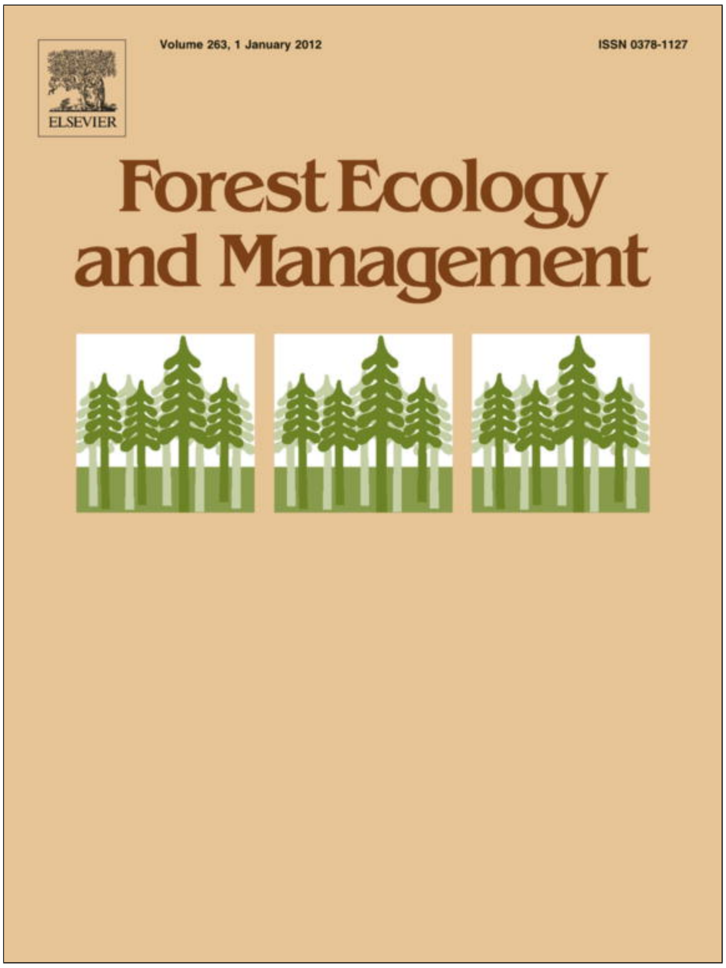

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Threshold effects of flood duration on the vegetation and soils of the Upper Mississippi River floodplain, USA

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ABSTRACT

Most large rivers have experienced major changes in hydrology and land use over the past century, with concomitant effects on sedimentation, nutrient cycling and biodiversity. To restore and/or enhance these ecosystems, managers need to know where their efforts are most likely to succeed under current hydrologic regimes as well as under potential future hydrologic regimes. We therefore examined changes in forest vegetation and soils across a hydrologic gradient, expressed as flood duration during the growing season, for 320 km of the Upper Mississippi River (UMR) floodplain.

Soil texture was highly variable but trended toward finer grained sediments and >5% organic matter as flood duration increased from 0% to ~40% of the growing season. Beyond 40%, soil texture was exclusively silt plus clay with >5% organic matter. The diversity of both the understory and overstory tree communities was also highly variable at sites that flooded for <40% of the growing season. However, understory diversity decreased as flood duration increased from 0% to ~25% of the growing season and overstory diversity declined as flood duration increased from 0% to ~40% of the growing season. Diversity estimates for both strata were uniformly low at sites that flooded for longer than ~40% of the growing season. Beyond this point the proportional abundance of *Acer saccharinum* in the overstory exceeded 70%.

Our results suggest that there is a threshold along the elevation gradient of this floodplain, corresponding with flood durations lasting ~40% of the growing season. At lower elevation sites, flooding exerts primary control over forest soils and vegetation, restricting the former to silt plus clay with higher organic matter and the latter to a few highly flood tolerant species. The existence of such thresholds have implications for management of floodplain soil nutrient dynamics and plant diversity under existing hydrologic regimes, more natural hydrologic regimes and more extreme hydrologic regimes that may result from climate change.

