SHORT COMMUNICATION

Effects of Flooding on Ion Exchange Rates in an Upper Mississippi River Floodplain Forest Impacted by Herbivory, Invasion, and Restoration

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Abstract We examined effects of flooding on supply rates of 14 nutrients in floodplain areas invaded by *Phalaris arundinacea* (reed canarygrass), areas restored to young successional forests (browsed by white-tailed deer and unbrowsed), and remnant mature forests in the Upper Mississippi River floodplain. Plant Root Simulator ion-exchange probes were deployed for four separate 28-day periods. The first deployment occurred during flooded conditions, while the three subsequent deployments were conducted during progressively drier periods. Time after flooding corresponded with increases in NO_3^--N, K^+ and Zn^{+2}, decreases in $H_2PO_4^--P$, Fe^{+3}, Mn^{+2}, and $B(OH)_4-B$, a decrease followed by an increase in NH_4^+-N, Ca^{+2}, Mg^{+2} and Al^{+3}, and an increase followed by a decrease for $SO_4^{-2}-S$. Plant community type had weak to no effects on nutrient supply rates compared to the stronger effects of flooding duration. Our results suggest that seasonal dynamics in floodplain nutrient availability are similarly driven by flood pulses in different community types. However, reed canarygrass invasion has potential to increase availability of some nutrients, while restoration of forest cover may promote recovery of nutrient availability to that observed in reference mature forests.

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Introduction

Flooding has traditionally been considered the main driver of soil nutrient dynamics in floodplains (Junk et al. 1989; Tockner et al. 2000; Junk and Wantzen 2004). Alternating wet/dry conditions stimulate rapid transformations of ions via changes in redox conditions and soil microbial communities (Thomas et al. 2009). Inundated (anoxic) conditions generally result in decreases in the oxidation state of most ions, while dry conditions generally promote increases in oxidation state. As a result, floodplains are known to undergo cyclical patterns in nutrient availability in response to seasonal flood dynamics (Junk et al. 1989).

Some nutrient transformations depend more on biotic mechanisms, while others rely more on abiotic processes (Mitsch and Gosselink 2007). Nitrogen (N) transformations are regulated by bacterial communities that can metabolize N either aerobically or anaerobically depending on soil saturation (Baldwin and Mitchell 2000; Olde Venterink et al. 2002). Phosphorus (P) transformations occur through biotic uptake, but they are also directly tied to physical and chemical processes related to soil redox conditions (Reddy et al. 1999; Darke and Walbridge 2000) and anaerobic microbial respiration (Roden and Edmonds 1997; Baldwin and Mitchell 2000). For example, iron-reducing bacteria convert ferric (Fe^{+3}) minerals to ferrous ions (Fe^{+2}) in anaerobic respiration, releasing P in the process, while sulfate-reducing bacteria reduce sulphate ions to hydrogen sulphide which reduces ferric oxides and causes more release of P (Baldwin and Mitchell 2000). Conversely, cycling of aluminum (Al) and other metals occurs mainly through abiotic processes (Gallardo 2003). As a consequence, biotic interactions that affect aboveground
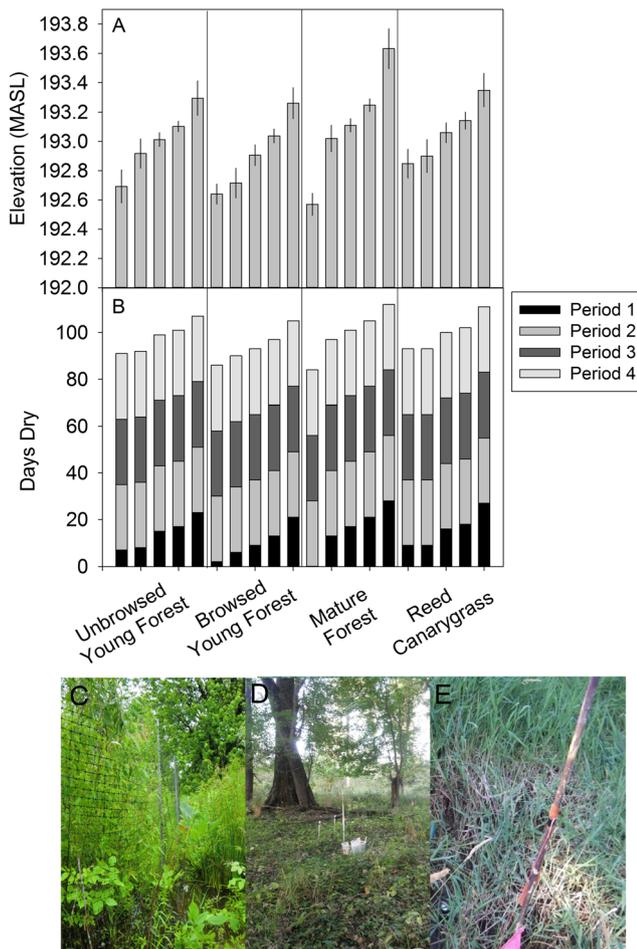
Fig. 1 Study plot characteristics. **a** Mean elevation (meters above sea level, ±1 standard error) of plots in four plant community types. **b** Cumulative number of days dry for each plot, grouped by time period. Picture depicts examples of all four communities: **c** exclosure delineating unbrowsed young-forest sites and browsed young-forest sites, **d** mature forest site, and **e** reed canarygrass site

