxic conditions, and then injected with 10 mL of acetylene. We used a pilot study to determine the appropriate incubation period, and ran assays in the dark for 24 h at room temperature ( $\sim 21^\circ\text{C}$ ). We took headspace gas samples at the beginning and end of the incubation period, and measured  $\text{N}_2\text{O}$  on a Varian model 3800 gas chromatograph (Varian Inc., Walnut Creek, California) equipped with a HayeSep R column and an electron capture detector. We corrected gas concentrations for  $\text{N}_2\text{O}$  dissolved in the aqueous phase with Bunsen's coefficient and calculated denitrification rates as  $\text{nmol N}_2\text{O generated kg}^{-1}$  sediment dry mass  $\text{h}^{-1}$  (Groffman et al. 1999). After final gas sampling, we dried sediments for  $>48$  h at  $60^\circ\text{C}$  and weighed them. In 2004, we combusted samples in a muffle furnace at  $550^\circ\text{C}$  for 4 h to determine sediment % organic matter.

#### Statistical analyses

We used mixed effects models (R software, version 2.8.1; R Project for Statistical Computing, <http://www.r-project.org/>) to assess how denitrification rates, water chemistry, and sediment organic matter differed as a function of the presence/absence of vegetation and river flow. We used mixed-effects models instead of repeated measures analysis of variance (ANOVA) because of their greater flexibility. This format allowed us to include sandbar samples with missing data and permitted us to control for temporal autocorrelation among samples (Pinheiro and Bates 2000). The basic sample unit of our study was the well observation. However, because each well was sampled multiple times over 2 y and represented a subsample of a given sandbar, wells were nested within sandbars by specifying them as random grouping factors. This model structure allows for unexplained variation among wells within bars, but assumes that wells can be treated as independent samples from a given bar.

River flow was the mean daily discharge at the Muscoda gauge on the day each sample was taken.

We used 2 categories of sandbar habitat type, vegetated and unvegetated, for denitrification analysis, whereas we used 3 categories (vegetated bars, unvegetated bars, river) for water-chemistry variables. We tested for temporal autocorrelation by comparing 2 versions of each model, 1 in which we controlled for temporal autocorrelation by including an autoregressive correlation structure of order 1 (where time was recorded as days since the 1<sup>st</sup> sampling period of 2004) and another in which we assumed all observations were independent. Each pair of models was compared with a likelihood ratio test. When they were not significantly different ( $p > 0.05$ ), the simpler model (i.e., no temporal autocorrelation) was used (Pinheiro and Bates 2000). Despite the clear temporal pattern in the data we collected, temporal autocorrelation was often insignificant because of the inclusion of flow as a fixed effect in the model. River flow and time were highly correlated ( $r = -0.47$ ) and, therefore, explained similar variability.

We normalized all dependent variables with  $\ln(x)$  transformations. We assessed the effects of amendments (control, +C, +N, +CN) and habitats (unvegetated and vegetated bars) on denitrification rates with a mixed model followed by least-square means comparisons with a Tukey's correction. We used linear regression to assess the relationship between river flow and both water chemistry and denitrification rates for each habitat type. Solute concentrations and denitrification rates were averaged by bar and  $\ln(x)$ -transformed for this analysis.

#### Results

The depth to water within all sandbars declined from early to late sampling periods, but was always shallower in unvegetated sandbars than vegetated sandbars (Table 1). In unvegetated sandbars, the water table was 0.1 to 0.3 m below the surface compared to 0.5 to 3 m in vegetated bars. DO concentrations measured early in the summer in 2005 during high flow differed significantly among habitats. DO was consistently lower in both bar types relative to in river water, and was lower in vegetated than in unvegetated bars. Concentrations were  $>2$  mg/L for 73% of the measurements made in the unvegetated bars; in contrast, only 27% of the vegetated bar measurements had DO concentrations above this hypoxia threshold. DOC varied from 3.1 to 12.6 mg/L, but did not differ among habitats or with river flow (Table 2). Average concentrations ( $\pm 1$  SE) in unvegetated and vegetated bars and the river were  $6.25 \pm 0.27$ ,  $6.59 \pm 0.33$ , and  $6.67 \pm 0.67$  mg/L, respectively. Sediment organic matter (OM) content

TABLE 1. Mean ( $\pm 1$  SE) water depth and dissolved O<sub>2</sub> in vegetated and unvegetated sandbars and river water in the Wisconsin River study reach. Mixed model results apply to differences between habitat types.

Variable	Habitat type			Mixed model result
	Unvegetated sandbars	Vegetated sandbars	Surface water (river)	
Depth to water (m)	0.19 $\pm$ 0.014 ( <i>n</i> = 9)	1.37 $\pm$ 0.16 ( <i>n</i> = 8)	–	$F_{1,4} = 52.4$ $p < 0.005$
Dissolved O <sub>2</sub> (mg/L)	2.74 $\pm$ 0.28 ( <i>n</i> = 39)	1.37 $\pm$ 0.29 ( <i>n</i> = 21)	6.0 $\pm$ 0.23 ( <i>n</i> = 12)	$F_{2,40} = 13.3$ $p < 0.001$

was very low in the sandy Wisconsin River, averaging 0.41 and 0.45% in unvegetated and vegetated bars. OM did not differ among habitat types, but it was significantly predicted by river flow and a habitat type  $\times$  river flow interaction (Table 2). As flow declined, OM decreased in unvegetated sandbars and increased in vegetated sandbars.