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1. Introduction

Floodplains are important elements of regional landscapes, providing ecosystem services such as flood control, commercial navigation, recreation and commercial harvest (Costanza et al., 1997; Postel and Carpenter, 1997; Haeuber and Michener, 1998). Perhaps most importantly, floodplains collect water, nutrients and energy from entire watersheds, making them biogeochemical and biodiversity hotspots (Junk et al., 1989; Malanson, 1993; Naiman et al., 1993; Forshay and Stanley, 2005). For example, denitrification, the conversion of nitrate to gaseous nitrogen (Knowles, 1982) occurs when nitrate rich water comes into contact with anaerobic soils (Pinay et al., 1995; Haycock et al., 1997; Sabater et al., 2003). Well connected river-floodplain systems can therefore reduce the amount of nitrogen transported to downstream coastal areas (Peterjohn and Correll, 1984; Noe and Hupp, 2009). Furthermore, biodiversity is often much greater in floodplains than adjacent upland ecosystems (Malanson, 1993; Naiman et al., 1993; Knutson and Klaas, 1998), increasing their value from a conservation perspective.

Across floodplain landscapes, substantial variation exists in local hydrological conditions due to topographic heterogeneity and river fluctuation. That variation often controls the spatial distribution of various ecological processes (e.g. sedimentation, nutrient cycling and community succession), ecosystem properties (e.g. soil texture and fertility and plant species composition) and associated ecosystem services (e.g. denitrification and biodiversity) (Wharton et al., 1982; Auble et al., 1994; Hodges, 1997; Mitsch and Gosselink, 1993; Pinay et al., 2000). Most critically, lower elevations flood more often and for longer periods of time than higher elevations. Differences in flood duration regulate the length of oxic and anoxic conditions (Patrick and Tusnem, 1972; Ponnamperuma, 1972; Keeney, 1973) which directly influences nutrient cycling

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(i.e. mineralization, nitrification and denitrification, Pinay et al., 1995, 2000) as well as the germination and growth of various plant species (Hosner and Minckler, 1963; Whitlow and Harris, 1979; Yin, 1998; Mitsch and Gosselink, 1993; Burke et al., 2003). Flooding also indirectly affects nutrient cycling and plant succession through variation in sediment deposition. Lower elevations often accumulate finer-grained sediments (Hupp and Morris, 1990; Mitsch and Gosselink, 1993; Hodges, 1997), which have higher water holding capacities and more organic matter than coarser grained sediments (Amato and Ladd, 1992; Hassink, 1994). These properties, along with the presence of anaerobic conditions, regulate local rates of denitrification (Pinay et al., 2000) and the suitability of various floodplain sites for different plant species (Whitlow and Harris, 1979; Robertson, 1992; Ewing, 1996; Wardrop and Brooks, 1998; Adamus et al., 2001; Walls et al., 2005). As a consequence, the vegetation and soils of floodplains are often distributed as spatially heterogeneous mosaics, corresponding with elevational differences in flood inundation (Auble et al., 1994; Hughes, 1997; Hodges, 1997; Toner and Keddy, 1997; Nilsson et al., 1997; Gergel et al., 2002).

Over the past 100 years, most large rivers have experienced extensive hydrologic modifications to support commercial navigation and to control flood impacts to urban and agricultural areas. Furthermore, the delivery of water and sediments to river systems has been altered by land use changes, including: forest clearing, wetland drainage, impervious surface construction and the use of agricultural drainage tile. As a result, the floodplains of most large rivers have undergone dramatic changes in flood duration, rates and patterns of sedimentation (Ligon et al., 1995; Friedman et al., 1998; Grant et al., 2003) and plant community composition (Teskey and Hinckley et al., 1977; Klimas et al., 1981; Auble et al., 1994; Hughes and Rood, 2003; Yin et al., 2009). Further changes in flooding and associated distributions of floodplain vegetation and soils are expected to occur during the next 100 years due to climate change (Olsen et al., 1999; Milly et al., 2002; Pinay et al., 2007; Palmer et al., 2008).