plant and belowground microbial communities have the potential to influence some ion transformations more strongly than others. Yet few studies have examined effects of flooding on the transformation of a broad suite of biotically and abiotically regulated nutrients in contrasting floodplain plant communities.

Understanding the relative effects of flooding and vegetation type on a broad range of nutrients is important because floodplains are increasingly at risk of invasion by non-native plant species. Flooding provides a constant supply of invasive propagules to floodplains (Tockner and Stanford 2002), and the presence of these species can disrupt historical patterns of plant succession following large floods (Zedler and Kercher 2004). Overly abundant herbivore populations also modify plant communities across a range of ecosystems (Danell

et al. 1994), including floodplains (Butler and Kielland 2008). In the Upper Mississippi River floodplain, De Jager et al. (2013) showed that the combined effects of flooding and browsing by white-tailed deer can promote invasion by *Phalaris arundinacea* (reed canarygrass), a widespread invader of North American wetlands (Lavergne and Molofsky 2004). Herbaceous monocultures of reed canarygrass could affect nutrient availability via high uptake rates or rapid decomposition rates (Conchou and Fustec 1988; Edwards et al. 2006). Reed canarygrass is also known to develop a thick thatch layer—a characteristic that modifies soil organic matter and a suite of abiotic properties, including soil temperature and moisture (Ehrenfeld 2003). In the absence of reed canarygrass invasion, deer herbivory can still influence nutrient cycling directly via deposition of dung and urine (Ruess and McNaughton 1987), and indirectly by altering tree species composition and causing associated changes in litter quantity and quality (Pastor et al. 1993).

Information on how herbivory, invasive plants, and floodplain forest restoration might alter effects of flooding on the availability of different nutrients is minimal. To try to understand these relationships, we deployed Plant Root Simulator (PRS) probes (Western Ag Innovations, Saskatchewan, CA) to measure nutrient supply rates during flooded and progressively unflooded conditions in an Upper Mississippi River floodplain site. This site has experienced a series of plant management actions (Thomsen et al. 2012; De Jager et al. 2013) which have led to the development of four different plant community types: 1) areas invaded by reed canarygrass; 2) areas restored to young successional forests (browsed), 3) areas restored to young successional forests and protected from deer herbivory by exclosures (unbrowsed), and 4) remnant mature forests. We tested the hypotheses that flooding, invasion, and herbivory interact to modify nutrient availability, and that the restoration of forest cover and suppression of herbivory can restore nutrient availability to that observed in reference mature floodplain forests.

