Received: 6 January 2017 | Revised: 29 April 2017 | Accepted: 29 May 2017

DOI: 10.1002/eco.1877

WILEY

RESEARCH ARTICLE

Effects of flood inundation and invasion by *Phalaris arundinacea* on nitrogen cycling in an Upper Mississippi River floodplain forest

Whitney Swanson[1] | **Nathan R. De Jager**[2] | **Eric Strauss**[1] | **Meredith Thomsen**[3]

[1] Biology Department and River Studies Center, University of Wisconsin-La Crosse, 1725 State St., La Crosse, WI 54601, USA

[2] US Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI 54603, USA

[3] Biology Department, University of Wisconsin La Crosse, 1725 State St., La Crosse, WI 54601, USA

Correspondence
Whitney Swanson, Biology Department and River Studies Center, University of Wisconsin-La Crosse, 1725 State St., La Crosse, WI 54601, USA.
Email: swanson.w22@gmail.com

Funding information
U.S. Army Corps of Engineers; U.S. Army Corps of Engineers' Upper Mississippi River Restoration Program

Abstract

Although floodplains are thought to serve as important buffers against nitrogen (N) transport to aquatic systems, frequent flooding and high levels of nutrient availability also make these systems prone to invasion by exotic plant species. Invasive plants could modify the cycling and availability of nutrients within floodplains, with effects that could feedback to promote the persistence of the invasive species and impact N export to riverine and coastal areas. We examined the effect of flooding on soil properties and N cycling at a floodplain site in Pool 8 of the Upper Mississippi River with 2 plant communities: mature native forest (*Acer saccharinum*) and patches of an invasive grass (*Phalaris arundinacea*). Plots were established within each vegetation type along an elevation gradient and sampled throughout the summers of 2013 and 2014. Spatial trends in flooding resulted in higher soil organic matter, porosity, and total nitrogen and carbon in low elevations. Nutrient processes and NH_4^+ and NO_3^- availability, however, were best explained by vegetation type and time after flooding. *Phalaris* plots maintained higher rates of nitrification and higher concentrations of available NH_4^+ and NO_3^-. These results suggest that invasion by *Phalaris* may make nitrogen more readily available and could help to reinforce this species' persistence in floodplain wetlands. They also raise the possibility that *Phalaris* may decrease floodplain N storage capacity and influence downstream transport of N to coastal zones.

KEYWORDS

disturbance, flood pulse, floodplain restoration, nitrogen, nitrogen cycling, *Phalaris arundinacea*, Upper Mississippi River

1 | INTRODUCTION

Excess nitrogen can easily move between terrestrial and aquatic ecosystems. For example, pools of excess nitrogen (N) in soil often accumulate as highly mobile nitrate (NO_3^-), which can be leached from soil through groundwater or run-off, and are partly responsible for nutrient pollution within streams and rivers (Aber, Nadelhoffer, Steudler, & Melillo, 1989; Galloway et al., 2008; Vitousek et al., 1997). Excess nutrients are transported downstream to coastal areas where nutrient pollution can cause eutrophication and "dead zones" (Howarth, 2008; Rabalais, 2002). However, floodplains can act as buffers between terrestrial and aquatic ecosystems by providing both nutrient storage in the form of organic matter and rapid biogeochemical cycling driven by spatial and temporal inundation patterns. Oscillating periods of wet and dry soil conditions promote different nitrogen cycling processes (Austin & Strauss, 2011; Hefting et al., 2004; Koschorreck & Darwich, 2003; Peralta, Ludmer, & Kent, 2013). Newly aerobic soils following the end of a flood support mineralization (the microbial conversion of organic N to NH_4^+) and nitrification (the microbial conversion of NH_4^+ to NO_2^- and then NO_3^-). Ammonium (NH_4^+) can be assimilated and stored in plant and microbial biomass. Nitrate also can be assimilated into biomass, leached from soil, or used as an energy source in dissimilatory reduction, that is, denitrification. Subsequent flooding leads to anoxic soil conditions caused by high anaerobic microbial respiration and/or decreased oxygen diffusion, thus promoting the release of gaseous N from the ecosystem via denitrification and reducing its downstream transport (Pinay et al., 2007). In well-connected river–floodplain systems, alternating wet–dry conditions and associated nutrient cycling processes may help to reduce effects of N enrichment.

N enrichment can also lead to local effects on species interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008). Invasion by nutrient-responsive plant species, for instance, has been shown to decrease the diversity and abundance of slower-growing native plants adapted to nutrient-poor conditions (Gilliam, 2006). Furthermore, some invasive species alter nutrient cycling (Alldred, Baines, & Findlay, 2016) and other important ecosystem functions, creating positive feedbacks, which promote their continued dominance (Gaertner et al., 2014; Hawkes, Wren, Herman, & Firestone, 2005; Suding & Hobbs, 2009). Nutrient-rich floodplains are highly vulnerable to invasion by exotic species (Hughes, Colston, & Mountford, 2005; Kercher & Zedler, 2004), and it is unclear how invasion might alter the capacity of floodplains to serve as nutrient buffers. Invasive plant species directly affect and are affected by N availability via their demand for nitrogen (Martina, Hamilton, Turetsky, & Phillippo, 2014; Vitousek, Walker, Whiteaker, Mueller-Dombois, & Matson, 1987) and by the quantity and nutrient content of their biomass and subsequent decomposing litter (Elgersma, Yu, Vor, & Ehrenfeld, 2012). Many invasive species have relatively high-N uptake rates, which allow them to grow more quickly and outcompete native species in high-N environments. Higher N uptake rates also result in litter with low C:N ratios, which decomposes rapidly and leads to further increases in soil N availability. Invasive species can indirectly influence N cycling by modifying the soil microclimate, including temperature and water availability, and by modifying the soil microbial community and activity in the rhizosphere (Ehrenfeld, 2003; Hawkes et al., 2005; Kao-Kniffin & Balser, 2010). N cycling, however, varies greatly among different ecosystems, and effects of invasion on N cycling in floodplain environments need to be addressed in the context of spatial and temporal patterns of flood inundation.

Phalaris arundinacea (reed canarygrass) is a strong competitor in wetlands across North America (Kercher, Herr-Turoff, & Zedler, 2007; Lavergne & Molofsky, 2004). Numerous attributes make *Phalaris* a strong competitor, including a high tolerance for variations in temperature, moisture, and nutrient availability, as well as multiple means of reproduction (Lavergne & Molofsky, 2004). Many studies have shown that *Phalaris* thrives in areas of elevated nitrogen availability (Wetzel & van der Valk, 1998; Green & Galatowitsch, 2001), which may explain high rates of invasion by *Phalaris* in the Upper Mississippi River (UMR) floodplain. *Phalaris* rapidly colonizes UMR forest canopy gaps, and it has been shown to suppress the growth of native herbaceous and woody species (Thomsen, Brownell, Groshek, & Kirsch, 2012). There is widespread concern about invasion of UMR floodplain forests by *Phalaris* due to its negative effect on community diversity (Reinhardt Adams, Kauth, & Sorenson, 2011; Romano, 2010; Thomsen et al., 2012), but little information exists regarding its effects on ecosystem functions, such as nutrient cycling.

