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ORIGINAL PAPER

Flood pulse effects on nitrification in a floodplain forest impacted by herbivory, invasion, and restoration

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Abstract We tested the hypothesis that management actions that alter floodplain plant communities will modify the effects of flooding on gross nitrification, a key process regulating the flux of nitrate along river-floodplains. Soils were collected from mature forests, patches of *Phalaris arundinacea*, an exotic grass, and areas restored to early successional forest (unbrowsed and browsed) in the Upper Mississippi River floodplain. Samples were collected across an elevation gradient and along the descending limb of the hydrograph to test for effects of flooding. In all three forest types, soil properties were less favorable for nitrification as elevation increased, due to decreasing organic matter, porosity, total nitrogen, and temperature. In contrast, *Phalaris* maintained high soil organic matter and porosity as floodplain elevation increased. Corresponding with the differences in soil properties found in forested plots, the highest rates of potential gross nitrification were found in the lower elevation sites immediately following the spring flood (1–8 days post inundation). These high rates were later followed by a rapid decline in both NH_4^+-N and nitrification with increasing time since inundation (>11 days post inundation). Nitrification rates were also highest following the flood in *Phalaris* sites, but rates did not depend on elevation, likely because of the lack of elevational differences in soil properties. Our results generally support the flood-pulse concept of river-floodplain connectivity, with the highest nitrification rates found in areas and during times immediately following inundation. Furthermore, restoration of forest cover in areas invaded by *Phalaris* appears likely to restore flood-pulse effects on abiotic soil properties and nitrification dynamics.

Keywords Connectivity · Disturbance · Flood pulse · Herbivory · Nitrogen · *Phalaris arundinacea* · Restoration

Introduction

The flood-pulse concept predicts that patterns of river-floodplain connectivity that promote alternating wet-dry conditions will increase rates of nutrient turnover, relative to patterns that lead to permanently or rarely inundated conditions (Junk et al. 1989; Tockner et al. 2000). Because floodplains often serve as critical buffers against elevated nitrogen concentrations in aquatic systems (Schlosser and Karr 1981), and because flooding is generally thought to be the main driver of nutrient dynamics within floodplains (Naiman and Décamps 1990; Pinay et al. 2007; Noe et al.

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2013), river management and restoration actions that focus on reducing river nitrogen loads often consist of modifying river-floodplain connectivity (Craig et al. 2008; Kaushal et al. 2008). However, flooding may interact with other factors that modify aboveground plant communities (e.g., herbivory, plant invasion, forest management) in ways that generate both direct and indirect effects on nutrient cycling (Windham and Ehrenfeld 2003; Butler and Kielland 2008). Although much is known about the effects of herbivory (e.g. Pastor et al. 1993, Frank et al. 2000) and plant invasion (e.g., Ehrenfeld 2001; Mack and D'Antonio 2003) on nitrogen cycling in terrestrial ecosystems, few studies have examined whether these factors might alter effects of flooding on nitrogen cycling in a floodplain ecosystem.

Nitrification (microbial oxidation of ammonium to nitrite and nitrate), is often considered the key process limiting nitrogen loss from ecosystems because it represents a source of nitrate, which is generally more mobile than ammonium (Vitousek et al. 1982). In upland forests, nitrate made available via nitrification can be associated with N leaching into rivers and streams. However, in wetland soils, nitrification can be coupled with denitrification, ultimately resulting in N loss to the atmosphere (Pinay et al. 2007). In continuously flooded soils, nitrification may occur in the uppermost oxygenated soil layer or in oxygenated root zones. Nitrate produced in oxygenated zones can then diffuse into nearby anaerobic zones to be denitrified (Shrestha et al. 2012). Similarly, in floodplains that experience alternating wet-dry phases, nitrification during dry periods may be coupled with denitrification during subsequent wet periods (Baldwin and Mitchell 2000). Hence, by regulating the timing and duration of soil anoxia, flooding can have large effects on nitrification rates and the potential for coupled nitrification–denitrification reactions.

In addition to effects of soil aeration, nitrification is known to be sensitive to a suite of other abiotic factors. For example, nitrification commonly increases monotonically with available NH_4^+-N (Vitousek et al. 1982; Parton et al. 1988; Strauss et al. 2002; Jicha et al. 2013), and soil temperature (Sabey et al. 1959; Malhi and McGill 1982; Gilmour 1984), and responds unimodally to pH (Strauss et al. 2002), and percent water filled pore space (wfps), with maximum estimates of nitrification observed around 55–60 % (Linn and Doran 1984; Parton et al. 1996)). In addition, organic carbon availability may affect nitrification rates in sediments with high C:N (>20, Strauss et al. 2002). The above ground plant community can influence many of these soil properties and could, therefore modify the effects of flooding on nitrification.

The forests of the Upper Mississippi River (UMR) floodplain are dominated by mature, even-aged stands of silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvaticus*), and American elm (*Ulmus americana*). Canopy gaps, created by either windthrow or harvesting, are often quickly invaded by reed canarygrass (*Phalaris arundinacea*; Romano 2010). The grass is a widespread invader of North American wetlands and is considered a model organism for understanding plant invasion dynamics (Lavergne and Molofsky 2004). It is a robust competitor above- and belowground, forming a thick thatch layer and a dense mat of rhizomes (Reinhardt Adams and Galatowitsch 2006; Annen 2008), which suppress the growth of other plants. Management actions targeting *Phalaris* promote the establishment of young trees (Thomsen et al. 2012), but flooding and intense herbivory from white-tailed deer (*Odocoileus virginianus*) can lead to high rates of tree mortality, re-open the plant canopy, and in some cases facilitate reinvasion (De Jager et al. 2013; Cogger et al. 2014).

The creation of canopy gaps and subsequent management decisions related to forest restoration and suppression of herbivory and re-invasion within them, could affect nitrogen cycling in floodplains. Mature forests are known to assimilate and store large amounts of nitrogen (Vitousek et al. 1982). As a consequence of low ammonium availability, nitrification rates are often slower in mature forests as compared with early successional forests. Herbivory in canopy gaps could further influence nutrient cycling in early successional floodplain forests via the deposition of dung and urine (Ruess and McNaughton 1987) or indirectly, by altering plant species composition and causing associated changes in litter quantity and quality (Pastor et al. 1993). Invasion of early successional forests by *Phalaris* could alter nitrogen availability via high uptake rates (Conchou and Fustec 1988; Edwards et al. 2006). Additionally, the development of a thick thatch layer has the potential to modify soil temperature and organic carbon. Finally, the dense roots of *Phalaris* may help to oxygenate soils during flooded periods, increasing the potential for nitrification (Forshay and Dodson 2011).