Methods

Study Site

The study took place at a floodplain site along the Mississippi River south of La Crosse, Wisconsin (43° 44.3' N, 91° 12.6'W). The site floods annually, with mean growing-season (April 1–Sept 30) flood durations lasting between 10 and 45 days depending on floodplain elevation (De Jager et al. 2013). In June 1998, straight-line

Table 1 Mean nutrient supply rate (±1 standard error) of all ions in each time period. Time periods that have the same letter are not significantly different. Nutrient supply rates are reported as µg $10\ cm^{-2}\ 4\ weeks^{-1}$

Ion	Period 1	Period 2	Period 3	Period 4	p-value
NO_3^--N	$7.6\pm1.4^{a,b}$	10.6 ± 4.2^a	$32\pm11^{b,c}$	47 ± 17^c	<0.01
NH_4^+-N	8.3 ± 1.0^a	1.5 ± 0.2^b	2.6 ± 0.3^c	5.2 ± 0.7^d	<0.01
$H_2PO_4^--P$	74 ± 9^a	12 ± 2^b	7.0 ± 0.9^b	9.6 ± 2.0^b	<0.01
K^+	17 ± 8^a	11 ± 3^a	72 ± 20^b	50 ± 10^b	<0.01
Ca^{+2}	2463 ± 91^a	1575 ± 30^b	$1933\pm95^{b,c}$	$2392\pm208^{a,c}$	<0.01
Mg^{+2}	594 ± 29^a	390 ± 15^b	496 ± 22^a	642 ± 53^a	<0.01
$SO_4^{-2}-S$	392 ± 64^a	806 ± 75^b	$570\pm92^{a,b}$	448 ± 66^a	<0.01
Fe^{+3}	436 ± 33^a	160 ± 14^b	57 ± 7^c	66 ± 20^c	<0.01
Cu^{+2}	1.3 ± 0.2	1.3 ± 0.1	1.2 ± 0.2	1.8 ± 0.4	n.s.
Mn^{+2}	78 ± 9^a	11 ± 1^b	3.7 ± 0.3^c	4.5 ± 0.8^c	<0.01
Zn^{+2}	3.4 ± 0.6	3.5 ± 0.7	4.0 ± 0.7	4.8 ± 0.6	n.s.
$B(OH)_4^--B$	1.7 ± 0.2^a	0.6 ± 0.1^b	0.7 ± 0.1^b	0.9 ± 0.1^b	<0.01
Pb^{+2}	1.4 ± 0.2	0.9 ± 0.2	1.2 ± 0.2	1.8 ± 0.3	n.s.
Al^{+3}	56 ± 3^a	23 ± 2^b	30 ± 3^b	55 ± 4^a	<0.01

winds blew down approximately 4.2 ha of forest within the site, and reed canarygrass quickly invaded the entire open area. Herbicide applications eliminated reed canarygrass from some areas by 2009, allowing a young forest consisting of *Acer saccharinum* (silver maple), *Fraxinus pennsylvaticus* (green ash), *Salix exigua* (sandbar willow), *S. nigra* (black willow) and *Populus deltoides* (eastern cottonwood) to establish (Thomsen et al. 2012). In 2009, five 20×20 m deer exclosures were constructed at the young forest site, eliminating deer herbivory within exclosures from Nov. 2009 to at least the end of 2012 (De Jager et al. 2013). During this time, browsing rates outside of the exclosures ranged from 0 to 85 % of all available stems from winter 2009 through fall 2012 (De Jager et al. 2013). Further site description and study results are available in Thomsen et al. (2012) and De Jager et al. (2013).

For this study, we selected five monoculture reed canarygrass plots (20×20 m), five exclosure plots in young forest (unbrowsed plots), five unfenced young forest plots (browsed plots), and five mature forest plots which were located along the edge of the canopy gap that was created in 1998 (Fig. 1). Plots from all four treatments captured the full elevation gradient of the floodplain, which was about 1 m (Fig. 1a). A previous study conducted at the same study site (De Jager et al., accepted) showed that soils from reed canarygrass plots tended to have lower soil bulk density and higher soil organic matter and porosity compared to soils from the three forest community types. Total nitrogen and carbon were lower in reed canarygrass plots as compared with the unbrowsed young forest and mature forest plots, but similar to estimates from the browsed young forest

plots. These previous results suggested that the availability of other ions may also differ by community type.