Recent studies have attempted to identify the effects of invasion and forest restoration actions on N cycling by contrasting the effects of flooding on soil abiotic properties, nutrient availability, and potential nitrification rates in UMR floodplain forests and patches invaded by *Phalaris* (De Jager, Swanson, Strauss, Thomsen, & Yin, 2015; Kreiling, De Jager, Swanson, Strauss, & Thomsen, 2015). Both studies showed that early and late successional forests had soil properties less favourable for nitrification as elevation increased, due to decreasing organic matter, porosity, total nitrogen, and temperature, reflecting long-term effects of flood inundation on sedimentation and organic matter accumulation. In contrast, *Phalaris* patches maintained high soil organic matter and porosity as floodplain elevation increased. *Phalaris* may increase soil organic matter because the grass remains rooted and decomposes in place, unlike leaf litter from forested areas, which may be transported to aquatic areas. In addition, *Phalaris* may trap suspended organic matter during flooded conditions, further increasing soil organic matter. Studies conducted in other environments have shown that *Phalaris* can block slow-moving water channels with its thick biomass, resulting in sediment accumulation (Forshay & Dodson, 2011). De Jager et al. (2015) showed that neither ammonium availability nor nitrification rates depended on floodplain elevation in *Phalaris* sites, whereas both measurements correlated with elevation in forested sites. Thus, *Phalaris* may sustain high nitrification rates across the floodplain elevation gradient, whereas nitrification is more spatially dependent and generally slower in mature floodplain forests. Although greater nitrification rates indicate that *Phalaris* has the potential to increase rates of nitrate production, its effects on nutrient availability and processing rates must be examined within the context of flood inundation.

Despite our current understanding of the effects of invasion on soil properties, the stochastic nature of flood inundation makes it difficult to identify when and where invasion is most likely to impact ecosystem processes. Differences in the timing and magnitude of peak river flows could alter flood inundation dynamics in ways that produce different patterns in plant growth and uptake, decomposition, and N cycling from 1 year to the next. It is possible that effects of invasion by *Phalaris* are more pronounced during years or times more weakly impacted by flood inundation. It is thus important to conduct studies that span multiple years and multiple flood events. For this reason, we extended the temporal extent of previous studies conducted at the same floodplain site in the UMR (De Jager et al., 2015; Kreiling et al., 2015). Specifically, we examined nitrogen cycling in areas dominated by mature stands of silver maple as well as adjacent open grassland patches of *Phalaris* throughout the growing seasons of 2013 and 2014, to examine how effects of invasion may differ during years of different flood patterns. In addition, we measured in situ rates of litter decomposition and nitrogen mineralization, which had not previously been measured at the site, to determine if invasion influences actual rates of N transformation in the field. The questions we addressed were as follows: (a) How do soil abiotic properties differ between native floodplain forests and herbaceous *Phalaris* monocultures, and how do such differences influence nitrogen cycling, such as litter decomposition, N mineralization, and nitrification? (b) How do temporal and spatial patterns in flood inundation affect these processes, and do the effects of flooding differ by vegetation type? (c) Which abiotic factors have the strongest influence on N processing measurements, and are these consistent between the two plant communities?

2 | METHODS

2.1 | Study area

The study area was located at a floodplain site in Navigation Pool 8 of the UMR owned by the U.S. Army Corps of Engineers (USACE) south

of La Crosse, Wisconsin (43° 44.3′ N, 91° 12.6′W). The site was situated along a backwater channel of the river that experiences seasonal spring–summer flooding, which typically lasts through mid-July (Figure 1). In the late 1990s, a high wind event created a large canopy gap within the study area, which was subsequently colonized by *P. arundinacea* (reed canarygrass). Although *Phalaris* is known to invade N rich sites (Green & Galatowitsch, 2001; Wetzel & van der Valk, 1998), the entire canopy gap was fully invaded due to the enhanced light availability and regardless of spatial variability in N availability. Our study used an established strip of mature forest, dominated by silver maple and a series of remaining adjacent canopy gaps, each consisting of 100% reed canarygrass cover.

Five 9 m^2 plots were established within each vegetation type to examine effects of invasion. Effects of flooding were examined both spatially and temporally by situating the series of plots along an elevation gradient (approximately 0.7 m in total) and by sampling across the spring–summer hydrograph. Sampling began in July, immediately following the end of the spring floods of 2013 and 2014, with the first soil samples collected on the first day that plots were accessible (Figure 1). Thereafter, sampling occurred monthly through the end of the growing seasons (September). We estimated the water surface elevation at the study site using linear regression between the nearest upstream and downstream gages. In addition, we used repeated site visits to measure flooding depths and durations for each plot.

2.2 | Data collection and laboratory analysis

Each sampling event included collecting at least 200 g of top soil within each plot. Three soil cores (5 cm diameter and 5 cm depth) were extracted randomly throughout each plot, composited and homogenized in one polyethylene bag per plot, and refrigerated until laboratory analyses. Soils were used to measure a series of abiotic properties, exchangeable N concentrations (NH_4^+ and NO_3^-), and gross rates of nitrification. Five additional cores (2.5 cm diameter and 5 cm depth) were extracted and immediately placed into polyethylene bags and then reinserted into the same location from which they were taken to incubate for 28 days in order to measure in situ rates of net mineralization and net nitrification (buried bag technique; Robertson, Wedin et al., 1999b). All soil extractions were performed within 48 hr of soil sampling. Extracts were refrigerated until analyses were performed, which was typically within 1 to 2 weeks, and never exceeded 4 weeks. A temperature data logger (Onset HOBO Water Temp Pro v2) was also deployed at each plot to monitor soil temperatures at half-hour increments throughout the experiment. Lastly, five leaf litter bags were deployed per plot in July of 2014 to be collected sequentially throughout the growing season to provide information on litter decomposition rates and changes in litter nitrogen and carbon (see below).

Soil physical properties, measured monthly, included soil water content (swc), percent organic matter, bulk density (D_B), total porosity, water-filled pore space (wfps), and pH. Properties were measured following standard procedures described by Elliott, Heil, Kelli, and Monger (1999) and Robertson, Sollins et al., (1999a). Total carbon (TC), total nitrogen (TN), and TC:TN molar ratios were measured for all dried samples using a vario Max CN Element Analyzer. Exchangeable ion concentrations of NH_4^+ and NO_3^- were obtained via KCL extraction according to the procedure described by Robertson et al. (1999a). Ammonium and NO_3^- concentrations were determined using a Lachat QuikChem 8500 Series 2 Flow Injection Analysis system. To determine in situ net mineralization and net nitrification rates for each plot, initial NH_4^+ and NO_3^- concentrations (N content from soil extraction on day zero) were subtracted from final concentrations obtained from incubated buried bags. Net mineralization rates were measured as the change in NH_4^+ concentrations, and net nitrification rates were estimated as the change in NO_3^- concentrations. Each incubated soil plug (five per plot) was homogenized and processed individually. All soil nutrient concentrations were expressed on a per unit soil volume by multiplying mean concentrations and daily rates by soil bulk density.