In this study, we examine the consequences of different floodplain vegetation management decisions on the nitrification potential of a UMR canopy gap. Differences in nitrification rates were compared in: (1) areas invaded by *Phalaris*, (2) recently restored unbrowsed early successional forests (inside exclosures), (3) recently restored browsed early successional forests (outside exclosures), and (4) a remnant, uninvaded mature forest. Plant community effects were examined along with flooding by establishing plots along the elevation gradient of the floodplain and by sampling along the descending limb of the spring-summer hydrograph. The specific questions we asked were: (1) How do abiotic soil characteristics relate to spatial and temporal patterns of flooding across contrasting plant communities? (2) How does the influence of flooding on spatial and temporal patterns of nitrification rates compare across plant communities? (3) Which abiotic factors have the greatest influence on nitrification rates, and are these consistent across all communities? Answers to these questions should contribute to a broader understanding of the role vegetation management actions might play in altering nitrogen dynamics within floodplains subject to periodic inundation.

Methods

Study area

Our study took place at a Mississippi River floodplain site owned by the U.S. Army Corps of Engineers south of La Crosse, Wisconsin (Fig. 1, 43° 44.3′N, 91° 12.6′W). The site floods periodically, with flood waters typically spreading across adjacent backwaters and onto the floodplain before gradually receding after floods. In 1998, straight-line winds blew down approximately 4.2 ha of forest within the site. After salvage logging, *P. arundinacea* L. (reed canarygrass) invaded the entire area. By 2009, repeated herbicide applications eliminated reed canarygrass from some areas as described in Thomsen et al. (2012), leaving a mosaic of 2–3 year-old *Acer saccharinum* L. (silver maple), *Fraxinus pennsylvaticus* Marshall (green ash), *Salix exigua* Nutt. and *S. nigra* Marshall (sandbar and black willow) and *Populus deltoides* W. Bartram ex Marshall (eastern cottonwood) interspersed with patches of reed canarygrass (former control plots). We selected five patches of reed canarygrass that were a minimum of ten years old to sample for this study. Each patch was a monoculture of the grass, was at least 20 × 20 m in size, and was situated along the elevation gradient of the floodplain (Figs. 1 and 2a).

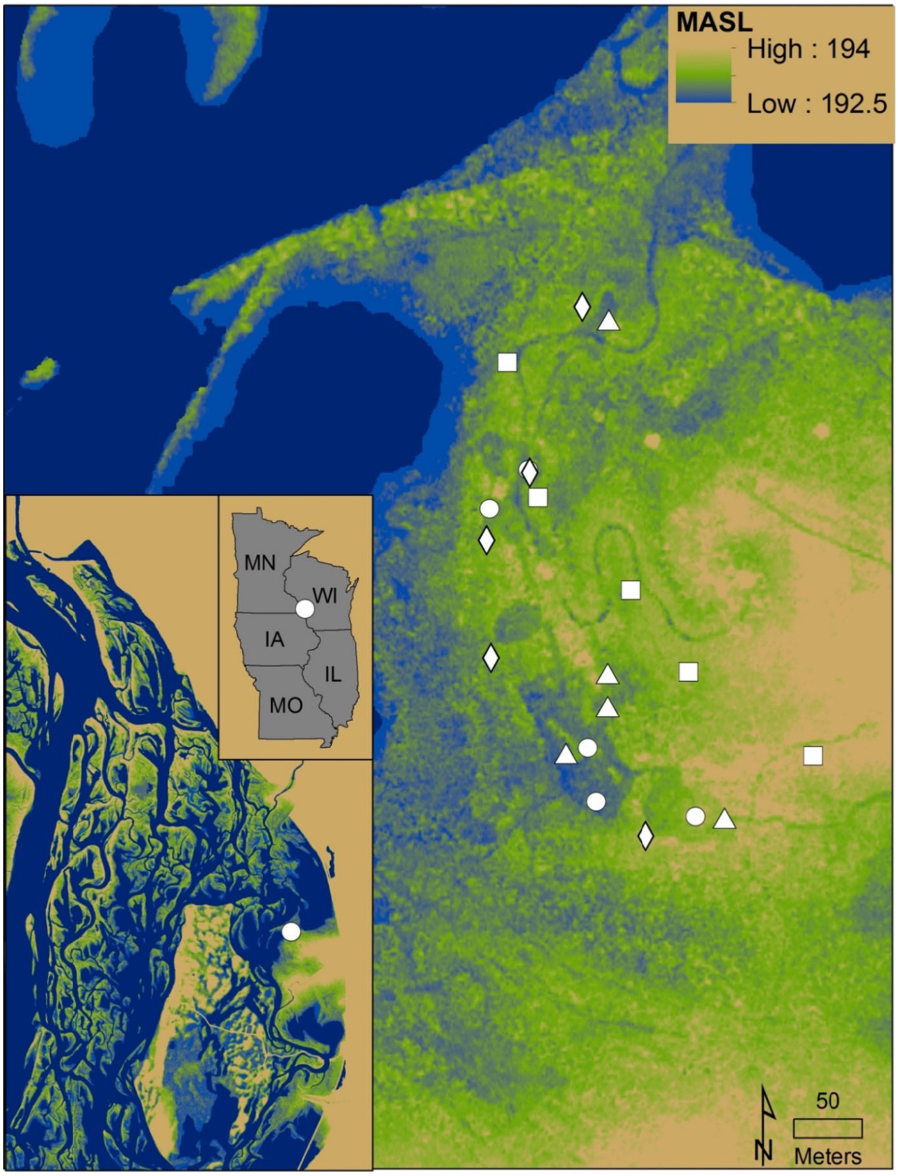
In 2009 five 20 × 20 m deer exclosures were constructed at the site, also situated along the elevation gradient of the floodplain (Figs. 1 and 2a). Fences were constructed of polypropylene mesh and were 2.4 m tall. These fences eliminated deer herbivory within exclosures from Nov. 2009 to the end of the present study in 2012. In contrast, browsing rates outside of the exclosures ranged from 40 to 85 % of all available stems during the winter of 2009, were reduced to near zero during three large magnitude floods in 2010 and 2011, and then ranged from approximately 15 % of available stems in spring 2012 to approximately 30 % of available stems in fall 2012. For this study, we sampled these five exclosures and five unfenced study plots, hereafter referred to as browsed early successional forests (Fig. 1). Sapling densities in the exclosures increased linearly from 5.4 trees m^{-2} in the lowest elevation plot to 13 trees m^{-2} in the highest elevation plot. Tree densities in the unfenced plots increased linearly from 0.06 trees m^{-2} in the lowest elevation plot to 7.3 trees m^{-2} in the highest elevation plot. These differences reflect past effects of both browsing and the floods of 2010 and 2011. Trees in the exclosures were approximately 2 m tall during this study while those in the browsed plots were approximately 1 m tall and these differences did not depend on elevation (De Jager et al. 2013).