Nutrient Sampling

PRS probes were deployed at each plot in the 0–15 cm soil layer on June 19, 2012. PRS probes consist of an ion-exchange membrane housed in a plastic probe. Anion probes have a positively-charged membrane to attract and adsorb all negatively-charged anions, while cation probes have a negatively-charged membrane to adsorb all positively-charged cations. Ions adsorb to the surface of the probes at a rate dependent on their activity and diffusion rate in the soil solution, thus PRS probes provide a measure of nutrient supply rate that correlates to the in situ nutrient pool available to plants (Qian and Schoenau 2002). For this study, separate anion and cation probes were placed in three subplots nested within each plot. All probes were later composited to provide a single measure for each plot. The anions measured were NO_3^--N, $SO_4^{-2}-S$, $H_2PO_4^--P$, and $B(OH)_4^--B$, and the cations measured were K^+, Fe^{+3}, NH_4^+-N, Ca^{+2}, Mn^{+2}, Al^{+3}, Mg^{+2}, Cu^{+2}, Pb^{+2} and Zn^{+2}. After 28 days, we extracted all PRS probes and inserted new ones in different locations within each subplot. This process was repeated for a total of four deployments, with the last set of probes collected on October 10.

Probes were shipped to Western Ag Innovations for analyses. Probes were eluted for one hour with a 0.5 N HCl solution. The eluate was analyzed for NO_3^--N and NH_4^+-N by colorimetry using an automated flow injection analysis system. For all other ions, the eluate was analyzed using inductively-coupled plasma spectrometry.

Data Analysis

During the spring flooding period which lasted from May through mid-July, all study plots were inundated except for one mature forest plot situated at the highest elevation (Fig. 2). We calculated the number of days that each plot was flooded and unflooded between the start of the experiment on June 19 to the time PRS probes were extracted. For example, the lowest elevation plot was flooded until July 16. As a result, the number of days since inundation (days dry) at the time of July sampling ranged from 0 days in the lowest elevation plot to 28 days in the highest elevation plot (Fig. 1b). After the first time period, all plots remained dry for the remainder of the study.

We initially conducted a two-way analysis of variance (ANOVA) with post-hoc Tukey tests for each ion to determine if there were significant differences ($\alpha=0.05$) among time periods and among community types, using SAS version 9.4 (SAS 2013). Because site elevation and spatial heterogeneity likely played a role in nutrient supply rate within plant communities, we also conducted analyses of covariance (ANCOVA) to determine if there were significant differences among community types after accounting for dry days as a covariate. Variables were also regressed against days dry to determine if there was a significant change over time. Both linear and non-linear regressions were fit to the data, and the regression that produced the highest R^2 and was significant was determined to be the best fit for the particular variable. All variables were log-transformed ($\ln(x)$) to meet assumptions of normality and homogeneity of variances. Nitrate, $B(OH)_4^--B$, NH_4^+-N, Mn^{+2}, Cu^{+2}, Pb^{+2}, and Zn^{+2} were log-transformed ($\ln(x+1)$) prior to analyses because some values were less than one.

We also conducted non-metric multi-dimensional scaling (NMDS) in PRIMER-E version 6 (Clarke and Gorley 2006) to distinguish differences in supply rate among community types and time periods based on Euclidean distance.

We further examined multivariate differences among time periods and community types using two-way Analysis of Similarities (ANOSIM). The log-transformed nutrient supply rates were used to generate a Euclidean distance matrix for ANOSIM analysis.

Results

Univariate Analysis

During the transition from flooded to unflooded conditions, nutrient supply rates for all ions except Cu^{+2}, Zn^{+2}, and Pb^{+2} were significantly different among the time periods (Table 1). Within increasing time since flooding, nutrient supply rates decreased for $H_2PO_4^--P$, Fe^{+3}, Mn^{+2}, and $B(OH)_4^--B$, whereas supply rates increased for NO_3^--N and K^+ (Fig. 3). Supply rates for NH_4^+-N, Ca^{+2}, Mg^{+2}, Al^{+3} and $SO_4^{-2}-S$ differed among time periods (Table 1) but there were no clear unidirectional trends with days dry (Fig. 3).