Potential gross nitrification rates were measured using a modified version of the nitrapyrin method (Strauss & Lamberti, 2000; Strauss et al., 2004). Two replicate analyses were conducted for each plot. A single replicate consisted of two 125 mL flasks each filled with 25 g field-wet soil and 81 mL deionized water. One of the flasks received 10 µL of nitrapyrin [2-chloro-6-(trichloromethyl)-pyridine], which is a known nitrification inhibitor, dissolved in dimethyl sulfoxide (DMSO). The second flask received only DMSO as a control. Flasks were capped

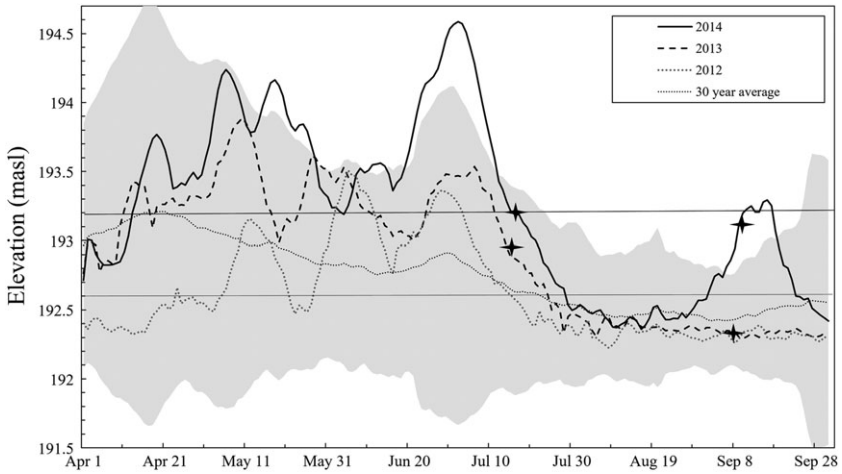

FIGURE 1 Water surface elevation (meters above sea level, masl) at the study site for the 2014, 2013, and 2012 growing seasons. Shaded region represents 95% CI based on the 30 year mean. Stars indicate first and last sampling event of that season. Horizontal bars indicate elevations of the highest and lowest plots used in the study. Durations of spring–summer flood from high to low elevations were 2012, 0–60 days; 2013, 29–85 days; 2014, and 82–113 days (not including the 2nd flood event in September)

with loose-fitting aluminium foil and aerated on an orbital shaker at 175 rpm for 72 hr at 27°C in a limited light environment. Initial and final NH_4^+ concentrations of the soil in both flasks were extracted with 1-N KCl, filtered, then analysed using a QuikChem 8500 Series 2 Flow Injection Analysis system. Gross nitrification rates over the incubation period were calculated by subtracting the change in NH_4^+-N concentrations within the uninhibited flasks (DMSO only) from the change in NH_4^+-N within the inhibited flasks (DMSO + nitrapyrin).

In 2014, leaf litter decomposition bags were constructed of fiberglass screen mesh (6 × 6 cm in size, 0.027 cm diameter) and filled with 5 g of either silver maple or *Phalaris* leaves (stems and stalks removed), which were collected after going through senescence the previous fall and dried to a constant weight. During the July soil sampling event, five bags filled with *Phalaris* litter were deployed at each *Phalaris* plot and five bags filled with silver maple leaf litter were deployed at forest plot. Bags were placed on the soil surface and buried under loose leaf litter if present. One bag per plot was removed during the August sampling event, two bags per plot were removed during the September sampling event, and the final two bags removed 2 weeks after the last soil sampling event. Each bag was rinsed in a water bath to remove excess sediment and then dried to a constant weight. We measured net loss or gain of mass, total nitrogen, total carbon, and TC:TN molar ratio by subtracting values at the end of the season with those of the initial litter bags. We did not estimate decay rates because the time between the first and last month of deployment was only 2.5 months. Hence, this is a measure of short-term net litter decomposition. Leaf litter was pulverized and stored in glass scintillation vials until total carbon and total nitrogen could be determined with a vario Max CN Element Analyzer.

2.3 | Data Analysis

Analysis of covariance was used to characterize variation in each measurement due to difference in elevation, time (month), and vegetation type. These analyses included each month (n = 6 for soil properties, n = 5 for potential gross nitrification, and n = 4 for in situ soil process measurements) and vegetation type (n = 2) as fixed factors and spatial differences in elevation as a continuous covariate. Analyses consisted of all main factors (month, vegetation type, and elevation) as well as all possible interaction terms. Nonsignificant factors and interaction terms were removed from models using significance tests (p < .05), and p values were adjusted for multiple comparisons using the Bonferoni method. For variables for which elevation was the only significant factor, we aggregated all data across vegetation type and month and used simple linear regression to characterize the relationship. All analyses were conducted using SPSS 22.0 (IBM SPSS Statistics 22.0 2015).

For litter measurements, we conducted analysis of covariance on the net change in mass as well as change in TC, TN, and TC:TN ratio, with vegetation type as the fixed factor and elevation as the continuous covariate. Again, the analyses consisted of all main factors and interaction terms and models were later simplified using significance tests (p = .05).

TABLE 1 Results of analysis of covariance analyses determining significant differences between forest and *Phalaris* communities as well as differences due to time after flooding and elevation for all measurements

Measurements	T	M	E	T × M	T × E	M × E	T × M × E
Soil							
Water content	<.001	.006	NS	NS	NS	NS	NS
Water-filled pore space	<.001	.005	NS	NS	NS	NS	NS
PH	.003	NS	<.001	0.047	NS	NS	NS
Daily temperature	.004	NS	NS	NS	NS	0.014	NS
Organic matter	NS	NS	<.001	NS	NS	NS	NS
Bulk density	NS	NS	<.001	NS	NS	NS	NS
Porosity	NS	NS	<.001	NS	NS	NS	NS
Nitrogen	NS	NS	<.001	NS	NS	NS	NS
Carbon	NS	NS	<.001	NS	NS	NS	NS
C:N ratio	<.001	NS	<.001	NS	0.005	NS	NS
Exchangeable ammonium	<.001	.039	NS	NS	NS	NS	NS
Exchangeable nitrate	.008	NS	NS	NS	NS	NS	NS
Net mineralization rate	<.001	NS	NS	NS	NS	NS	NS
Net nitrification rate	NS	NS	NS	NS	NS	NS	NS
Gross nitrification rate	<.001	NS	NS	NS	0.001	NS	NS
Litter							
Change in mass loss	NS	NA	NS	NA	NS	NA	NA
Change in nitrogen	.036	NA	NS	NA	NS	NA	NA
Change in carbon	NS	NA	<.001	NA	NS	NA	NA
Change in C:N	<.001	NA	NS	NA	NS	NA	NA

Note. Vegetation type (T) and month (M) were main effects, and elevation (E) was added as a covariate. Significant p values are given, NS = not significant, NA = not applicable.

3 | RESULTS

3.1 | Soil physiochemical properties

During the two study years, typical spring–summer flooding lasted through mid-July. In 2013, one *Phalaris* plot was saturated during the first sampling event, and all other plots were dry 1–9 days prior. All plots remained unflooded the rest of the 2013 growing season. Flooding was more prevalent at the site in 2014. The highest two plots of both vegetation types were dry 4–5 days prior to the July sampling event and remained dry for the duration of the growing season. The lowest three plots of each vegetation type were saturated or flooded during the July sampling event, then dry 23–32 days leading up to August sampling. A second flood occurred in September, leaving the lowest three plots of each vegetation type saturated or flooded 1–5 days prior to the final sampling event. Vegetation type and month were significant predictors of soil water content (swc) and water-filled pore space (wfps), but elevation was not significant (Table 1). Both measurements were highest during flooded months (July 2013 and 2014 and September 2014; Table 2) and lower during drier months (August and September 2013). *Phalaris* soils, however, retained more water during each month compared to forest soils with the highest measurements seen in July 2014 (Table 2). Soil water content in *Phalaris* communities was 1.5–1.8 times higher than in forest communities in all months except the driest (Sept 2013) in which it was 2.2 times higher.