Finally, five plots were established in a strip of mature forest situated along the edge of the canopy gap that was created in 1998. Saplings were not present in these plots and the herb layer was also poorly developed. The basal area of large trees (>20 cm dbh) within a 12 m radius of each plot ranged from 37.2 to 63.50 m^2 ha^{-1} and showed no trends with elevation. Each site had a mix of large silver maple, green ash, and eastern cottonwood. Each mature forest plot was also situated along the elevation gradient of the floodplain (Figs. 1 and 2a).

Data collection and laboratory analyses

Sampling took place within three 1 × 1 m subplots nested within each plot. Subplot elevations were estimated by comparing the water surface elevation

Fig. 1 Map of the study area, including floodplain elevation (in meters above sea level, MASL), the location of sample plots (*squares* are mature forests, *circles* are unbrowsed early successional forests, *triangles* are browsed early successional forests, and diamonds are patches of reed canarygrass. The location of the study site is shown relative to the larger river reach and Upper Midwestern United States (*inset, large white circles*)



adjacent to the site with the land elevation recorded in each subplot. Subplot elevations were averaged and soil samples were composited to avoid pseudoreplication. Soil samples were collected in July, August and September following a spring flood, which lasted from May to mid-July 2012. All study plots were inundated during the flood, except for a single mature forest plot situated at the highest elevation (Fig. 2a, b). Maximum flood depth in the lowest elevation plot was just less than 1 m. From May 1 to the first soil sampling episode in July, flood durations ranged from 0 days in the single unflooded plot to 60 days in the lowest elevation plot (Fig. 2b). The first soil samples were collected from the lowest elevation plot on the first day that it was unflooded. Because of the elevation gradient of the floodplain, the nature of the decline in water levels during the first sampling episode (Fig. 2a), and the timing of our sample collection, the average time since inundation at the time of July sampling differed along the elevation gradient of the floodplain. Average time since inundation for July sampling ranged from 1 to 14 days in

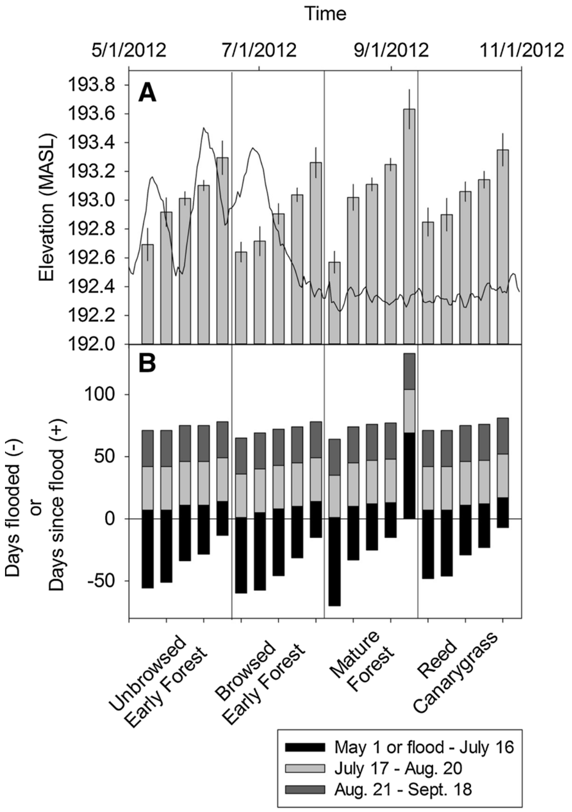


Fig. 2 **a** Mean (± SE) of sample plots in four different plant community types used for this study (*bars*), and water surface elevation at the study area from May 1 to November 1, 2012 (*time series*). **b** Black bars depict the number of days each sample plot was flooded (*negative values*) or dry (*positive values*) during May 1 to July 16 (when first soil samples were collected). No plots were flooded following the first soil sampling episode. *Light gray bars* depict the 35 days between the first and second sampling episodes and *dark gray bars*, the 29 days between the second and third sampling episodes. Top *x*-axis pertains to the time series of water surface elevation

browsed early forest plots, 7–14 days in unbrowsed early forest plots, 7–17 days in patches of reed canarygrass, and 1–69 days in mature forest plots (days since May 1 for the highest elevation plot). However, the two lowest elevation plots from each plant community type were saturated at the time of July soil sampling. All plots remained unflooded for the remainder of the study.

Soil samples were collected using polycarbonate tubes that measured 2.5 cm in diameter and 20 cm in length. Cores were taken from the top 5 cm of soil within each subplot and composited at the plot level before laboratory analyses. We measured the following soil physical properties during a single sampling period (August): soil organic matter, bulk density, total porosity, total carbon, total nitrogen, and TN:TC. We measured soil moisture, exchangeable NH_4^+-N, and gross nitrification rates monthly. Finally, soil temperature was measured at half hour increments from June 19 to October 19, 2012 with buried temperature data loggers (HOBO PRO V2) and the data were later summarized using monthly means.

Soil organic matter was measured via mass loss after combustion in a 600° C oven for 20 min. We then used the following pedotransfer function to estimate soil bulk density (D_B, g cm^{-3}) (Robertson et al. 1999):

$$D_B\left(\text{g cm}^{-3}\right) = \text{Exp}[0.23 - 0.037 \times \text{SOM}(\%)],$$

$$S_{y,x} = 0.05\ \text{g cm}^{-3}$$

Total porosity (S_t,%) was then estimated using estimated bulk density and a standard particle density (P_D) of 2.65 g cm^{-3} (Blake and Hartge 1986):

$$S_t(\%) = [1 - D_B/P_D] \times 100$$

Water filled pore space (wfps) was determined using the equation:

$$\text{wfps}\ (\%)\ =\ [P_W \times (D_B/S_t)] \times 100$$

where P_W is gravimetric water content (g H_20 g^{-1} dry soil, measured monthly at each plot), estimated by weighing soils before and after drying in an oven at 60 °C for 72 h or until a constant weight was achieved. A 60 °C temperature was used instead of the more traditional 105 °C to avoid N losses due to volatilization (Robertson et al. 1999). Total carbon (TC), total nitrogen (TN) and TC:TN ratios (molar) were determined with a Variomax CN analyzer (Elementar). Ashed samples were used to determine total organic carbon and TOC:TN ratios (atomic) by comparing them with non-ashed samples.