The two-way ANOVA suggested that supply rates for $H_2PO_4^--P$, Fe^{+3}, K^+, NO_3^--N, and Mn^{+2} differed significantly among community types (Table 2), with reed canarygrass plots having higher rates compared to some forest plots (Tukey pairwise tests, $p<0.05$). However, when days dry was accounted for in the ANCOVA analyses, community types did not differ and changes in nutrient supply rates were best characterized by days dry alone (Table 2). Based on fitted regression curves (Table 2, Fig. 3), four types of supply-rate responses could be identified with respect to days dry: 1) NO_3^--N, K^+, and Zn^{+2} increased, 2) $H_2PO_4^--P$, Fe^{+3}, Mn^{+2}, and $B(OH)_4^--B$ decreased, 3) NH_4^+-N, Ca^{+2}, Mg^{+2}, and Al^{+3} initially declined following flooded conditions and later increased during the driest period, and 4) $SO_4^{-2}-S$ increased but then decreased again.

Multivariate Analyses

The NMDS analysis also showed a distinct separation in the study plots by time (Fig. 4). The majority of plots from period one were clustered in the upper left corner of the NMDS array and more closely associated with flooded conditions (dark blue to purple background), plots from period 2 were generally clustered in the upper right corner, while plots from periods 3 and 4 were in the lower portion of the NMDS array and associated with longer durations of unflooded conditions (orange and red background). During flooded conditions, all study plots had relatively high NH_4^+-N, $H_2PO_4^--P$, Fe^{+3}, and Mn^{+2}, which decreased when the site dried. Nitrate and K^+ increased after the site dried, whereas NH_4^+ Ca^{+2}, Mg^{+2} and Al^{+3} decreased when the site first dried out (between periods

Fig. 2 Daily water surface elevation (*thick line*) and precipitation (*vertical bars*) during the study period. Thin *horizontal lines* represent the lowest and second highest study plot elevations, excluding one outlier plot at 193.63 MASL that never flooded. *Dots* represent dates of PRS probe deployment, with numbers corresponding to four successive time periods

Table 2 P-values for effects of plant community type and the days dry covariate from ANOVA and ANCOVA analyses, and best-fit regressions of nutrient supply rate on days dry. *n.s.* not significant

Ion	Community Type Effect (ANOVA)	Community Type Effect (ANCOVA)	Days Dry Covariate (ANCOVA)	Best-Fit Regression on Days Dry	Regression R^2
NO_3^--N	0.03	n.s.	<0.01	$\ln(y+1)=0.0154x+1.5156$	0.1622
NH_4^+-N	n.s.	n.s.	n.s.	$\ln(y+1)=0.0004x^2 - 0.0461x+2.4904$	0.3687
$H_2PO_4^--P$	0.02	n.s.	<0.01	$\ln(y)=0.0006x^2 - 0.0876x+5.0503$	0.6176
K^+	<0.01	n.s.	<0.01	$\ln(y)=0.0216x+1.746$	0.4190
Ca^{+2}	n.s.	n.s.	n.s.	$\ln(y)=0.0001x^2 - 0.0125x+7.845$	0.1159
Mg^{+2}	n.s.	n.s.	n.s.	$\ln(y)=0.0001x^2 - 0.0112x+6.3787$	0.1445
$SO_4^{-2}-S$	n.s.	n.s.	n.s.	$\ln(y)=-0.0009x^2+0.0327x +5.5144$	0.1351
Fe^{+3}	0.02	n.s.	<0.01	$\ln(y)=-0.028x+6.2054$	0.6489
Cu^{+2}	n.s.	n.s.	n.s.	$\ln(y+1)=0.0016x+0.7056$	0.0188
Mn^{+2}	0.03	n.s.	<0.01	$\ln(y+1)=0.0004x^2 - 0.0784x+5.0066$	0.7834
Zn^{+2}	n.s.	n.s.	n.s.	$\ln(y+1)=0.0059x+1.1154$	0.1155
$B(OH)_4^--B$	n.s.	n.s.	n.s.	$\ln(y+1)=0.0001x^2 - 0.0176x+1.0984$	0.3051
Pb^{+2}	n.s.	n.s.	n.s.	$\ln(y+1)=0.002x+0.6445$	0.0245
Al^{+3}	n.s.	n.s.	n.s.	$\ln(y)=0.0003x^2 - 0.0355x+4.232$	0.3380