Daily soil temperature was influenced by vegetation type and the interaction between month and elevation, and soil pH was influenced by elevation and the interaction between vegetation type and month (Table 1). pH was consistently lower, and soil temperatures were consistently warmer in *Phalaris* soils and low elevation plots (Table 2, Figure 2). *Phalaris* soils on average were 1.1 °C warmer compared to forest soils throughout both growing seasons with pH about 1 unit lower at all times except July 2014 in which soils were most flooded and all sites had similar pH of around 7.

3.2 | Soil bulk properties

Soil organic matter, bulk density, and total porosity did not depend on vegetation type, month, or any of the interactions among these variables. Instead, all variables were significantly affected by elevation alone (all: $p < .001$; Table 1). Soils of both vegetation types

TABLE 2 Monthly means (±SE) of soil physiochemical and bulk properties of forest and *Phalaris* plots for 2013 and 2014 ($n = 5$)

Vegetation type	Month	Temperature (°C)	Water content ($g \cdot H_2O \cdot cm^{-3}$)	Water-filled pore space (%)	pH	Organic matter (%)
2013						
Forest	July	20.1 ± 0.22	0.57 ± 0.04	66.00 ± 4.26	6.78 ± 0.2	36.35 ± 6.89
	August	17.6 ± 0.27	0.38 ± 0.03	46.44 ± 6.33	6.78 ± 0.38	34.40 ± 9.56
	September	20.1 ± 0.31	0.19 ± 0.03	24.62 ± 5.39	6.44 ± 0.36	29.37 ± 7.16
Phalaris	July	22.28 ± 0.25	0.86 ± 0.07	107.25 ± 9.51	6.29 ± 0.33	27.04 ± 5.45
	August	18.83 ± 0.24	0.66 ± 0.04	78.51 ± 5.02	6.26 ± 0.26	29.70 ± 2.17
	September	20.43 ± 0.46	0.42 ± 0.04	51.09 ± 6.21	5.89 ± 0.29	27.76 ± 2.49
2014						
Forest	July	20.48 ± 1.34	0.96 ± 0.12	121.13 ± 12.49	7.41 ± 0.09	22.58 ± 4.20
	August	18.88 ± 0.49	0.44 ± 0.02	54.19 ± 1.41	6.67 ± 0.36	28.61 ± 6.98
	September	18.70 ± 0.28	0.71 ± 0.10	85.26 ± 10.30	7.02 ± 0.26	30.50 ± 6.34
Phalaris	July	23.51 ± 0.92	1.44 ± 0.12	179.25 ± 13.57	7.30 ± 0.07	23.94 ± 1.48
	August	20.56 ± 0.40	0.66 ± 0.04	80.84 ± 4.83	6.14 ± 0.22	26.26 ± 2.96
	September	19.09 ± 0.18	1.32 ± 0.09	160.83 ± 7.36	6.87 ± 0.09	27.20 ± 3.60
Vegetation type	**Month**	**Bulk density (mg soil cm^{-3})**	**Total porosity %**	**Soil nitrogen %**	**Soil carbon %**	**Soil CN ratio**
2013						
Forest	July	0.37 ± 0.07	86.18 ± 2.82	0.92 ± 0.22	12.49 ± 2.90	15.96 ± 0.33
	August	0.44 ± 0.12	83.53 ± 4.52	1.03 ± 0.26	14.20 ± 4.00	15.60 ± 0.63
	September	0.48 ± 0.10	81.87 ± 3.94	0.97 ± 0.23	12.81 ± 3.12	15.18 ± 0.34
Phalaris	July	0.50 ± 0.09	81.16 ± 3.44	0.95 ± 0.19	12.28 ± 2.70	14.85 ± 0.52
	August	0.42 ± 0.03	83.97 ± 1.30	1.08 ± 0.12	13.17 ± 1.66	14.16 ± 0.33
	September	0.46 ± 0.05	82.69 ± 1.71	1.04 ± 0.10	12.21 ± 1.19	13.71 ± 0.23
2014						
Forest	July	0.57 ± 0.08	78.47 ± 2.99	0.75 ± 0.16	9.87 ± 2.28	15.17 ± 0.31
	August	0.49 ± 0.10	81.48 ± 3.91	0.91 ± 0.23	12.87 ± 3.46	16.09 ± 0.69
	September	0.45 ± 0.09	82.99 ± 3.57	1.02 ± 0.20	14.56 ± 3.24	16.30 ± 0.52
Phalaris	July	0.52 ± 0.03	80.30 ± 1.13	0.84 ± 0.08	10.08 ± 0.85	14.00 ± 0.28
	August	0.49 ± 0.05	81.62 ± 1.85	0.94 ± 0.13	11.35 ± 1.68	14.13 ± 0.46
	September	0.48 ± 0.07	81.98 ± 2.59	1.00 ± 0.15	12.75 ± 2.07	14.73 ± 0.52

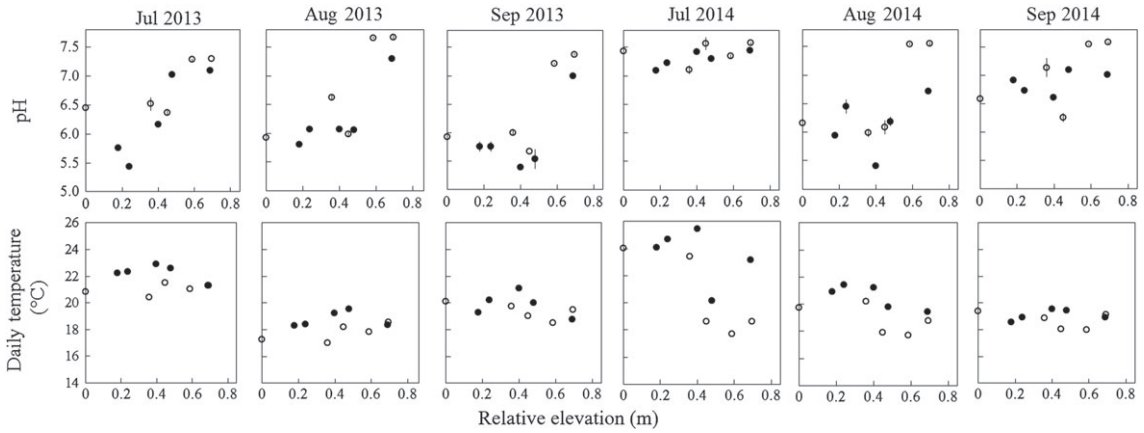

FIGURE 2 Trends in soil pH and daily temperature across time and elevation (0.7 m between lowest and highest plots) within forest (open circles) and *Phalaris* (closed circles) plots. Error bars for pH represent one standard deviation of lab replicates. Daily temperature was collected by a single data logger per plot

accumulated more organic matter and had higher porosity in lower elevations (R^2 = .49 and .61, respectively), and soil bulk density was highest for both vegetation types in higher elevations (R^2 = .61; Figure 3). Soil total nitrogen and carbon were similarly affected by elevation alone (p < .001 for both). Both measurements were highest in low elevations, independent of type or month, and decreased as elevation increased (R^2 = .44 and .43, respectively). However, soil C:N molar ratios depended on vegetation type, elevation, and their interaction (Table 1). Forest soil C:N declined from 17 to 15 with increasing elevation (R^2 = .72), and *Phalaris* soil C:N ratios ranged between 13 and 15 and had no observable trend with elevation (R^2 = .02).