Habitat type, river flow, the interaction between these 2 factors, and the interaction between habitat and year were significant predictors of parafluvial NO<sub>3</sub><sup>-</sup>-N concentrations (Table 2). NO<sub>3</sub><sup>-</sup>-N was highest in the early summer when river flow was high in both years and significantly declined as flow declined in all habitats in both years (Fig. 3A, B). NO<sub>3</sub><sup>-</sup>-N concentrations declined at a faster rate in 2005 than in 2004, but in both years, the fastest decline was in unvegetated bars (Fig. 3A, B). NO<sub>3</sub><sup>-</sup>-N was highest in unvegetated bars early in the summer when river

flow was high, with an average concentration  $\sim 7\times$  greater than in the river and almost  $20\times$  higher than in the parafluvial zone of vegetated bars. Concentrations subsequently declined as flow declined in all habitats. In 2004, NO<sub>3</sub><sup>-</sup>-N in unvegetated bars declined below concentrations observed in the river at low flow (Fig. 3A). However, in 2005, NO<sub>3</sub><sup>-</sup>-N concentrations maintained the pattern of highest levels in unvegetated sandbars and lowest in vegetated sandbars as flow declined (Fig. 3B). The decline in vegetated bars from moderate to low flow was relatively small (0.03 mg N/L) because average NO<sub>3</sub><sup>-</sup>-N concentration across the 7 vegetated bars in both years had already fallen below 0.10 mg N/L after flows declined from flood stages.

NH<sub>4</sub><sup>+</sup>-N concentrations were significantly predicted by habitat type and habitat type  $\times$  river flow interaction. Concentrations were higher in both

TABLE 2. Mixed model results for variable = habitat + river flow + (habitat  $\times$  river flow) for samples taken in one year and variable = habitat + river flow + year + (habitat  $\times$  river flow) + (habitat  $\times$  year) for samples taken in both years. River flow was recorded the day samples were taken. Habitats were vegetated and unvegetated bars for sediment organic matter, and vegetated bars, unvegetated bars, and surface (river) water for dissolved organic C (DOC), NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, and SO<sub>4</sub><sup>2-</sup>. NS = not significant ( $p > 0.05$ ).

Variable (sample size)	Factor	df	<i>F</i>	<i>p</i>
Sediment organic matter, 2004 ( <i>n</i> = 35)	Habitat	1,4	0.3	NS
	River flow	1,15	4.6	<0.05
	Habitat $\times$ river flow	1,15	8.1	<0.05
DOC, 2005 ( <i>n</i> = 80)	Habitat	2,16	0.4	NS
	River flow	1,45	2.0	NS
	Habitat $\times$ river flow	2,45	1.7	NS
NO <sub>3</sub> <sup>-</sup> -N ( <i>n</i> = 511)	Habitat	2,99	18.7	<0.001
	River flow	1,380	160.4	<0.001
	Year	1,380	1.6	NS
	Habitat $\times$ river flow	2,380	25.9	<0.001
	Habitat $\times$ year	2,380	27.3	<0.001
NH <sub>4</sub> <sup>+</sup> -N ( <i>n</i> = 511)	Habitat	2,99	106.4	<0.001
	River flow	1,380	1.5	NS
	Year	1,380	1.7	NS
	Habitat $\times$ river flow	2,380	39.8	<0.001
	Habitat $\times$ year	2,380	0.4	NS
SO <sub>4</sub> <sup>2-</sup> ( <i>n</i> = 511)	Habitat	2,99	17.0	<0.0001
	River flow	1,380	1.5	NS
	Year	1,380	12.5	<0.001
	Habitat $\times$ river flow	2,380	2.3	NS
	Habitat $\times$ year	2,380	0.02	NS