one and two) but increased throughout the rest of the growing season (Fig. 3). ANOSIM indicated that there were significant differences among the four time periods (Global $R=0.588$, $p=0.001$), but no effect of community type (Global $R=0.015$, $p=0.35$) suggesting that across all ions, nutrient supply rates were similar among community types and most strongly driven by changes in flooding.

Discussion

Flooding influenced the availability of soil nutrients similarly in all four plant community types studied in this floodplain site, as we detected no interactive effects between flooding and plant community type. Instead, we observed different patterns in nutrient availability during flooded conditions compared to the dry period as supply rates for ten nutrients significantly changed throughout the growing season. Flooding is known to be a major determinant of ion availability and distribution in floodplain soils (Baldwin and Mitchell 2000; Olde Venterink 2002). Nutrients in the soil are cycled mainly by biological and geological processes that are different for each ion (Van Cappellen 2003). These differences suggested the hypothesis that some nutrients might be more strongly influenced by invasion, herbivory, or forest restoration effects on aboveground plant communities. However, flooding may act as the main driver of both biological and geological processes by changing the oxidation status of the soil, making the soil more anaerobic, and increasing the weathering of mineral particles (Gallardo 2003). As flood waters recede, soils become more oxidized, resulting in further nutrient transformation. Although our study design did not strictly control for effects

of flooding, our results are consistent with current understanding of how inundation influences nutrient availability in floodplains (Reddy and D'Angelo 1994; Mitsch and Gosselink 2007). Changes in the N ions with time since inundation suggested that aerobic conditions promoted nitrification of NH_4^+-N to NO_3^--N as well as more available SO_4^{-2}-S from microbial sulfur oxidation. Decreasing Mn^{+2} suggested increased microbial and abiotic oxidation to Mn^{+4}, and declining levels of both Fe^{+3} and $H_2PO_4^-$-P suggested that co-precipitation occurred.

While there were distinct differences in nutrient supply rates during wet and dry conditions, plant community type had little apparent influence: only five nutrients differed among communities in the initial ANOVA analysis, but not when time period was accounted for as a covariate. To the extent that $H_2PO_4^-$-P, NO_3^-, K^+, and Fe^{+3} may have been slightly more available in reed canarygrass plots than in some of the forested plots, a possible reason is greater organic matter decomposition. Reed canarygrass plots tended to have greater soil organic matter than the forested plots (De Jager et al., accepted), and reed canarygrass litter has a lower C:N ratio (~21) compared to tree litter (~27) (W. Swanson, unpublished data), both of which could contribute to faster decomposition rates. Hence, differences in litter quantity and quality may promote elevated nutrient concentrations in invaded areas. Such increases in nutrient availability may further promote the growth and persistence of reed canarygrass, similar to other aggressive invaders (Ehrenfeld 2003).