3.3 | Litter decomposition

Net mass loss from leaf litter bags deployed during 2014 did not show significant differences between the two vegetation types and ranged

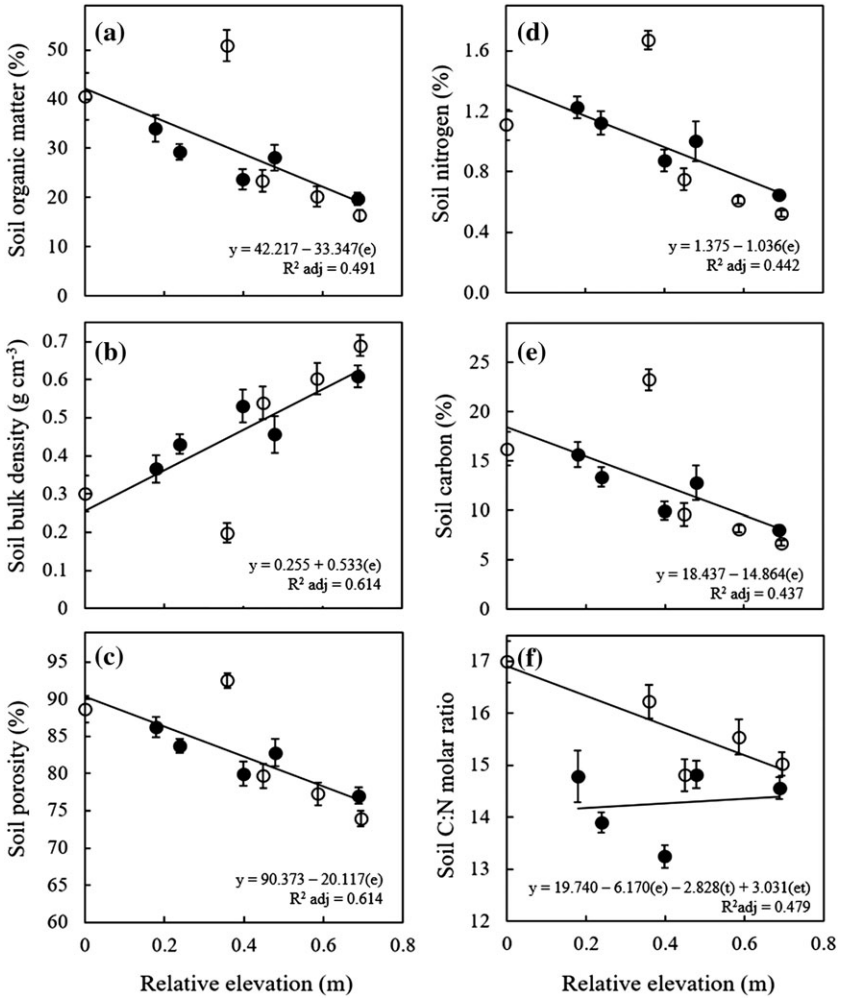

FIGURE 3 Trends in soil bulk properties across elevations within forest (open) and *Phalaris* (closed) plots. (a) soil organic matter, (b) soil bulk density, (c) soil porosity, (d) soil nitrogen, (e) soil carbon, (f) soil C:N molar ratio. Month and vegetation type were combined for all linear regressions (n = 12) except soil C:N in which vegetation type had a significant effect (p < .005). Dummy variables were used for vegetation type in the equation for C:N (forest = 1, *Phalaris* = 2). Error bars = 1 SE; e = elevation, t = vegetation type, et = interaction of elevation and vegetation type

between 41% and 76%. Elevation and vegetation type were important factors in changes of litter %C and %N, respectively (Table 1). By the end of the 2.5-month incubation period, more carbon was lost from litter in low elevation plots than high elevations (Figure 4). regardless of litter type. Changes in percent, litter N differed by vegetation type (Figure 5). Nitrogen content of forest litter increased 1% by the end of the study, and *Phalaris* litter N increased by <0.5%. Different rates of carbon loss (across elevations) and nitrogen gain (between vegetation types) led to significantly different changes in litter C:N molar ratios that depended most on litter type (Figure 6). Forest litter had an initial C:N ratio 2× that of *Phalaris* litter (66 and 32, respectively) and decreased at a faster rate. By the end of the study, both litter types had C:N ratios <30. Thus, carbon was lost similarly from both litter types, but forest litter gained a greater percent of N resulting in a greater decline in C:N ratios in forest litter. C:N ratios were also significantly higher in forest soil than invaded soils (Figure 6).

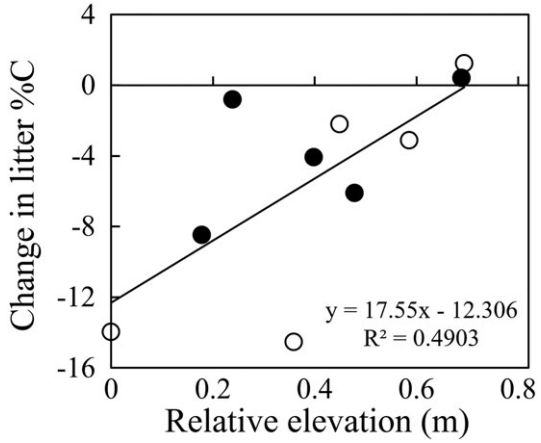

FIGURE 4 Change in litter C content of final litter collection after a 2.5-month incubation period during the 2014 growing season. Significant effects of elevation only; forest = open circles, *Phalaris* = closed circles

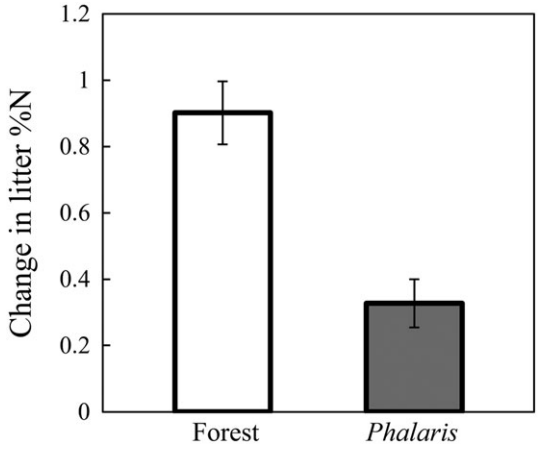

FIGURE 5 Mean change in litter N content (p = .036) after a 2.5-month incubation period during the 2014 growing season, elevation combined. Error bars = 1 SE. Average initial and final % N content in forest litter was 0.84 and 1.72, respectively. Average initial and final % N content in Phalaris litter was 1.55 and 1.84 respectively. Average initial and final % N content in forest litter was 0.84 and 1.72, respectively. Average initial and final % N content in *Phalaris* litter was 1.55 and 1.84, respectively

3.4 | Nitrogen availability and processing rates

Differences in soil exchangeable NH_4^+ were significantly influenced by vegetation type and month (Table 1). *Phalaris* soils consistently maintained higher concentrations of exchangeable NH_4^+ in all months compared to forest soils, with the highest concentrations during flooded conditions (Table 3). Nitrate concentrations also differed by vegetation type, and these differences did not depend on month, elevation, nor any of the interaction terms (Table 1). *Phalaris* soils consistently maintained higher NO_3^- concentrations than forest soils (Figure 7).with the highest concentrations in the driest months. Flooded soils typically had zero or low soil NO_3^-, but *Phalaris* soils continued to maintain higher average monthly NO_3^- concentrations. Average forest soil NO_3^- concentrations never exceeded 1.5 μg/cm^3.