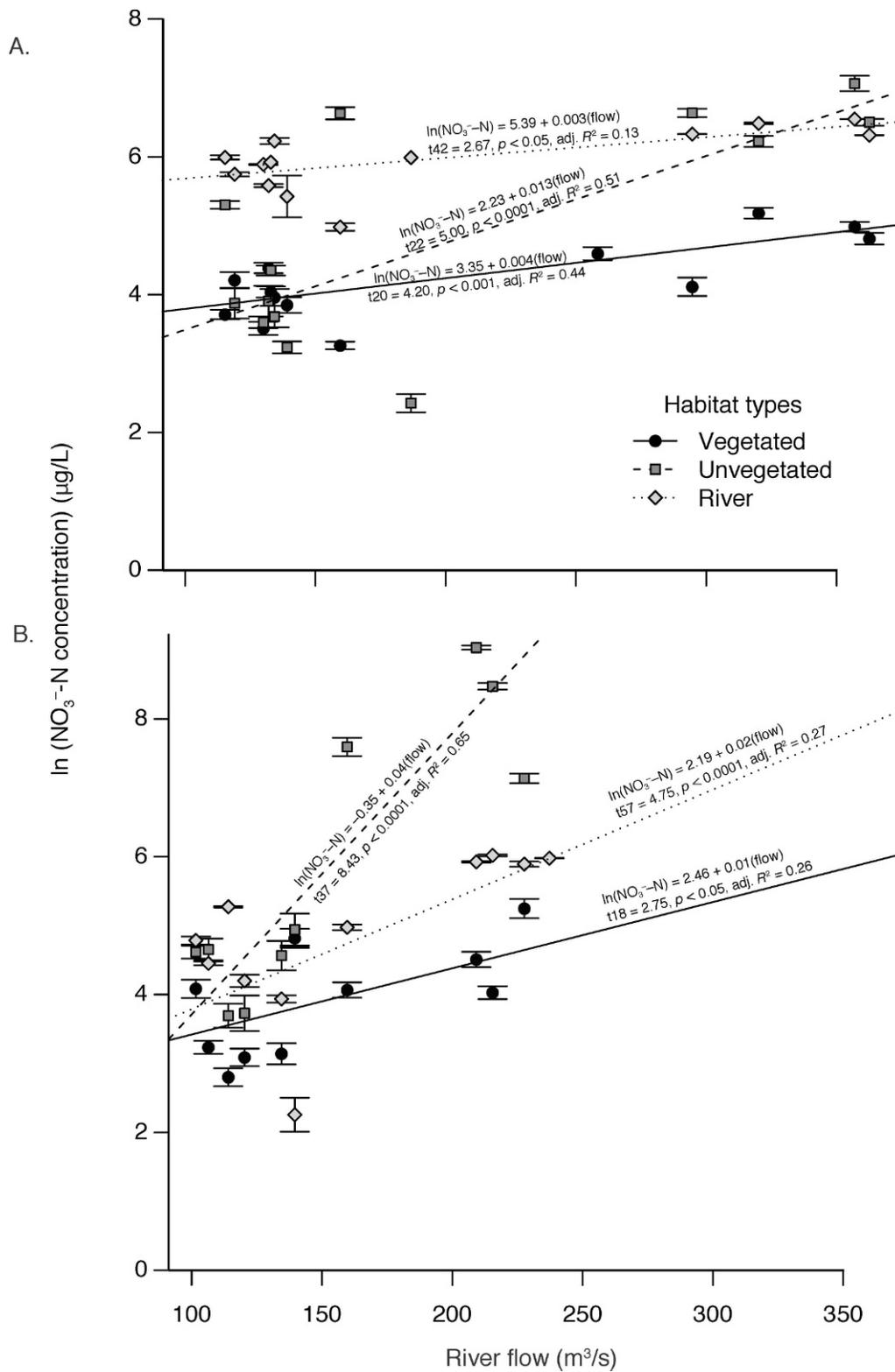


FIG. 3. Mean ( $\pm 1$  SE)  $\text{NO}_3^- \text{-N}$  concentrations in the parafluvial zone of unvegetated and vegetated bars and surface water in the river as a function of river flow in 2004 (A) and 2005 (B). Fitted lines were obtained from a regression of  $\ln(\text{NO}_3^- \text{-N})$  concentration on river flow for each habitat type, and significant regression results are reported on the figure. Each point is an average of habitats sampled during 1 d ( $n = 3\text{--}12$ ). Adj. = adjusted.

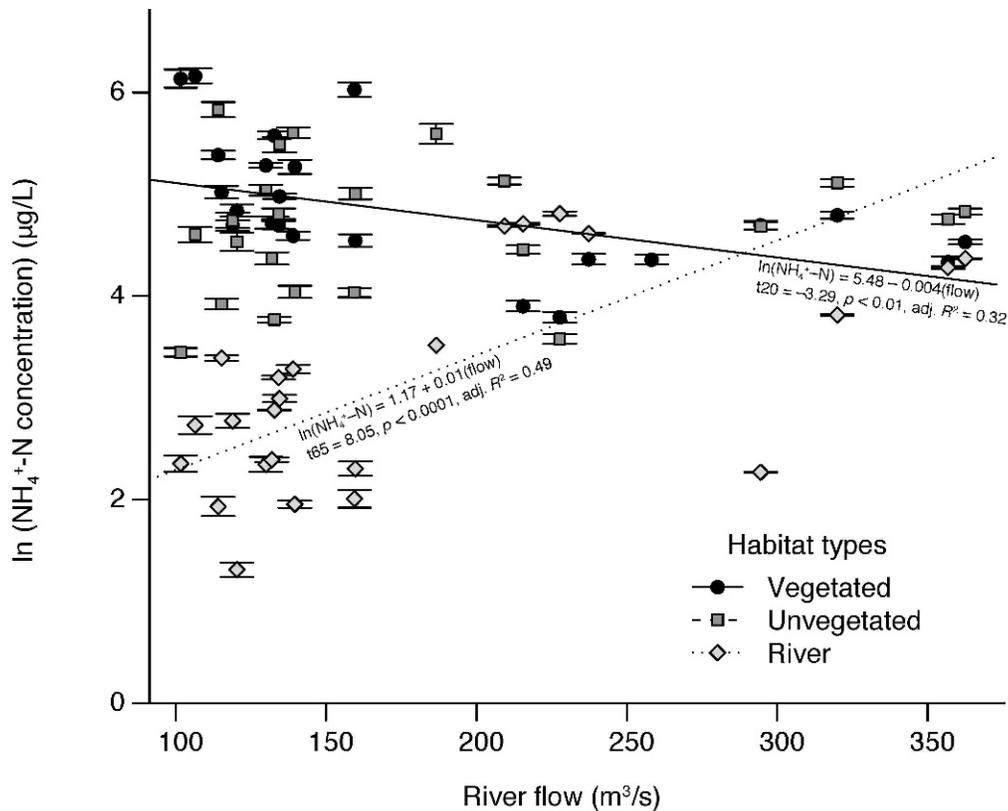


FIG. 4. Mean ( $\pm 1$  SE)  $\text{NH}_4^+\text{-N}$  concentrations in the parafluvial zone of unvegetated and vegetated bars and surface water in the river as a function of river flow. Fitted lines were obtained from a regression of  $\ln(\text{NH}_4^+\text{-N})$  concentration on river flow for each habitat type, and significant regression results are reported on the figure. Each point is an average of habitats sampled during 1 d ( $n = 3\text{--}12$ ). Adj. = adjusted.

sandbar types than in the river. As flow declined,  $\text{NH}_4^+\text{-N}$  increased significantly in vegetated sandbars and decreased significantly in surface water (Fig. 4). Concentrations of  $\text{SO}_4^{2-}$  were significantly predicted by habitat type and year (Table 2). Concentrations were lowest in vegetated bars and increased significantly in surface water as flow decreased (Fig. 5).

Denitrification rates varied significantly in response to amendments (additions of C or N) and the interactions of amendment with river flow and habitat (alone and in combination) (Table 3, Fig. 6A, B). Overall, denitrification rates in both vegetated and unvegetated sandbars were primarily  $\text{NO}_3^-$ -N limited (significant increase in +N treatments) and secondarily organic C limited (additional increase in +CN treatments). Based on the ratio of amended:control rates as an index of the magnitude of limitation (Francoeur 2001), N and CN additions to sediments from unvegetated bars resulted in an average rate increase of 4 $\times$  and 6 $\times$ , respectively. In comparison, these additions increased denitrification by 12 $\times$  and 21 $\times$  in vegetated bars, indicating a greater C limitation in vegetated bars than unvegetated bars.

In unvegetated bars, control and +C treatments peaked at moderately low flow rates (134 cms) and decreased to minimum rates as flow rates declined. Average +N and +CN rates were highest at low flow rates, and rates for these 2 treatments decreased significantly as flow declined (Fig. 6A). In vegetated bars, denitrification rates in control and +C treatments were consistently low at all flow rates, and were often lower than in unvegetated bars. Addition of N alone and in combination with C resulted in higher rates, and highest overall denitrification activity occurred in response to +CN under moderate river flow (160 cms). Denitrification rates were variable in vegetated bars, and no significant relationships with flow were found for individual amendments (Fig. 6B).