Effective management of floodplain nutrient dynamics and biodiversity in such altered systems requires a quantitative understanding of how spatial variation in flood duration drives the distribution of ecosystem properties such as plant species composition and soil texture and fertility at landscape scales. First, it has been suggested that the success of restoration and/or management actions in floodplains could be improved through establishment of more natural flow regimes (Rood et al., 2005). Quantitative relationships between flooding and ecological properties can be used to derive benchmarks for water-level management actions that support particular ecosystem services (e.g. biodiversity and/or nutrient processing) (Auble et al., 1994; Toner and Keddy, 1997; Yin et al., 2009). Secondly, where social and economic factors preclude large-scale hydrologic manipulations, floodplain managers need to know where opportunities for restoration success are greatest under the current hydrologic conditions. Finally, the global hydrologic cycle is expected to change greatly over the next 100 years in response to climate and land-use changes (IPCC, 2001). It is not possible to make predictions about the likely effects of climate change on the spatial distribution of ecosystem services that floodplains provide without knowing how the diversity of native plant communities and/or the processing of nutrients relate to flooding. Such relationships need to be expressed visually, in the form of maps, so that managers can evaluate alternative management or environmental scenarios.

In this study, we examined the vegetation and soils of the Upper Impounded Reach of the Upper Mississippi River (UMR) (Fig. 1), a 320 km stretch that has undergone major changes in hydrology, sedimentation, nutrient transport and processing and plant community composition over the past 200 years (Yin and Nelson, 1995; Nelson, 1997; Leake and Johnson, 2006; Yin et al., 2007, 2009). During the late 1930s a series of low-head dams were constructed to support commercial navigation by deepening the main channel from ~1.4 m (4.5 ft) to 2.7 m (9 ft). This action created a series of successive navigation pools between dams by increasing water levels at low discharges (Wlosinski and Hill, 1995; Johnson and Hagerty, 2008). Unlike the more southern portion of the Mississippi River, few levees exist in this reach and the river remains highly connected to the floodplain. In fact, given the increase in water level and spatial extent at low discharges, the floodplain of this reach is often considered overly connected to the river. Consequently, the floodplain is now dominated by highly flood and sediment tolerant species such as silver maple (*Acer saccharinum*), while less flood tolerant hard-mast oak (*Quercus* spp.) and hickory (*Carya* spp.) communities have almost completely disappeared (Yin et al., 1997, 2009; Knutson and Klaas, 1998; Nelson et al., 1998). In addition to hydrological modifications, much of the UMR basin has been converted from a prairie and forest mosaic to a watershed dominated by cropland and pastureland during the past 200 years. As a consequence, Knox (2006) estimated that vertical accretion of sediments in the UMR floodplain increased from about 0.9 mm year^{-1} between 10,000 and 200 years ago to between 2 and 20 mm year^{-1} during the past 200 years. Changes in sedimentation rate and type can further influence plant community composition (Whitlow and Harris, 1979; Robertson, 1992; Ewing, 1996; Wardrop and Brooks, 1998; Adamus et al., 2001; Walls et al., 2005) as well as nutrient cycling (Pinay et al., 2000). Nutrient cycling, particularly denitrification, is of interest to the UMR management community because Rabalais et al. (2002) reported a tripling in nitrate export to the Gulf of Mexico since the 1950s, fueling the second largest coastal hypoxic zone in the world. If it is a goal of the UMR management community to manage plant species composition and sedimentation in order to enhance biodiversity and nutrient processing in the UMR floodplain, they need to know where their efforts are most likely to succeed under the current hydrologic regime as well as under alternative hydrologic regimes created by either management actions or changing environmental conditions.

The purpose of this study was to improve our basic understanding of hydrologic controls over the vegetation and soils of the UMR floodplain and use this information to develop predictive maps of the spatial distribution of flood duration and associated ecosystem services (i.e. biodiversity and nutrient processing). We therefore quantified changes in soil texture and fertility as well as the understory and overstory tree communities across sites that spanned a gradient of mean growing season flood duration (i.e. elevation). We tested two alternative hypotheses and one null hypothesis for how vegetation and soils would relate to the mean duration of the growing season that sites were flooded, each with different implications for how potential biodiversity and/or nutrient processing might be distributed across the floodplain (Table 1).