There was a significant effect of vegetation type on in situ rates of mineralization (p < .001, Table 1, Figure 8). *Phalaris* soils had lower net rates of mineralization than forest soils in all incubation periods, with

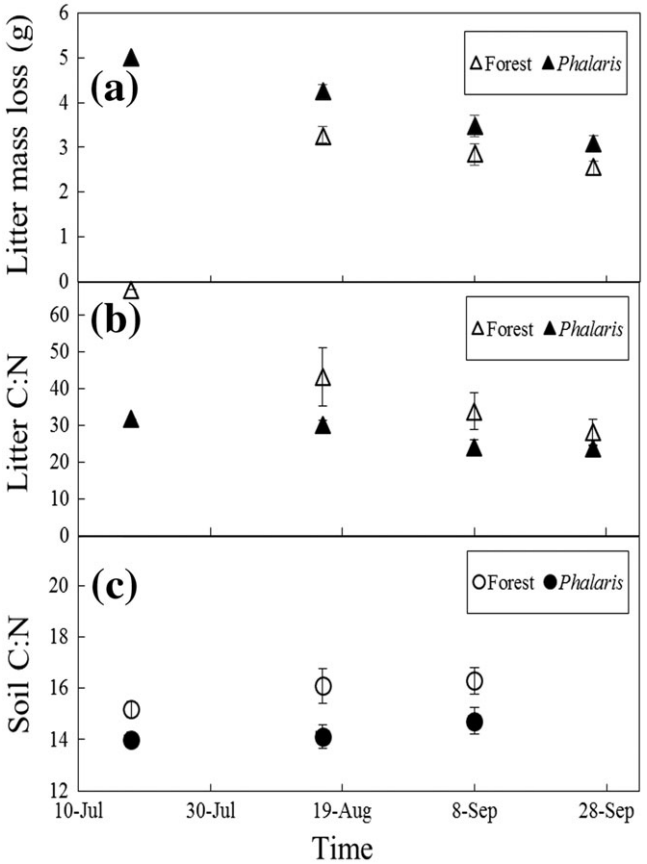

FIGURE 6 (a) Leaf litter mass loss; (b) leaf litter C:N ratios; and (c) soil C:N ratios from forest and *Phalaris* plots throughout the 2014 growing season (elevations combined, error bars = SE). Leaf litter in July represents initial mass and C:N ratios of litter collected and dried the previous fall (n = 25). In the following sampling events n = 5, 10, 9, respectively in each community type. One litter bag within each community type was removed from calculations due to removal by animals or significant sedimentation. Soil C:N ratios are from all three soil collections of the growing season (n = 5)

TABLE 3 Monthly means (±SE) of soil exchangeable nitrogen and nitrogen processing rates of forest and *Phalaris* plots for 2013 and 2014 (n = 5)

Vegetation type	Month	Exchangeable NH_4^+–N (μg/cm^{-3})	Exchangeable NO_3^-–N (μg/cm^{-3})	Gross nitrification (μg·N·cm^{-3}·day^{-1})	Net mineralization (μg·N·cm^{-3}·day^{-1})	Net nitrification (μg·N·cm^{-3}·day^{-1})
2013						
Forest	July	6.79 ± 0.95	0.31 ± 0.11	1.02 ± 0.35	−0.06 ± 0.03	0.00 ± 0.01
	August	5.69 ± 0.69	0.96 ± 0.21	2.32 ± 1.78	0.05 ± 0.05	0.55 ± 0.08
	September	8.75 ± 0.98	0.78 ± 0.53	1.25 ± 0.70		
Phalaris	July	18.37 ± 4.99	7.28 ± 6.57	5.13 ± 2.65	−0.43 ± 0.18	−0.02 ± 0.24
	August	12.21 ± 1.77	8.41 ± 4.43	6.15 ± 1.85	−0.17 ± 0.06	1.88 ± 0.50
	September	11.17 ± 1.25	5.76 ± 2.88	1.11 ± 0.38		
2014						
Forest	July	8.22 ± 1.43	0.00 ± 0.00	0.96 ± 0.66	−0.01 ± 0.04	0.04 ± 0.01
	August	7.26 ± 1.18	1.13 ± 0.14	1.92 ± 0.72	0.06 ± 0.04	0.18 ± 0.11
	September	12.48 ± 2.26	0.85 ± 0.46			
Phalaris	July	27.02 ± 5.32	0.15 ± 0.15	7.33 ± 1.60	−0.58 ± 0.22	0.22 ± 0.11
	August	10.47 ± 1.05	12.59 ± 7.88	5.66 ± 2.20	−0.16 ± 0.03	−0.08 ± 0.11
	September	19.38 ± 2.30	1.31 ± 0.57			

the most negative rate during the wettest incubation period (July–August 2014; Table 3). No rates exceeded 0.06 μg·N·cm^3·day^{-1}. Net nitrification rates were not significantly associated with any of the environmental factors (Table 1). The driest incubation period (August 2013) was the only period in which nitrification rates exceeded 0.5 μg·N·cm^3·day^{-1} in either vegetation type and rates were almost four times greater in *Phalaris* soils in that month alone than in forest plots (Table 3).

Gross nitrification, measured under laboratory settings, was affected by type and the interaction between type and elevation (Table 1). Both vegetation types supported higher rates of gross potential nitrification in the lowest elevation plots (Figure 9). where soil organic matter, porosity, and temperature tended to be highest, and soil pH tended to be lowest Nevertheless, *Phalaris* soils maintained higher average rates of gross nitrification across the elevation gradient, ranging 1.4–11 times higher than forest soils.

4 | DISCUSSION

Floodplain forests are highly productive ecosystems due to seasonal flood events, which recharge soil nutrients, supporting rapid nutrient turnover, and high plant productivity. In the UMR, spring floods deposit organic matter and nutrient-rich water onto floodplain soil from upstream sources and watershed run-off. Both are high in nutrients, in part due to surrounding agricultural activity. Not only does flooding provide a new source of nutrients to the floodplain, it is also the primary driver of soil redox potential and thus controls microbial

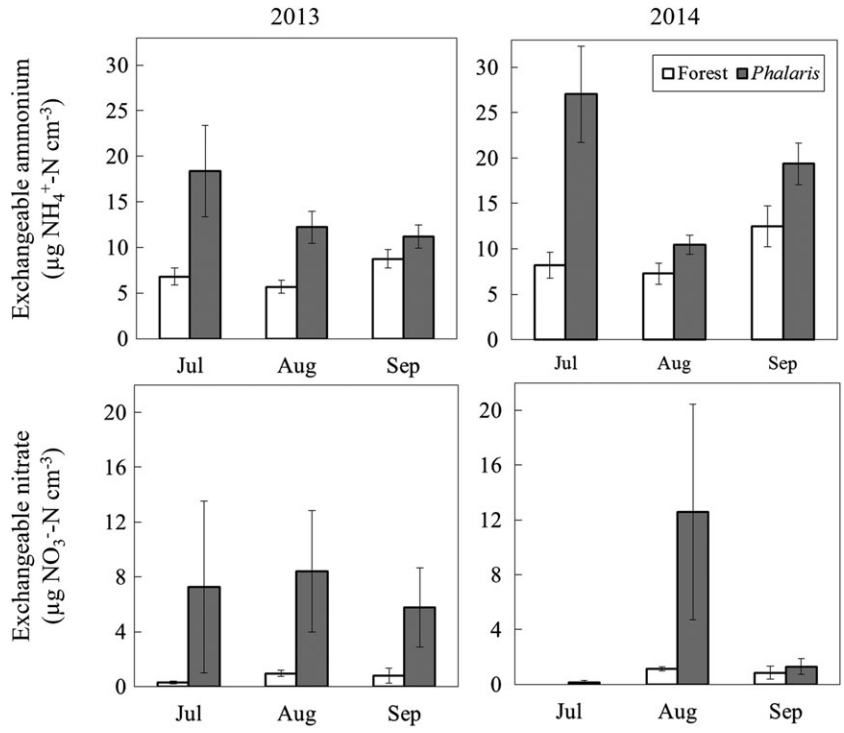

FIGURE 7 Monthly trends (±SE) of soil exchangeable N within forest and *Phalaris* plots, elevations combined (n = 5)