## Discussion

Parafluvial N concentrations and denitrification activity showed substantial variation between vegetated and unvegetated bars and with flow in the Wisconsin River.  $\text{NO}_3^-$ -N declined as flow decreased over time in all habitats, suggesting net N retention in

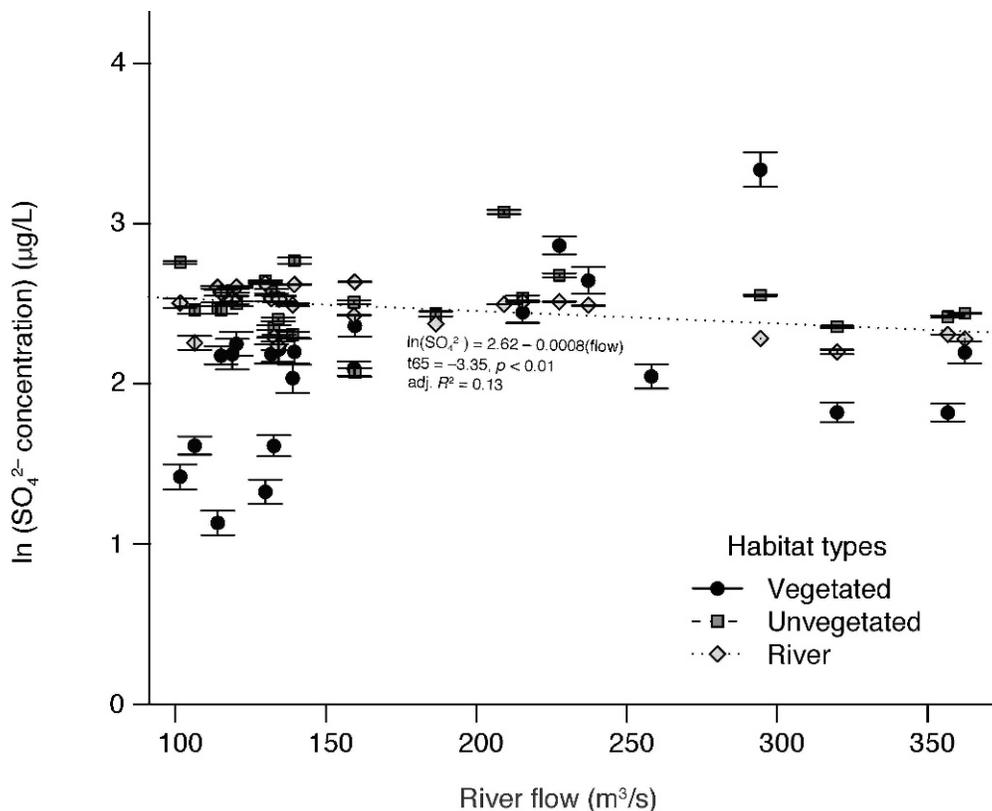


FIG. 5. Mean ( $\pm 1$  SE)  $\text{SO}_4^{2-}$  concentrations in the parafluvial zone of unvegetated and vegetated bars and surface water in the river as a function of river flow. Fitted lines were obtained from a regression of  $\ln(\text{SO}_4^{2-})$  concentration on river flow for each habitat type, and significant regression results are reported on the figure. Each point is an average of habitats sampled during 1 d ( $n = 3-12$ ). Adj. = adjusted.

the river and within interstitial environments in particular. However, the balance between parafluvial  $\text{NO}_3^-$ -N source and sink was affected by both presence/absence of vegetation and flow conditions.

During high flow, unvegetated bars clearly were acting as sources of  $\text{NO}_3^-$ -N. However, as flow declined, denitrification rates increased and  $\text{NO}_3^-$ -N declined within unvegetated bars, results suggesting that these habitats became  $\text{NO}_3^-$ -N sinks when flow

rates were low in the late summer. Conversely, vegetated bars already were functioning as  $\text{NO}_3^-$ -N sinks when flow rates were high. When flow declined to low levels, the depleted  $\text{NO}_3^-$ -N stores, increasing  $\text{NH}_4^+$ -N concentrations, and muted denitrification response to N and C amendments pointed to a collapse of the denitrifier community, minimal N retention, and a shift to  $\text{SO}_4^{2-}$  reduction as the dominant respiratory pathway in vegetated bars.

TABLE 3. Mixed model results for denitrification rates in parafluvial sediments ( $n = 359$ ) in the Wisconsin River in response to amendments (control, +C, +N, +CN), habitat type (unvegetated and vegetated bars), and river flow recorded the day samples were taken. NS = not significant ( $p > 0.05$ ). NC = no categorical comparison possible.

Factor	df	F	p	Tukey's comparison
Amendment	3,326	40.0	<0.0001	+CN > +N > +C = control
Habitat	1,4	1.5	NS	NS
Year	1,326	0.2	NS	NS
River flow	1,326	3.8	NS	NC
Amendment $\times$ river flow	3,326	1.3	NS	NC
Amendment $\times$ habitat	3,326	0.4	NS	NC
Habitat $\times$ river flow	1,326	13.6	<0.001	NC
Amendment $\times$ habitat $\times$ river flow	3,326	4.3	<0.01	NC