Gross nitrification rates were measured in each plot and during each month with laboratory incubations using a modification of the nitrapyrin method as described in Strauss and Lamberti (2000) and Strauss et al. (2004). Two replicate analyses were conducted for each plot. For each replicate, two 125-mL flasks were filled with 25 g of soil and 81 mL of water. One of the flasks received an additional 10 µL of a known nitrification inhibitor, nitrapyrin [2-chloro-6-(trichloromethyl)-pyridine], dissolved in dimethyl sulfoxide (DMSO). The other flask received only DMSO. Each flask was covered loosely with aluminum foil and aerated on an orbital shaker (175 r.p.m) for 72 h at 27 °C. Filtered 1-N KCl extracts were used to determine initial and final NH_4^+-N concentrations in both flasks. Concentrations of NH_4^+-N were determined on a Lachat QuikChem 8500 Series 2 FIA system. Potential gross nitrification rates over the incubation period were calculated by subtracting the change in NH_4^+-N concentration in the flask containing DMSO (uninhibited flask) from the change in NH_4^+-N concentration in the flask receiving both nitrapyrin and DMSO (inhibited flask). Initial NH_4^+-N concentrations were averaged between the two flasks and later used to help explain variation in nitrification rates. The mean of the replicates for each plot was used in further statistical analyses. Nitrification rates were expressed on a per unit soil volume basis by multiplying daily rates by soil bulk density.

Data analysis

We examined effects of elevation and plant community type using analysis of covariance with community type as the categorical variable and relative elevation as the continuous covariate. This analysis was conducted once for measurements made during a single time period (soil organic matter, percent porosity, TN, TC, TN:TC). Independent analyses were conducted for each month for mean daily soil temperature, mean daily temperature range (daily high minus daily low), wfps, exchangeable NH_4^+-N and gross nitrification rates. We compared models consisting of (1) intercept only (no effect of community type or elevation), (2) effect of community type only, (3) effect of elevation only, (4) community type plus elevation (different y-intercepts among community types but a common slope), (5) the effect of community type plus an interaction term (different y-intercepts and slope terms for community type), and (6) removal of the individual main effect for community type, while maintaining the interaction term (common y-intercepts among community types but different slope terms). We refer back to these model numbers throughout the results section. The most parsimonious model was determined using Akaike Information Criterion (AIC) weights. AIC weights are interpreted as the probability that a given model is the best Kullback–Leibler model, given the data and set of candidate models (Burnham, and Anderson 2001). If the best model included effects of community type and elevation, we then used a form of factor-level reduction to test for significant differences in the y-intercept and slope terms for all combinations of community types. This was accomplished by grouping community types by all possible combinations, and using analysis of variance (with Bonferroni corrected P values < 0.05) to compare and contrast each model. If no significant differences were found among models from different community types, then the data from those community types were grouped before final model estimation.

We developed a full dataset by linking the measurements made in each plot during a single time period to the measurements made in each plot during each time period to further examine linear associations (Pearson correlation coefficients) between nitrification rates and measurements of TN, TC, TN:TC, mean daily soil temperature and mean daily temperature range, and NH_4^+-N availability; and unimodal associations between nitrification rates and wfps (by using both water filled pore space and water filled pore space squared). Separate analyses were conducted for the data from each community type and for the entire data set. We then used stepwise regression, again with AIC weights, to identify the most parsimonious model for predicting nitrification rates for each community type and for the entire data set. Finally, we also examined relationships between the number of days that plots were unflooded and exchangeable NH_4^+-N and gross nitrification rates by creating bi-plots and applying hyperbolic decay functions. All analyses were done in the 'stats' package in R3.0.2 (R Core Team 2013).

Results

Effects of flooding and vegetation type on soil abiotic factors

The best models based on AIC for predicting percent soil organic matter and percent soil porosity consisted of the interaction between relative elevation and community type (Model 6, $AIC_w = 0.98$ and 0.99 respectively, Fig. 3). The highest estimates of percent organic matter (20–25 %) and porosity (75–85 %) were observed at the lowest elevations, regardless of community type. Both measurements declined with increasing elevation, with rates that depended on community type (Fig. 3). Factor-level reduction showed that mature forest and unbrowsed early

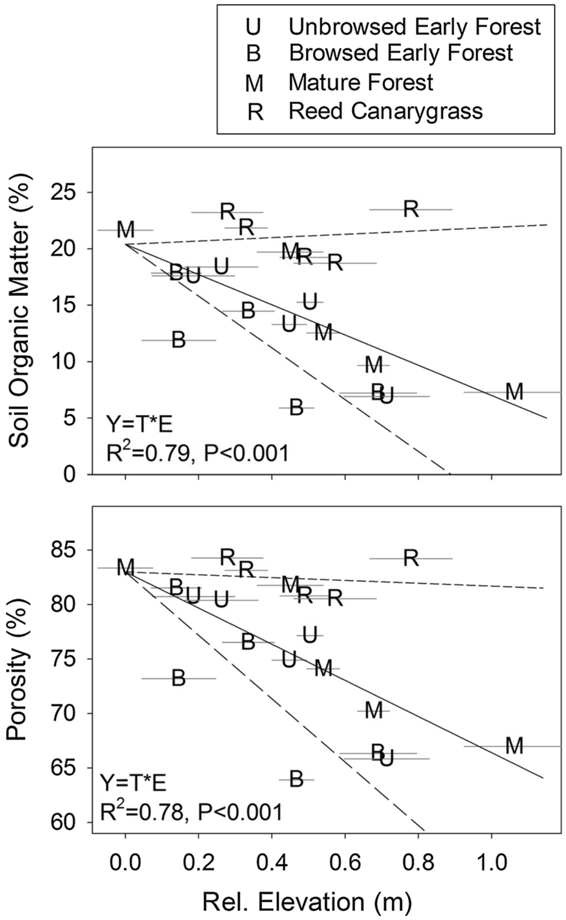


Fig. 3 Trends in percent soil organic matter and porosity with increasing floodplain elevation (E) for four different community types (T) and associated best models based on AIC. Both soil properties were greatest in low elevation plots, regardless of community type, but declined with increasing elevation at rates that depended on community type (Model 6, see methods). The most rapid rates of decline were observed in browsed early successional forest plots (*long dashes*) and the slowest rates of decline were in patches of reed canarygrass (*non-significant, short dashes*). Declines in soil organic matter and porosity were similar for mature forest and unbrowsed early successional forests (*solid black line*)

successional forest plots lost organic matter and porosity at approximately equal rates with increasing elevation, to lows of approximately 7 % organic matter and 65 % porosity. The browsed early successional forests lost organic matter and porosity with increasing elevation at the fastest rates. In contrast to the forested plots, neither soil organic matter nor soil porosity decreased with increasing elevation in reed canarygrass plots (Fig. 3).