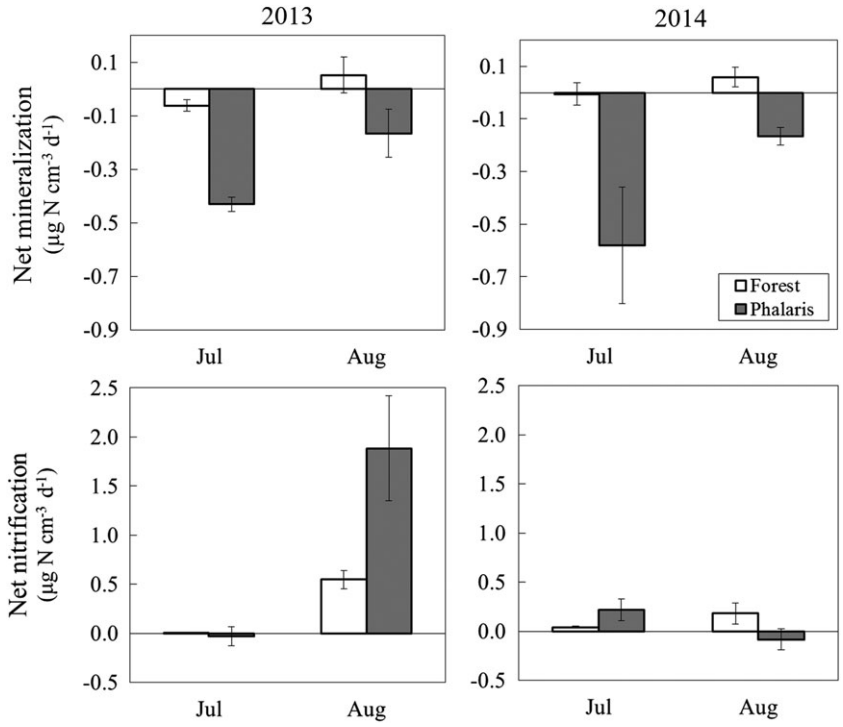

FIGURE 8 Trends in in-situ N processing rates across time within forest and *Phalaris* plots, elevations combined (n = 5). Error bars = 1 SE

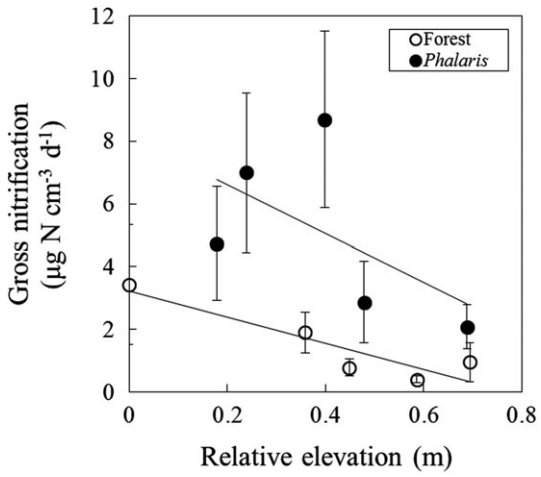

FIGURE 9 Trends in gross nitrification rates across elevations within forest and *Phalaris* plots, months combined (n = 5). Dummy variables were used for vegetation type (forest = 1, *Phalaris* = 2). Error bars = 1 SE. R2adj = 0.291. Model: y = −1.925 + 5.077(t) – 3.970(te); t = type, te = interaction of type and elevation

activity, which is responsible for most N cycling processes. A floodplain's ability to lessen nutrient loading downstream and act as an N sink depends on the amount of N being sequestered long-term in biomass (such as in woody tissue) and the frequency and length of time in which soils are inundated or dry (Pinay & Decamps, 1988). Invasion by *P. arundinacea* (reed canarygrass) has been shown to hinder forest regeneration (Hovick & Reinartz, 2007; Reinhardt Adams et al., 2011; Thomsen et al., 2012) and also to alter soil properties and microbial activity enough to potentially influence ecosystem functions, such as N cycling (De Jager et al., 2015). There have been some studies regarding the impacts of various degrees of flood events and also the interactive effects of flooding and invasion on N cycling within the UMR floodplain forest system (Jicha et al., 2014; De Jager et al., 2015; Kreiling et al., 2015) but these studies span limited flood scenarios. Collecting data throughout varying flood types provides a better understanding of the relationship between invasion and flooding on nutrient cycling. This study compared soil properties and N availability and processing rates of mature forest soils and those invaded by *Phalaris* throughout two summers, which experienced above-average flood events. Results suggest that the severity of flooding most greatly influences soil properties, but invasion by *Phalaris* ultimately leads to greater production of nitrate.

4.1 | Influences of spatial and temporal trends in flooding

Long-term patterns of flooding contribute to spatial differences in floodplain soils. Low elevations flood more often and for longer durations than higher areas, apparently leading to the accumulation of fine sediments and high organic matter content in low elevations. Our results revealed a spatial gradient of soil conditions, with higher soil total nitrogen and carbon in low elevations. These results support previous findings at broader spatial scales in the UMR (De Jager, Thomsen, & Yin, 2012).

At the same study site, De Jager et al. (2015) found that *Phalaris* patches maintained higher soil organic matter than early and mature forest soils, even as floodplain elevation increased. *Phalaris* was hypothesized to trap organic matter during flooded conditions, as well as produce a dense root mass and litter layer. In the present study, organic matter content and porosity were greater than in the 2012 growing season with no differences between forest and invaded communities. Although we did not focus on the growth patterns of *Phalaris*, it was clear from visual inspection that higher water levels during 2013

and 2014 reduced *Phalaris* biomass production compared to 2012. It is possible that increased flooding led to more deposition of organic matter in both types of sites, and that the lack of *Phalaris* growth limited its ability to trap organic matter at higher elevations, ultimately resulting in similar distributions of organic matter and other soil bulk properties across the elevation gradient. This result underscores the importance of studying floodplain biogeochemical processes over a number of years with different flood events and growing conditions.

In the current study, spatial variation in bulk properties were correlated with trends in some nitrogen processes. Higher rates of gross nitrification in low elevations were associated with soil properties (such as greater organic matter and greater porosity) and greater microbial activity. Decomposition rates were also greater at lower elevations, as litter of both vegetation types lost the greatest percentage of carbon in low elevation sites.