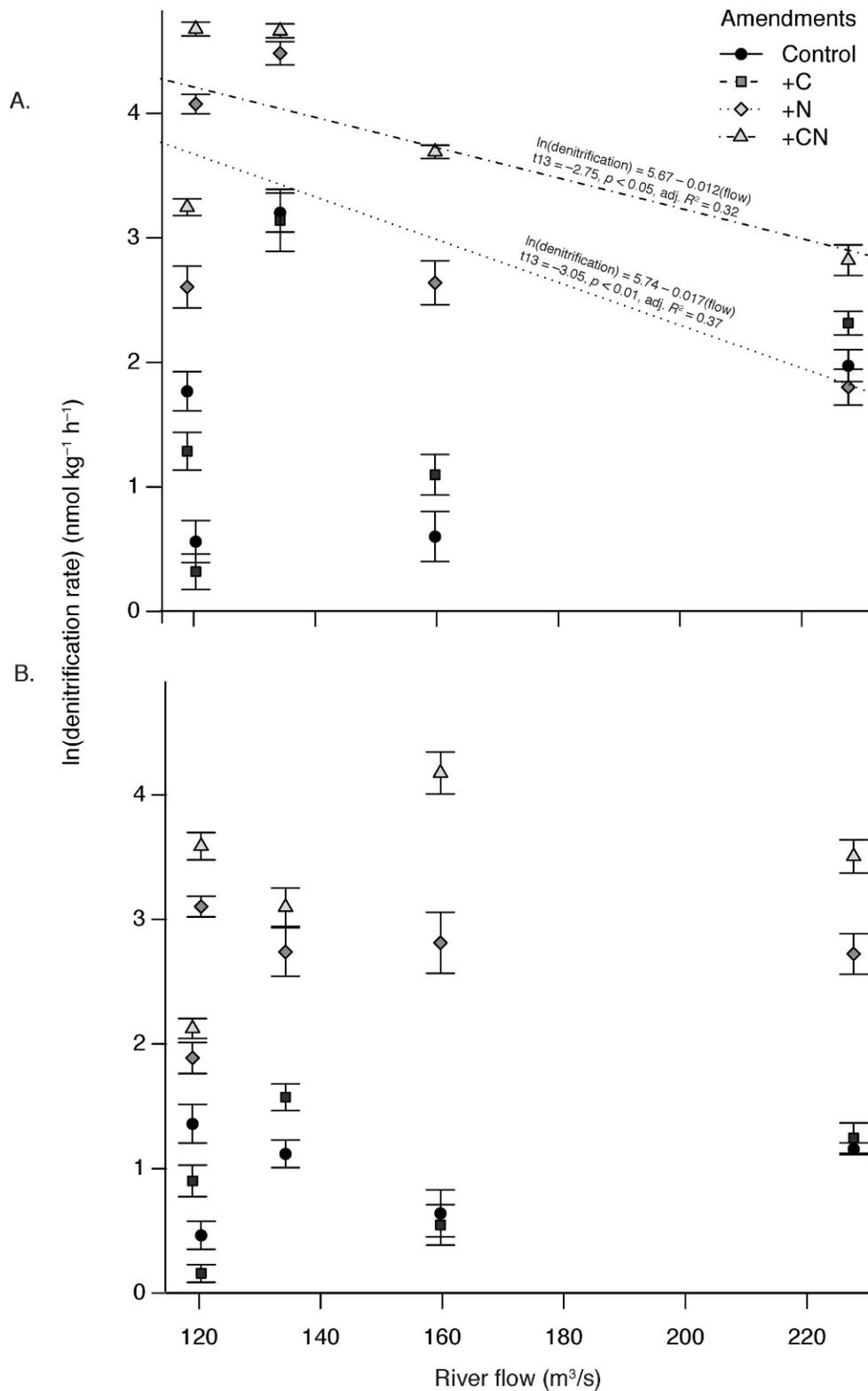


FIG. 6. Mean ( $\pm 1$  SE) denitrification rates ( $\mu\text{mol N}_2\text{O kg}^{-1} \text{h}^{-1}$ ) for hyporheic sediments in unvegetated (A) and vegetated (B) bars in the Wisconsin River in response to different nutrient amendment treatments (control, +N, +C, +CN) as a function of river flow. Fitted lines were obtained from a regression of  $\ln(\text{denitrification rate})$  on river flow for each amendment type, and significant regression results are reported on the figure. Each point is an average of habitats sampled during 1 d ( $n = 9$ ).

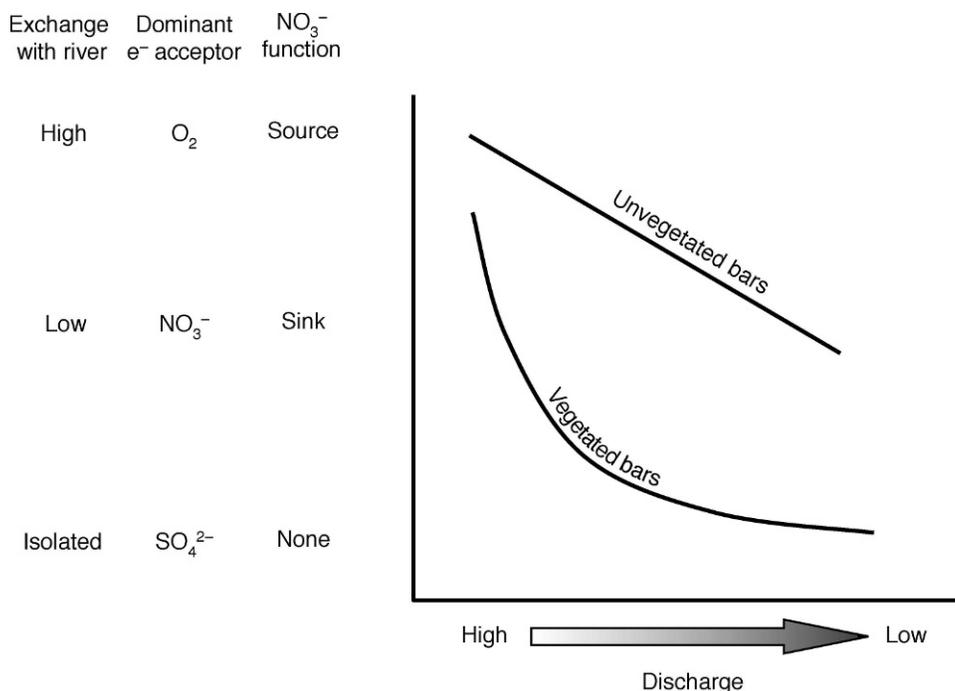


FIG. 7. Conceptual figure showing the relationship between N retention and river discharge on vegetated and unvegetated bars.