Although high herbivory rates occurred in our browsed forest plots (De Jager et al. 2013), we did not observe any differences in nutrient supply rates between the browsed and unbrowsed plots. Deer and other large herbivores can add
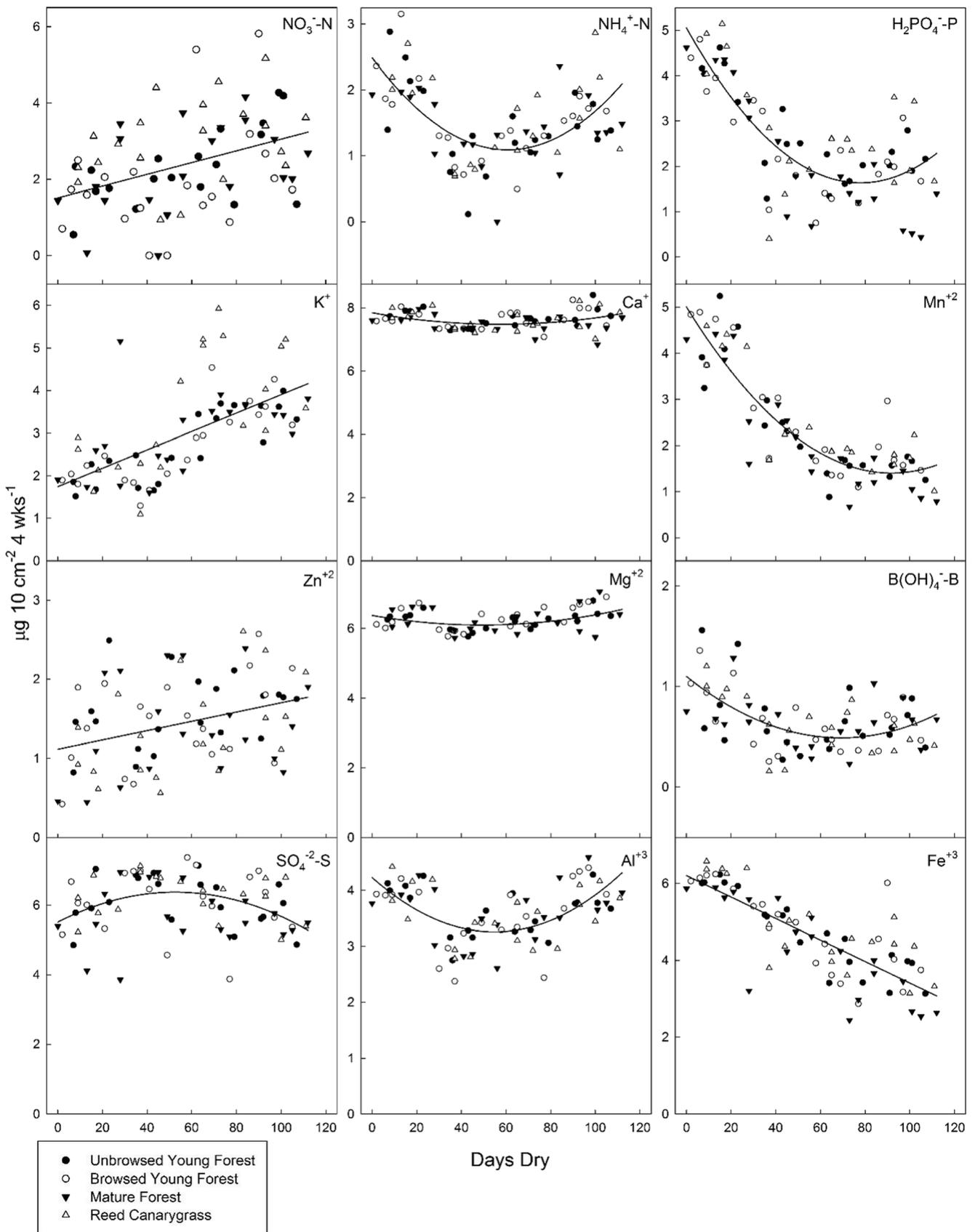
◀ **Fig. 3** Relationship of days dry to nutrient supply rate for each ion at the study plots, with plots of all community-types combined for analysis. *Fitted lines* represent the linear or nonlinear model that provided the largest R^2 value for the data and was significant. Fitted regressions and R^2 are provided in Table 2. Only variables that had significant regressions are shown

nutrients to the soil via fecal input (Butler and Kielland 2008) or remove available nutrients through grazing or browsing that reduces inputs to the litter layer (Pastor et al. 1993; Danell et al. 1994). In this study, it appears that any subtle herbivory effects were overridden by the strong effects of flooding on nutrient availability.