Total organic carbon (TOC) displayed similar spatial patterns as soil organic matter, with the best AIC model consisting of the interaction between community type and elevation (Model 6, $AIC_w = 0.98$, $R^2 = 0.78$, $P < 0.001$). TOC was highest in low elevation plots, regardless of community type (~0.06 g C cm^{-3}), and declined with increasing elevation most rapidly in browsed early successional forests, at equally moderate rates in unbrowsed early and mature forest plots, and did not decline in reed canarygrass plots. Organic carbon constituted over 98 % of total carbon for all community types. Total nitrogen (TN) declined with increasing elevation similarly for all community types (Model 3, $AIC_w = 0.91$, $R^2 = 0.38$, $P = 0.003$). TOC:TN ratios depended on both community type and the interaction between community type and elevation (Model 5, $AIC_w = 0.82$, $R^2 = 0.65$, $P = 0.005$). Highest TOC:TN was observed in low elevation mature forest plots (~17) and declined with increasing elevation to approximately 13. Browsed and unbrowsed early successional forests showed a non-significant decline in TOC:TN with increasing elevation. TOC:TN increased from 14 to a high of 18 with increasing elevation in reed canarygrass plots.

The best AIC model for predicting mean daily soil temperature in July consisted of independent effects of community type and elevation (Model 4, $AIC_w = 0.91$, $R^2 = 0.41$, $P = 0.01$). Soil temperatures declined with increasing elevation in all community types, but mature forests maintained slightly cooler soil temperatures than the other types across the range of elevations. During August and September, mean daily soil temperature did not depend on either elevation or community type (Model 1, $AIC_w = 0.99$). The best model for daily temperature range (daily high minus daily low) consisted of the interaction between community type and elevation during all three months (Model 6, $AIC_w > 0.95$, $R^2 > 0.56$, $P < 0.001$). At the lowest elevations, soil temperatures fluctuated approximately 0.5 °C in July and 1.0 °C in August and September, regardless of community type. Factor-level reduction showed that rates of increase in daily soil temperature range with increasing elevation were most rapid in browsed early successional forests during each month, while the other community types showed equally slower rates of increase in temperature range with increasing elevation during each month.

Water filled pore space (wfps) was generally highest in July, immediately following the flood pulse and lower in August and September. The best model based on AIC for wfps in July consisted of the interaction between elevation and community type (Model 6, $AIC_w = 0.96$, $R^2 = 0.38$, $P = 0.02$). Factor-level reduction indicated that wfps increased with increasing elevation approximately equally in the browsed and unbrowsed early successional forests and this rate was greater than the rate of increase observed in the mature forest and reed canarygrass plots, which were also approximately equal. In August and September, wfps also increased with increasing elevation, but rates of increase were not different among community types (Model 3, $AIC_w = 0.99$, $R^2 = 0.19$, $P = 0.04$ in August and $AIC_w = 0.94$, $R^2 = 0.35$, $P = 0.005$ in September). Increases in wfps with elevation were caused by decreases in available pore space with increasing elevation (Fig. 3).

Effects of flooding and vegetation type on nitrification

The best model based on AIC for predicting the pool size of NH_4^+-N during July consisted of effects of community type and the interaction between community type and elevation (Model 5, $AIC_w = 0.95$, Fig. 4). Estimates of NH_4^+-N declined with increasing elevation in the forested plots, but from a higher y-intercept and at a faster rate in early successional forests as compared with mature forests. NH_4^+-N was uniformly low across all elevations in patches of reed canarygrass. In August and September NH_4^+-N was uniformly low across all elevations and ecosystem types (Model 1, $AIC_w = 0.99$, Fig. 4). Across all community types, nitrification rates were higher in July than in August or September ($P < 0.01$). The best model for predicting gross nitrification rates in July consisted of effects of community type and the interaction between community type and elevation (Model 5, $AIC_w = 0.96$, Fig. 4). Nitrification rates declined from a higher y-intercept, but at a faster rate with increasing elevation in the early successional forests (both browsed and unbrowsed) as compared with mature forests. However, nitrification rates in reed canarygrass patches were not affected by elevation (Fig. 4). In August and September, nitrification rates were uniformly low in all community types and elevations (Model 1, Fig. 4).

Spatial and temporal trends in NH_4^+-N in the forested plots could be explained as a function of the number of days that plots were unflooded (Fig. 5). We model this association with a hyperbolic decay function, which describes high initial pools of NH_4^+-N in forests (N_F), followed by a rapid rate of decline in NH_4^+-N with any increase in the number of days since flooding (D_{uf}):

$$N_F = \frac{23.05 \times 2.8}{2.8 + D_{uf}} \quad R^2 = 0.93,\ P < 0.001$$

A similar association was not found for reed canarygrass plots, as NH_4^+-N was uniformly low regardless of time since flooding ($P = 0.17$, Fig. 5). As for pool sizes of NH_4^+-N, patterns in nitrification could be explained as a function of the number of days that plots were unflooded (Fig. 5). We modeled associations between nitrification and days unflooded for all community types with a hyperbolic decay function:

$$N_{EF} = \frac{10.27 \times 5.2}{5.2 + D_{uf}} \quad R^2 = 0.37,\ P < 0.001$$

which describes a rapid decline in nitrification with increasing days since flooding.

Correlations between soil abiotic factors and nitrification rates

Across all community types, nitrification rates were positively associated with extractable NH_4^+-N ($r = 0.57$), which was the single best predictor of nitrification rates (Table 1). However, association strength varied by community type. Nitrification rates increased significantly with increasing NH_4^+-N in unbrowsed ($r = 0.66$), browsed ($r = 0.78$), and mature ($r = 0.51$) forest plots, but not significantly in patches of reed canarygrass ($r = 0.22$). The second best single predictor of nitrification rates across all community types was wfps ($r = 0.39$). The strength of association again varied by community type: significant unimodal associations were found for browsed early successional forest plots ($r = 0.55$) and patches of reed canarygrass ($r = 0.57$) and non-significant unimodal associations were found for unbrowsed early successional forests ($r = 0.42$) and mature forests ($r = 0.33$).

Extractable NH_4^+-N and wfps together explained 42 % of the variance in nitrification rates across all