Collectively, these results suggest that N retention capacity of parafluvial zones in the Wisconsin River is a function of presence/absence of vegetation (Heffernan et al. 2008) and seasonal flow conditions (Deforet et al. 2008). In particular, the transition from NO<sub>3</sub><sup>-</sup>-N source to sink occurs rapidly with seasonal changes in stage in vegetated bars, but steadily in unvegetated bars (Fig. 7).

We expected that presence of vegetation would increase sediment or interstitial C stocks (Deforet et al. 2008, Gurnell et al. 2008), and in turn, would support higher rates of respiration and denitrification (Schade et al. 2001). Sediment OM appeared to follow this expectation because stocks declined with flow in unvegetated bars but increased in vegetated bars. Although interstitial DOC was similar between bar types, it is possible that the labile DOC pools were greater in vegetated bars via supply from root exudates and litter leachates (Deforet et al. 2008, Heffernan et al. 2008). However, the stronger response to added C in vegetated bars indicates that labile DOC supplies were, if anything, lower than in unvegetated bars. We suggest that this C limitation is not caused by lower production of labile DOC, but instead results from limited movement of DOC into saturated parafluvial sediments within bars. Therefore, we conclude that establishment of vegetation minimizes the hydrologic connection between the

river and bars, and thus, reduces overall N retention capacity in this system.

Establishment and growth of vegetation on bars on the Wisconsin River reduced the hydrologic exchange between bars and the river. Persistent anoxia in interstitial environments, as observed in vegetated bars, occurs because DO-rich surface waters are unable to penetrate into sediments. The presence of vegetation fosters trapping of fine sediments (Gurnell et al. 2008), which in turn, decreases hydraulic conductivity (Freeze and Cherry 1979). We did not compare sediment grain sizes among bar types, but vegetated bars clearly were effective sediment traps because their greater depth to water was the result of accumulation of sand on bar surfaces. We attempted to perform slug tests (addition of water to a well to measure the rate at which the head declines) to estimate hydraulic conductivity in vegetated and unvegetated bars. Added heads declined slowly in vegetated bars, but an elevated water column could not be maintained in unvegetated bars, a result revealing extremely high hydraulic conductivity in unvegetated bars and low conductivity in vegetated bars. Consistent with this idea of hydrologic isolation of vegetated bars in the Wisconsin River, Heffernan et al. (2008) found that establishment of riparian vegetation in a sand-bed desert stream significantly reduced surface–subsurface hydrologic exchange.

After plant colonization, the subsurface environment was persistently anoxic, even after flash floods that normally would recharge parafluvial and hyporheic sediments with well-oxygenated water in these desert systems (Jones et al. 1995).

We suspect that the dominant mechanism of hydrologic connection between the river and vegetated bars in the Wisconsin River is vertical exchange driven by the rise and fall of river stage, as has been reported in a braided cobble-bed river (Clilverd et al. 2008). In this scenario, high spring flows would saturate parafluvial sediments and potentially introduce DO- and  $\text{NO}_3^-$ -N-rich water early in the year. In vegetated bars, any initial infusion of DO and  $\text{NO}_3^-$ -N would be quickly depleted (in our case, long before we were safely able to sample), and metabolic conditions would become progressively more reduced as flow declined over the course of summer in the absence of any new inputs of DO or  $\text{NO}_3^-$ -N. The quick progression to hydrologic isolation means that the window of opportunity for N retention might be limited to a brief period of time when flow rates are high in the spring (Fig. 7). High flows that are typical during early spring months could potentially infuse bars with a steady supply of DO and  $\text{NO}_3^-$ -N, but water temperatures in the river at this time typically are 5 to 10°C, and these temperatures together with frequent ice formation around bar edges, suggest limited metabolic activity.

Establishment and persistence of riparian vegetation on bare sand surfaces is a function of a river's flow regime (Stromberg and Patten 1990, Johnson 2000, Rood et al. 2005). Like many rivers, the Wisconsin has experienced modern changes in system hydrology following construction of multiple dams. The net effect has been a reduction in overall flow variability and magnitude of spring flooding and an increase in summertime baseflow (Krug and House 1980, Dixon and Turner 2006). This flow homogenization has fostered greater recruitment of riparian vegetation on exposed sediments (Dixon and Turner 2006) and reduction of N retention on floodplains during spring floods (Forshay and Stanley 2005, Gergel et al. 2005). The results of our study suggest that an increased conversion of unvegetated bars to vegetated bars also will reduce N retention capacity within the main channel of the river.

If vegetated bars and islands represent an alternate stable state (Dent et al. 2002, Corenblit et al. 2007, Heffernan 2008), the loss of N retention capacity is unlikely to be restored under current climate and management regimes because substantial effort would be required to move back to an unvegetated state (Mayer and Rietkerk 2004). This pattern of flow

modification and enhanced tree recruitment is by no means unique to the Wisconsin River. For example, flow stabilization has allowed riparian forests to encroach into active channel areas of the Platte River (Johnson 1994) and has fostered establishment of dense stands of invasive salt cedars in the southwestern US (Beauchamp and Stromberg 2007). Flow modulation and riparian encroachment are occurring in concert with long-term increases in N loading to many rivers, especially in the Mississippi River basin (Goolsby and Battaglin 2001), a pattern suggesting that hydrologic changes are acting to isolate progressively more N-rich river flow from the environments that can retain this N.