We also found no notable differences in nutrient supply rates between mature forest plots and browsed young successional forests. The similarities are somewhat surprising given that nutrient content often differs between old and young forests (Schwendenmann 2000). Thus, our results suggest that restoration of forest cover may promote rapid recovery of nutrient exchange dynamics. Forest acreage in the Upper Mississippi River basin has drastically declined since European settlement due to anthropomorphic factors such as timber harvesting and river hydrological modifications (Yin et al. 1997). Restoring floodplain forests is important because forests deliver many ecosystem services to the riverine community including providing critical habitat for migratory birds (Knutson et al. 2005), and stabilizing soil to reduce erosion during flooding (Goodwell et al. 2014).

Ion-exchange resins provide an efficient and affordable way to simultaneously measure the availability of a broad suite of nutrients (Qian and Schoenau 1996). However, ion-exchange resins only provide an index of plant nutrient availability that is correlated with, but not directly comparable to, chemical extractions (Qian et al. 1992). Thus, it is difficult to

quantitatively compare measurements made among studies. Nutrient supply rates also depend on the duration of deployment and the environmental conditions of the soil (Qian and Schoenau 2002). We standardized our deployments to 28 days, a duration found to be sufficient for the accumulation of a broad range of ions and for detecting differences among experimental treatments (Drohan et al. 2005). However, it could be argued that the changing environmental conditions during our study influenced the effectiveness of the PRS probes. Although we cannot rule this out, our results were consistent with prior understanding of nutrient transformations during anaerobic and aerobic conditions, suggesting that ion-exchange resins are a valid means of detecting flood-pulse effects on nutrient availability.

In conclusion, our study suggests that flood duration influences nutrient supply rates in the Upper Mississippi River floodplain more than plant community composition. Nutrient cycling has a large effect on this riverine ecosystem because the floodplain may be a source or a sink for nutrients (Junk et al. 1989). Available nutrients in floodplain soils can be flushed into the river during flooding (Kreiling et al. 2013). High loading of nutrients spurs localized eutrophication and algal blooms (Houser and Richardson 2010), and the load can be transported to the Gulf of Mexico where it contributes to forming the large annual hypoxic zone (Turner et al. 2008). Meanwhile, nutrients that are transported to the floodplain during floods can be taken up by plants and other organisms, cycled through various microbial processes, or can be incorporated into the soil matrix (Johnston 1991; Kreiling et al. 2013). Thus it is important for managers to identify potential areas and time periods where increased biogeochemical cycling may be occurring (McClain et al. 2003) and also to identify areas of potential nutrient release. Our results suggest that nutrient dynamics could be modeled at larger scales by simply relating nutrient supply rates from localized areas of known elevation to the hydrograph, making it possible to identify potential locations and times of rapid nutrient transformation.
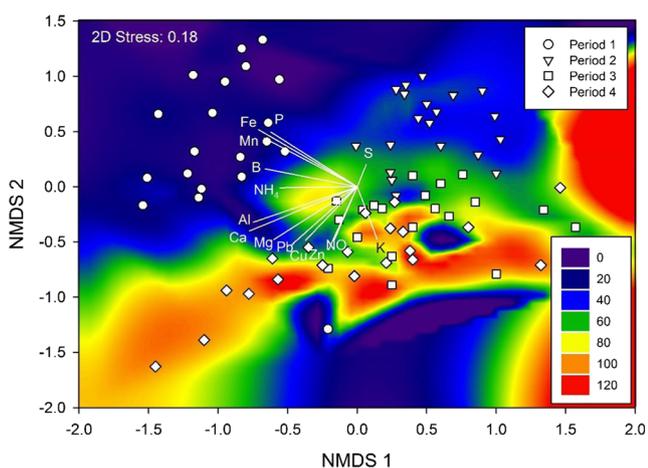
Fig. 4 Non-metric multi-dimensional scaling (NMDS) ordination of nutrient supply rates in twenty floodplain plots during four time periods. Vectors represent the correlation of each ion to the ordination coordinates. The background is a color-coded contour plot showing the distribution of dry days associated with each study plot/time combination

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