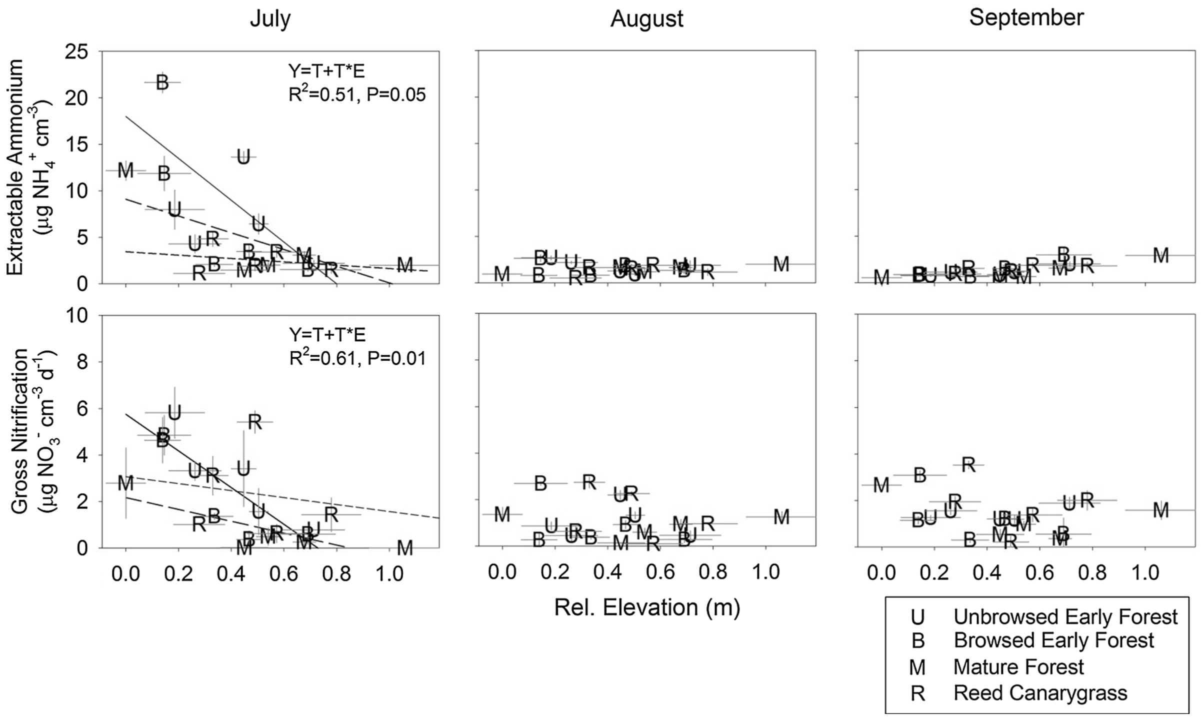


Fig. 4 Trends in extractable NH_4^+-N and potential gross nitrification rates with increasing elevation (E) for four community types (T). Data are means and SE of replicate samples from each plot. Model 5 (see methods) best explained patterns of extractable NH_4^+-N and gross nitrification rates during July. Extractable NH_4^+-N declined with increasing elevation at similar rates for the two early successional forest types in July (*solid black line*), at a slower rate for mature forests (*long dashes*) and was uniformly low in patches of reed canarygrass in July (*non-significant short dashes*). Gross nitrification declined with increasing elevation at a similar rate for both early successional forest types (*solid black line*) at a slower rate in mature forests (*long dashes*) and did not change with elevation in patches of reed canarygrass in July (*non-significant dashes*)

community types, with maximal rates occurring at intermediate wfps (∼40–60 %) and high NH_4^+-N (Fig. 6). Variables that explained additional variance in nitrification rates included total soil nitrogen and carbon, which together explained an additional 5 % of the variance in nitrification rates, and along with available NH_4^+-N and wfps, made up the best model based on AIC (Table 2). Although temperature was a significant predictor of nitrification rates alone (Table 1), it accounted for very little variance that was not accounted for by available NH_4^+-N or wfps (1–2 %, Table 2).

Models fit to individual community types accounted for more variance in nitrification rates than models fit without respect for community type. The best model based on AIC for predicting nitrification rates in unbrowsed early successional forests included extractable NH_4^+-N, wfps, and total nitrogen and carbon, and explained 84 % of the variance in nitrification rates. Temperature variables were most important in browsed early successional forests (Tables 1 and 2). The best model based on AIC for predicting nitrification rates in browsed forests included extractable NH_4^+-N, wfps, and both mean daily temperature and daily range in temperature, and explained 95 % of the variance in nitrification rates (Table 2). Total nitrogen or carbon was most important in mature forests (Tables 1 and 2). The best model for predicting nitrification rates in mature forests included extractable NH_4^+-N, wfps, and total nitrogen and carbon ($R^2 = 0.74$). Reed canarygrass was the only community type that did not include extractable NH_4^+-N as a component in the best AIC model for predicting nitrification rates (Table 2), likely due to the fact that NH_4^+-N exhibited little variation in reed canarygrass patches. The best model based on AIC

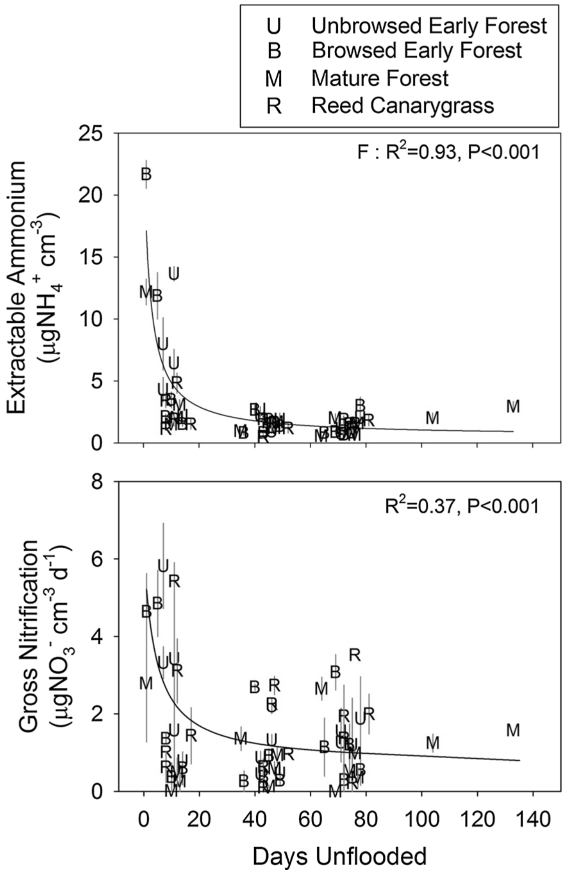


Fig. 5 Extractable NH_4^+-N and gross nitrification plotted as functions of the number of days separating soil sampling from the last day each plot was flooded. Data are means and SE of replicate samples. Extractable NH_4^+-N declined with increasing days unflooded similarly for all three forest types (*solid black line*) and was uniformly low in patches of reed canarygrass (*no line shown*). Gross nitrification declined similarly for all types (*solid black line*) with increasing days unflooded

included wfps alone, but this model only accounted for 33 % of the variance in nitrification rates. Inclusion of all variables in Table 1 improved model fit to $R^2 = 0.53$ for reed canarygrass patches, but there was little support for this model based on AIC weights (Table 2).

Discussion

The flood-pulse concept predicts that nutrient turnover will be faster in floodplain areas that experience periodic flooding, as compared with areas that are either permanently or rarely inundated (Junk et al. 1989). Of particular interest in floodplains is how inundation affects nitrification because nitrification represents a source of nitrate, which can be subsequently lost via leaching or denitrification (Baldwin and Mitchell 2000, Shrestha et al. 2012). As a result, floodplain management actions often focus on establishing patterns of river-floodplain connectivity that promote alternating wet-dry cycles (Craig et al. 2008, Kaushal et al. 2008; Welti et al. 2012). Our results generally support the flood-pulse hypothesis in the UMR floodplain, with the highest rates of nitrification typically occurring immediately following the spring flood and declining rapidly with increasing time since inundation. Therefore, efforts that promote river-floodplain connectivity along the UMR are likely to influence the nitrification potential of the floodplain.