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### Literature Cited

- ALEXANDER, R. B., R. A. SMITH, AND G. E. SCHWARZ. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature* 403:758–761.
- BEAUCHAMP, V. B., AND J. C. STROMBERG. 2007. Flow regulation of the Verde River, Arizona encourages *Tamarix* recruitment but has minimal effect on *Populus* and *Salix* stand density. *Wetlands* 27:381–389.
- BERNHARDT, E. S., AND G. E. LIKENS. 2002. Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. *Ecology* 83:1689–1700.
- BOULTON, A. J., S. FINDLAY, P. MARMONIER, E. H. STANLEY, AND H. M. VALETT. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* 29:59–81.
- CLARET, C., P. MARMONIER, J. M. BOISSIER, AND D. FONTVIELLE. 1997. Nutrient transfer between parafluvial interstitial water and river water: influence of gravel bar heterogeneity. *Freshwater Biology* 37:657–670.
- CLILVERD, H. M., J. B. JONES, AND K. KIELLAND. 2008. Nitrogen retention in the hyporheic zone of a glacial river in interior Alaska. *Biogeochemistry* 88:31–46.
- COLLINS, M. J., AND J. C. KNOX. 2003. Historical changes in Upper Mississippi River water areas and islands. *Journal of the American Water Resources Association* 39:487–500.
- COOKE, J. G., AND R. E. WHITE. 1987. The effect of nitrate in stream water on the relationship between denitrification

- and nitrification in a stream-sediment microcosm. *Freshwater Biology* 18:213–226.
- CORENBLIT, D., E. TABACCHI, J. STEIGER, AND A. M. GURNELL. 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth Science Reviews* 84:56–86.
- DAHM, C. N., N. B. GRIMM, P. MARMONIER, H. M. VALETT, AND P. VERVIER. 1998. Nutrient dynamics at the interface between surface waters and groundwaters. *Freshwater Biology* 40:427–451.
- DEFORET, T., P. MARMONIER, D. RIEFFEL, N. CRINI, C. FRITSCH, P. GIRAUDOUX, AND D. GILBERT. 2008. The influence of size, hydrological characteristics and vegetation cover on nitrogen, phosphorus and organic carbon cycling in lowland river gravel bars (Doubs River, France). *Fundamental and Applied Limnology* 171/2:161–173.
- DENT, C., G. CUMMING, AND S. CARPENTER. 2002. Multiple states in river and lake ecosystems. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 357:635–645.
- DIXON, M. D., AND M. G. TURNER. 2006. Simulated recruitment of riparian trees and shrubs under natural and regulated flow regimes on the Wisconsin River, USA. *River Research and Applications* 22:1057–1083.
- DUFF, J. H., AND F. J. TRISKA. 1990. Denitrification in sediments from the hyporheic zone adjacent to a small forested stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1140–1147.
- EDWARDS, P. J., J. KOLLMANN, A. M. GURNELL, G. E. PETTS, K. TOCKNER, AND J. V. WARD. 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. *Wetlands Ecology and Management* 7:141–153.
- FORSYAY, K. J., AND E. H. STANLEY. 2005. Rapid nitrate loss and denitrification in a temperate river floodplain. *Biogeochemistry* 75:43–64.
- FRANCOEUR, S. N. 2001. Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. *Journal of the North American Benthological Society* 20:358–368.
- FREEZE, R. A., AND J. A. CHERRY. 1979. *Groundwater*. Prentice Hall, Upper Saddle River, New Jersey.
- GERGEL, S. E., S. R. CARPENTER, AND E. H. STANLEY. 2005. Do dams and levees impact nitrogen cycling? Simulating the effects of flood alterations on floodplain denitrification. *Global Change Biology* 11:1352–1367.
- GILVEAR, D., AND N. WILLBY. 2005. Channel dynamics and geomorphic variability as controls on gravel bar vegetation, River Tummel, Scotland. *River Research and Applications* 21:1–18.
- GOOLSBY, D. A., AND W. A. BATTAGLIN. 2001. Long-term changes in concentrations and flux of nitrogen in the Mississippi River Basin, USA. *Hydrological Processes* 15:1209–1226.
- GROFFMAN, P. M., M. A. ALTABET, J. K. BÖHLKE, K. BUTTERBACH-BAHL, M. B. DAVID, M. K. FIRESTONE, A. E. GIBLIN, T. M. KANA, L. P. NIELSEN, AND M. A. VOYTEK. 2006. Methods for measuring denitrification: diverse approaches to a difficult problem. *Ecological Applications* 16:2091–2122.
- GROFFMAN, P. M., E. A. HOLLAND, D. D. MYROLD, G. P. ROBERTSON, AND X. ZOU. 1999. Denitrification. Pages 272–288 in G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins (editors). *Standard soil methods for long-term ecological research*. Oxford University Press, New York.
- GURNELL, A. M., T. D. BLACKWELL, AND G. E. PETTS. 2008. Characteristics of freshly deposited sand and finer sediments along an island-braided, gravel-bed river: the roles of water, wind and trees. *Geomorphology* 99: 254–269.
- GURNELL, A. M., AND G. E. PETTS. 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. *Freshwater Biology* 47:581–600.
- GURNELL, A. M., G. E. PETTS, D. M. HANNAH, B. P. G. SMITH, P. J. EDWARDS, J. KOLLMANN, J. V. WARD, AND K. TOCKNER. 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms* 26:31–62.
- HALE, B. W., E. M. ALSUM, AND M. S. ADAMS. 2008. Changes in the floodplain forest vegetation of the lower Wisconsin River over the last fifty years. *American Midland Naturalist* 160:454–476.
- HEFFERNAN, J. B. 2008. Wetlands as an alternative stable state in desert streams. *Ecology* 89:1261–1271.
- HEFFERNAN, J. B., R. A. SPONSELLER, AND S. G. FISHER. 2008. Consequences of a biogeomorphic regime shift for the hyporheic zone of a Sonoran Desert stream. *Freshwater Biology* 53:1954–1968.
- HINKLE, S. R., J. H. DUFF, F. J. TRISKA, A. LAENEN, E. B. GATES, K. E. BENCALA, D. A. WENTZ, AND S. R. SILVA. 2001. Linking hyporheic flow and nitrogen cycling near the Willamette River—a large river in Oregon, USA. *Journal of Hydrology* 244:157–180.
- HOLMES, R. M., S. G. FISHER, AND N. B. GRIMM. 1994. Parafluvial nitrogen dynamics in a desert stream ecosystem. *Journal of the North American Benthological Society* 13:468–478.
- HOLMES, R. M., J. B. JONES, S. G. FISHER, AND N. B. GRIMM. 1996. Denitrification in a nitrogen-limited stream ecosystem. *Biogeochemistry* 33:125–146.
- JOHNSON, W. C. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. *Ecological Monographs* 64:45–84.
- JOHNSON, W. C. 2000. Tree recruitment and survival in rivers: influence of hydrological processes. *Hydrological Processes* 14:3051–3074.
- JONES, J. B., S. G. FISHER, AND N. B. GRIMM. 1995. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran Desert stream. *Ecology* 76:942–952.
- JONES, J. B., AND R. M. HOLMES. 1996. Surface-subsurface interactions in stream ecosystems. *Trends in Ecology and Evolution* 11:239–242.
- KOLLMANN, J., M. VIEL, P. J. EDWARDS, K. TOCKNER, AND J. V. WARD. 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Applied Vegetation Science* 2:25–36.
- KRUG, W. R., AND L. B. HOUSE. 1980. Streamflow model of Wisconsin River for estimating flow frequency and