Flood frequency, duration, and time of occurrence all strongly influence microbial activity by controlling soil moisture and redox potential (Peralta et al., 2013; Reddy & Patrick, 1975). Alternating flooded and unflooded conditions can enhance N turnover by supporting a greater number of microbial processes, which occur under the various stages of inundation. Permanently flooded or permanently dry environments may hinder N turnover by only supporting select microbial communities and processes. Seasonal flooding also increases nitrogen availability by providing organic nitrogen for mineralization, depositing free ammonium from upstream, and run-off sources and by releasing ammonium bound to soil clay particles (Koschorreck & Darwich, 2003). Ammonium is typically the dominant N species during inundation due to anaerobic decomposition releasing NH_4^+ (Reddy, Rao, & Jessup, 1990) and denitrification removing any available NO_3^- (Pinay et al., 2007). As soils dry, vegetation uptake, microbial immobilization, and nitrification then lower NH_4^+ availability.

Previous work at this study site and throughout Navigation Pool 8 of the UMR noted stronger seasonal trends in soil NH_4^+ and NO_3^- availability from flooding than what was observed in this study (De Jager et al., 2015; Jicha et al., 2014; Kreiling et al., 2015). Ammonium availability was greatest in these studies immediately following the end of the flood pulse, and NO_3^- became more dominant as soils dried. Jicha et al. (2014) found that gross nitrification was greatest in mature *Acer* forests that were historically moderately rarely flooded, and Kreiling et al. (2015) found that invasion by *Phalaris* had minimal impacts on ion availability compared to time after flooding. Both studies were conducted in years with substantially lower flood pulses prior and during sampling periods. It is possible that greater periods of anoxic soil conditions in the present study lessened seasonal variation and resulted in overall greater N availability. Longer periods of flooding prior to sampling allowed for greater transport of organic matter and nutrients onto the study site and also supported denitrification, which would have removed nitrate brought to or created at the site.

Although not measured in this study, denitrification is an important anaerobic N process influencing the ecosystem's overall potential to remove N. Hefting et al. (2004) found that mineralization was the primary N process in riparian ecosystems experiencing a water table from zero to −10 cm and that nitrification was the primary process in sites with water tables below −30 cm, but denitrification remained an important process throughout the entire range of water table levels and was the dominant process between −10 and −30 cm. Pinay et al. (2007) also found that denitrification was optimal between 60% and 80% soil moisture as microsites supporting aerobic microbial nitrification supplied nitrate. These patterns suggest that coupled nitrification–denitrification could have played an important role throughout our study as well and was likely the cause of significant loss of NO_3^- in *Phalaris* soils from August to September 2014.

4.2 | Influences of invasion

Invasion of floodplain forest canopy gaps by *Phalaris* has the potential to modify nitrogen cycling in ways that promote its persistence. First, microbial decomposition appears to be less limited by available NH_4^+ in invaded soils. *Phalaris* litter had significantly lower ratios of C:N than forest litter, which resulted in less immobilization of N from the soil to the organic matter pool over time. This may explain why both NH_4^+ and NO_3^- were higher in soils from *Phalaris* plots as compared to soils from forest plots where nitrogen was immobilized from soil to the organic matter pool. Furthermore, rates of potential gross nitrification were highest in *Phalaris* plots, as was in situ net nitrification during the driest time period. These results collectively suggest that invasion of forest canopy gaps by *Phalaris* triggers an increase in nitrogen cycling rates that may serve to reinforce its persistence in high-N environments. Interestingly, legacy effects of litter quality on soil microbial activity have been shown to persist for more than 17 months after removal of litter (Elgersma et al., 2012), suggesting that invasion by *Phalaris* can continue to influence ecosystem functions during a growing season with poor biomass growth due to flooding, such as the case in our study in 2014. This may explain why invasion remained influential in N processing rates despite having a lack of influence on bulk properties, which was documented in previous studies. Furthermore, the presence of *Phalaris* resulted in trends similar to those hypothesized by Ehrenfeld (2003) for sites dominated by N responsive invaders, including production of litter that decays more rapidly than native litter, greater soil available nitrogen, faster nitrogen processing rates (especially nitrification), lower C:N molar ratios, and higher soil moisture.

The abundance of *Phalaris* also has the potential to impact adjacent riverine and coastal areas by either increasing or decreasing the amount of NO_3^- exported from the floodplain. Nitrate is more mobile and more easily leached from soils than NH_4^+, and it is possible that increased nitrification rates and NO_3^- availability in *Phalaris* soils could result in higher rates of N loss to the river. On the other hand, denitrification is often limited by the availability of nitrate in flooded wetland soils where N is most commonly in the form of NH_4^+. Higher rates of nitrification in *Phalaris* soils could, therefore, promote higher rates of denitrification and N loss from the river–floodplain ecosystem to the atmosphere. In fact, it is possible that the results from the buried bag experiment reflect greater coupled nitrification–denitrification in *Phalaris* soils compared to forest soils. During the wet incubation periods (July 2013 and 2014 and August 2014), we noted net negative mineralization and neutral net nitrification rates. This could have resulted from high rates of nitrification causing a loss of NH_4^+, coupled with high rates of denitrification causing a lack of NO_3^- accumulation. Another explanation is that immobilization caused the decrease in

NH_4^+ during the flooded periods. However, immobilization is only favoured over mineralization on residues with high C:N ratios, such as fresh forest litter (>30; Norton & Schimel, 2011). It seems more likely that coupled nitrification–denitrification is responsible for negative mineralization rates during flooded conditions and that *Phalaris* could ultimately promote the loss of N from the system when soils remain inundated for extended periods of time and especially if inundation occurs after NO_3^- accumulates from an extended dry period.

5 | CONCLUSION

Our results highlight the challenges of predicting consequences of floodplain invasion for ecosystem functions like N cycling. Due to large flood events, we hypothesize that invasion in this study did not impact soil properties similarly to previous studies at the same location. However, it is clear that invasion by *Phalaris* increased the pool of mobile NO_3^- via more rapid decomposition and nitrification rates. Such increases in N availability could maintain this species' dominance in forest canopy gaps, as *Phalaris* is known to thrive in high-N environments. Whether or not invasion also corresponds to an increase in NO_3^- released downstream or removed by denitrification depends on the frequency, duration, and timing of inundation. Floodplain management actions aimed at reducing N transport to the main channel need to consider how the interactive effects of flooding and invasion change from year to year with different flood types. Future research could focus on learning about the fate of NO_3^- in *Phalaris* dominated wetlands or consider the possible benefits of maintaining mosaics of native and invasive communities throughout a floodplain, which could reduce restoration time and effort and still provide high-nutrient turnover and N buffering capacity.

ACKNOWLEDGEMENTS

Funding for this research was provided to N.R. De Jager through the U.S. Army Corps of Engineers' Upper Mississippi River Restoration Program. W. Swanson was supported through a cooperative research agreement between the USGS Upper Midwest Environmental Sciences Center and the University of Wisconsin-La Crosse River Studies Center. Helpful comments on a previous version of this manuscript was provided by Rebecca Kreiling, USGS. Any use of trade names of products does not imply endorsement by the United States Government.

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How to cite this article: Swanson W, De Jager NR, Strauss E, Thomsen M. Effects of flood inundation and invasion by *Phalaris arundinacea* on nitrogen cycling in an Upper Mississippi River floodplain forest. *Ecohydrology*. 2017:e1877. https://doi.org/10.1002/eco.1877