Relative to the number of studies examining flood-pulse effects on nitrogen cycling, far fewer studies have examined how vegetation management actions might alter nutrient dynamics along floodplains. Studies from upland systems have indicated a strong potential for exotic species invasions to modify soil nutrient cycling (Windham and Ehrenfeld 2003), because they differ from native communities in biomass, productivity, tissue chemistry, and decomposition rates. In our study, *P. arundinacea*, an exotic grass, invaded areas that were formerly forested, leading to open grassland and corresponding differences in soil organic matter, porosity, nutrient availability, and the factors most strongly associated with nitrification. In comparison, young forests (both browsed and unbrowsed) had similar soil properties as remnant mature forests. These results suggest that vegetation management actions that alter aboveground plant communities have the potential to alter the soil environment and potentially modify the effects of flooding on nitrogen cycling.

Invasion modifies spatial patterns of soil properties

Differences in soil abiotic properties along floodplain elevation gradients may reflect long-term inundation frequencies. In our study, soils from low elevation forested sites (both remnant mature and early successional) had properties generally more favorable for nitrification as compared to higher elevation forested sites: higher porosity, total soil nitrogen, and warmer soil temperatures. Low elevation forested areas probably accumulate plant litter and other forms of

Table 1 Pearson correlation coefficients for associations between gross nitrification rates and each variable listed for 4 plant community types studied

Variable	Unbrowsed early forest	Browsed early forest	Mature forest	Reed canarygrass	All
Total nitrogen (g cm^{-3})	0.20	0.14	0.42	0.26	0.14
Total carbon (g cm^{-3})	0.03	0.10	0.47	0.24	0.06
C:N (molar)	**−0.53**	−0.24	0.17	0.07	−0.22
Mean daily temperature (°C)	0.41	0.20	−0.10	0.22	0.24
Mean daily temp range (high-low, °C)	−0.48	**−0.89**	−0.30	0.17	**−0.30**
Percent water filled pore space	0.42	**0.55**	0.33	**0.57**	**0.39**
Extractable ammonium (μg NH_4^+ cm^{-3})	**0.66**	**0.78**	**0.51**	0.22	**0.57**

Significant associations are shown in bold ($P < 0.05$)

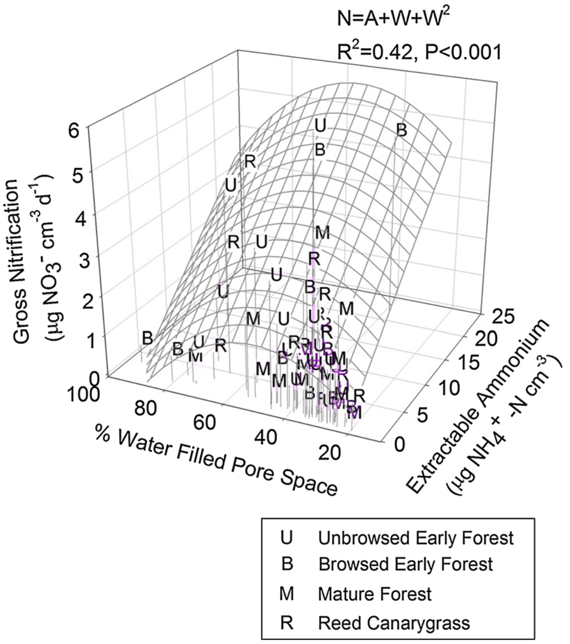


Fig. 6 Gross nitrification (N) increased with increasing extractable NH_4^+-N (A) and responded unimodally to increasing water filled pore space (W)

suspended organic material as flood waters recede, generally improving soil porosity and providing abundant organic matter for microbial processing. It should be pointed out that our study site was located far from the main channel of the UMR and is typically not subject to scour during flood events. Rather, flood waters gradually enter and exit the site and most likely slowly redistribute organic material.

In contrast to forest soils, invaded grassland patches maintained high soil organic matter and porosity across the full range of elevations sampled. Other studies have suggested that the accumulation of a year-round thick litter layer is a major factor controlling *Phalaris* invasion, due in part to its influence on soil resource availability (Eppinga et al. 2011). We suggest that this property is also key in removing elevational trends in soil abiotic factors seen in uninvaded forests. Whereas the leaf litter produced in high elevation forested areas can wash down to and accumulate in lower elevations during flood events, the litter produced by *Phalaris* is more likely to remain rooted and decompose in place. Also, we have observed a tendency for free floating plant material to become trapped by *Phalaris* during flooded conditions. The net effect of these phenomena appears to be that *Phalaris* patches are high in soil organic matter, carbon, and porosity, regardless of floodplain elevation. It is possible that invasion could over-ride the long-term effects of flooding on basic soil properties, resulting in a lack of spatial patterning along elevation gradients. Furthermore, the similar spatial patterns in soil properties found among all three forest types suggest that restoration of forest cover in areas invaded by *Phalaris*, should promote the recovery of soil properties to those observed in mature forests.

Short-term flood-pulse effects on nitrification

The short-term effects of flooding on N cycling play out across the spatial template of soil properties formed by longer-term flood frequencies and plant

Table 2 Table of R^2 and AIC weights for models predicting nitrification rates using backward stepwise regression