- volume. U.S. Geological Survey Water-Resources Investigations Open-File Report 80-1103. US Geological Survey, Reston, Virginia.
- LEOPOLD, L. B., M. G. WOLMAN, AND J. P. MILLER. 1964. Fluvial processes in geomorphology. Freeman, San Francisco, California.
- LEWIS, D. B., N. B. GRIMM, T. K. HARMS, AND J. D. SCHADE. 2007. Subsystems, flowpaths, and the spatial variability of nitrogen in a fluvial ecosystem. *Landscape Ecology* 22: 911–924.
- MALARD, F., K. TOCKNER, M. J. DOLE-OLIVIER, AND J. V. WARD. 2002. A landscape perspective of surface-subsurface hydrological exchanges in river corridors. *Freshwater Biology* 47:621–640.
- MAYER, A. L., AND M. RIETKERK. 2004. The dynamic regime concepts and ecosystem management and restoration. *BioScience* 54:1013–1020.
- ORR, C. H., E. H. STANLEY, K. A. WILSON, AND J. C. FINLAY. 2007. Effects of restoration and reflooding on soil denitrification in a leveed Midwestern floodplain. *Ecological Applications* 17:2365–2376.
- PETERSON, B. J., W. M. WOLLHEIM, P. J. MULHOLLAND, J. R. WEBSTER, J. L. MEYER, J. L. TANK, E. MARTÍ, W. B. BOWDEN, H. M. VALETT, A. E. HERSHEY, W. H. MCDOWELL, W. K. DODDS, S. K. HAMILTON, S. GREGORY, AND D. D. MORRALL. 2001. Control of nitrogen export from watersheds by headwater streams. *Science* 292:86–90.
- PINHEIRO, J. C., AND D. M. BATES. 2000. Mixed-effects models in S and S-PLUS. Springer, New York.
- POPP, A. S. 2005. Longitudinal patterns of dissolved organic carbon, chlorophyll, and nutrients in a seventh order river: the Wisconsin River, U.S.A. MS Thesis, University of Wisconsin, Madison, Wisconsin.
- PUCKETT, L. J., C. ZAMORA, H. ESSAID, J. T. WILSON, H. M. JOHNSON, M. J. BRAYTON, AND J. R. VOGEL. 2008. Transport and fate of nitrate at the ground-water/surface-water interface. *Journal of Environmental Quality* 37:1034–1050.
- ROOD, S. B., G. M. SAMUELSON, J. H. BRAATNE, C. R. GOURLEY, F. M. R. HUGHES, AND J. M. MAHONEY. 2005. Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment* 3:193–201.
- SCHADE, J. D., S. G. FISHER, N. B. GRIMM, AND J. A. SEDDON. 2001. The influence of a riparian shrub on nitrogen cycling in a Sonoran Desert stream. *Ecology* 82: 3363–3376.
- SEITZINGER, S. P., R. V. STYLES, E. W. BOYER, R. B. ALEXANDER, G. BILLEN, R. W. HOWARTH, B. MAYER, AND N. VAN BREEMAN. 2002. Nitrogen retention in rivers: model development and application to watersheds in the Northeastern U.S.A. *Biogeochemistry* 57/58:199–237.
- SJODIN, A. L., W. M. LEWIS, JR, AND J. F. SAUNDERS. 1997. Denitrification as a component of the nitrogen budget for a large plains river. *Biogeochemistry* 39:327–342.
- SMITH, M. S., AND J. M. TIEDJE. 1979. Phases of denitrification following oxygen depletion in soil. *Soil Biology and Biochemistry* 11:261–267.
- STANLEY, E. H., AND A. J. BOULTON. 1995. Hyporheic processes during flooding and drying in a Sonoran Desert stream. I. Hydrologic and chemical dynamics. *Archiv für Hydrobiologie* 134:1–26.
- STROMBERG, J. C., AND D. T. PATTEN. 1990. Riparian vegetation instream flow requirements: a case study from a diverted stream in the eastern Sierra Nevada, California, USA. *Environmental Management* 14:185–194.
- TRUSH, W. J., S. M. MCBAIN, AND L. B. LEOPOLD. 2000. Attributes of an alluvial river and their relation to water policy and management. *Proceedings of the National Academy of Sciences of the United States of America* 22: 11858–11863.
- TURNER, M. G., E. H. STANLEY, M. BÜRGLI, AND D. J. MLADENOFF. 2008. Changes in the Wisconsin River and its floodplain. Pages 229–249 in D. M. Waller and T. P. Rooney (editors). *The vanishing present: ecological change in Wisconsin*. University of Chicago Press, Chicago, Illinois.
- VAN DER HOVEN, S. J., N. J. FROMM, AND E. W. PETERSON. 2008. Quantifying nitrogen cycling beneath a meander of a low gradient, N-impacted, agricultural stream using tracers and numerical modeling. *Hydrological Processes* 22:1206–1215.
- VAN KESSEL, J. F. 1977. Factors affecting the denitrification rate in two water-sediment systems. *Water Research* 11: 259–267.
- ZANONI, L., A. GURNELL, N. DRAKE, AND N. SURIAN. 2008. Island dynamics in a braided river from analysis of historic maps and air photographs. *River Research and Applications* 24:1141–1159.

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