Community type	Model	R^2	AIC_w
All	W + W^2 + TN + TC + CN + T + R + A	0.51	0.09
	W + W^2 + TN + TC + CN + T + A	0.48	0.00
	W + W^2 + TN + TC + A	0.48	0.07
	W + W^2 + TN + TC + A	**0.47**	**0.83**
	W + W^2 + TN + A	0.42	0.00
	W + W^2 + TC + A	0.41	0.00
	W + W^2 + A	0.41	0.00
	W + W^2	0.15	0.00
	A	0.32	0.00
Unbrowsed early forest	W + W^2 + TN + TC + CN + T + R + A	0.87	0.00
	W + W^2 + TN + TC + CN + T + A	0.87	0.14
	W + W^2 + TN + TC + CN + A	0.85	0.19
	W + W^2 + TN + TC + A	**0.84**	**0.67**
	W + W^2 + TN + A	0.75	0.00
	W + W^2 + TC + A	0.74	0.00
	W + W^2 + A	0.74	0.00
	W + W^2	0.18	0.00
	A	0.43	0.00
Browsed early forest	W + W^2 + TN + TC + CN + T + R + A	0.95	0.00
	W + W^2 + TN + TC + T + R + A	0.95	0.00
	W + W^2 + TN + T + R + A	0.95	0.15
	W + W^2 + T + R + A	**0.95**	**0.85**
	W + W^2 + R + A	0.93	0.00
	W + W^2 + A	0.74	0.00
	W + W^2	0.29	0.00
	A	0.61	0.00
Mature forest	W + W^2 + TN + TC + CN + T + R + A	0.77	0.00
	W + W^2 + TN + TC + CN + T + A	0.76	0.01
	W + W^2 + TN + TC + CN + A	0.76	0.13
	W + W^2 + TN + TC + A	**0.74**	**0.54**
	W + W^2 + TN + A	0.67	0.02
	W + W^2 + TC + A	0.69	0.31
	W + W^2 + A	0.39	0.00
	W + W^2	0.11	0.00
	A	0.26	0.00
Reed canarygrass	W + W^2 + TN + TC + CN + T + R + A	0.53	0.00
	W + W^2 + TN + TC + T + R + A	0.53	0.00
	W + W^2 + TN + TC + R + A	0.41	0.00
	W + W^2 + TN + TC + A	0.39	0.00
	W + W^2 + TN + A	0.39	0.01
	W + W^2 + TN	0.36	0.08
	W + W^2 + A	0.33	0.02
	W + W^2	**0.33**	**0.89**
	A	0.05	0.00

Bold font is applied to the best AIC model. AIC weights are the probability that a given model is the best Kullback–Leibler model, given the data and set of candidate models shown (Burnham and Anderson 2001)

W water filled pore space (wfps), *TN* total nitrogen, *TC* total carbon, *CN* TN:TC ratio (molar), *T* mean daily temperature, *R* the daily range in temperature, *A* extractable NH_4-N (units for each variable are given in Table 1) community dynamics. Corresponding with the elevational differences in soil properties found in forested sites, the highest rates of potential gross nitrification were observed in the lower elevations immediately following the spring flood pulse (from 1 to 8 days post inundation). These high rates were later followed by a rapid decline in both NH_4^+-N and nitrification with increasing time since inundation (beyond 11 days post inundation). Although both NH_4^+-N and nitrification rates were comparatively lower in mature forests, the highest rate we observed in this community type was in the lowest elevation plot immediately following the flood. Mature terrestrial forests are known to support higher fine root densities and higher NH_4^+-N uptake rates than early successional forests (Vitousek et al. 1982), which may explain the reduced NH_4^+-N availability and post-flood nitrification rates in mature forests relative to early successional forests.

The initially high post-flood rates of nitrification in forested communities were due to increased availability of NH_4^+-N and the maintenance of moderate wfps (~40–60 %) in low elevation sites. These results support previous findings that nitrification rates increase with NH_4^+-N availability and respond unimodally to increasing wfps (Vitousek et al. 1982; Linn and Doran 1984; Parton et al. 1988, 1996; Strauss et al. 2002). Furthermore, nitrification rates in saturated soils commonly decrease after dewatering because of NH_4^+-N depletion, but also because nitrifying bacteria are sensitive to desiccation (Cavanaugh et al. 2006; Austin and Strauss 2011). Hence, both the longer term effects of flooding on soil properties and shorter-term effects of flooding on NH_4^+-N availability appear to work in concert to produce classical oscillations in nitrification in floodplain forests of the UMR: from inhibition of nitrification during prolonged flooded conditions, to maximal rates immediately following flooded conditions, and finally to a rapid decline in nitrification during the dry phase of the hydrograph. The similar flood-pulse dynamics observed among all three forest types suggests that restoration of forest cover is likely to correspond with recovery of this ecosystem function and we suggest that over time, the early successional forests studied here will begin to display the more damped oscillations in nitrification rates observed in mature forests.

Nitrification rates were also highest in *Phalaris* sites during July, suggesting that short-term inundation durations continue to play a key role in regulating N cycling in invaded grassland patches. However, high nitrification rates in July were found despite low NH_4^+-N availability, indicating that nitrification may depend more on NH_4^+-N made available via mineralization of organic matter during the incubation period, as opposed to the initial pool of available inorganic NH_4^+-N. The lack of a distinct pulse of available NH_4^+-N may reflect higher in situ nitrification rates during the flooded period that preceded our study, as *Phalaris* has been shown to oxygenate sediments and increase nitrification rates in streams (Forshay and Dodson 2011). Or, low NH_4^+-N may be due to high nutrient uptake rates. Conchou and Fustec (1988) documented high uptake rates by *Phalaris*, leading to the recommendation that it be used as a sink for nutrients in water treatment wetlands. Additionally, Edwards et al. (2006) showed that high root densities in *Phalaris* were associated with high rates of microbial nutrient accumulation. Thus, the dense litter layer found in *Phalaris* patches may support rapid organic–inorganic nutrient transformations, while the high root densities may be responsible for higher porosity and nutrient uptake rates, collectively leading to low inorganic N availability. Regardless of the cause of lower post-flood NH_4^+-N availability, our results suggest that invasion by *Phalaris* has the potential to modify the factors most limiting to nitrification in floodplain wetlands.

Despite high rates of herbivory by white-tailed deer, and strong effects on canopy openness and soil temperature, we observed little effect on nitrification rates when compared with unbrowsed early successional forests. Large herbivores can alter nutrient cycling in terrestrial forests by reducing plant height growth and survival, which often leads to an opening of the plant canopy and associated reductions in litter quantity and rates of nitrogen cycling that more than offset any nutrients added via dung and urine (Pastor et al. 1993; Butler and Kielland 2008). In our study, browsing probably reduced litter quantity, resulting in rapid losses of soil organic matter, porosity, and organic carbon with increasing elevation. However, effects of browsing on these soil properties were most pronounced at high elevations, where nitrification rates were uniformly low, regardless of plant community type. It is possible that herbivory has significant effects on the soil environment in high elevation floodplain areas, but any effect on nitrification appears to be offset by the lack of an effect of flooding. From a management perspective, the effects of herbivory in this ecosystem are probably most strong when they promote invasion by *Phalaris* (De Jager et al. 2013; Cogger et al. 2014), which as we have shown can influence soil properties.

Conclusions

Our results support the flood-pulse concept in the UMR floodplain, suggesting that management and restoration actions that promote alternating wet-dry conditions are also likely to promote rapid nitrogen transformations. Further, floodplain vegetation management actions that focus on transitions between forest cover and invasion by *Phalaris* could modify the spatial template of soil properties upon which annual flood-pulses operate. In particular, conversion of invaded areas to early successional forests is predicted to recover spatial patterns in soil organic matter and porosity that may have been altered by invasion. Future studies could account for other N transformation processes (e.g. denitrification) to gain a more complete understanding of how invasion, restoration, and river-floodplain connectivity might modify nutrient fluxes along large floodplain rivers.

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