2. Materials and methods

2.1. Study site

This study occurred along approximately 320 river kilometers (200 miles) of the Upper Mississippi River floodplain from Dam 2 in the north near Hastings, Minnesota, to Dam 10 in the south, located near Guttenburg, Iowa (Fig. 1). The majority of this river reach is within the Upper Mississippi River National Wildlife and Fish Refuge and is characterized by an island-braided channel form that has developed over the last 10,000–12,000 years (Nielsen et al., 1984). The low-head dams on the Mississippi River do not store floodwaters; the river still experiences a flood pulse in the

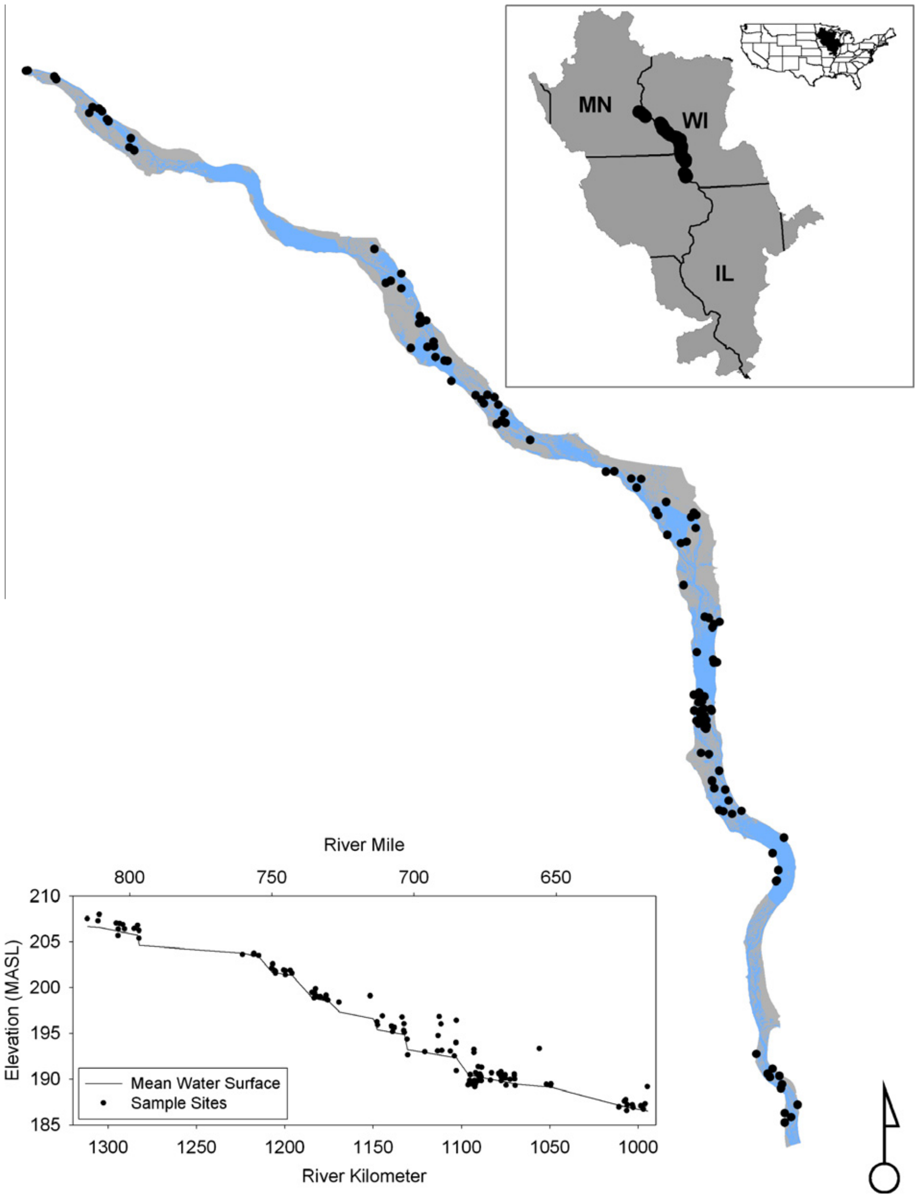

Fig. 1. Location of the Upper Mississippi River (UMR) reach studied here within the UMR basin (inset upper right) and the location of 121 sampling locations (filled circles, not to scale) that were surveyed. Also shown (inset lower left) is the elevation (MASL) of each sample site (filled circles) relative to mean river stage (1974–2004, line) plotted according to river kilometer (measured as the upstream distance from the confluence with the Ohio river).

spring, but not the extreme low-flow conditions during summer that characterized the historical river condition (Wlosinski and Hill, 1995).

Prior to lock and dam construction, the elevational distribution of tree species is thought to have followed a pattern determined by flood frequency and duration. Low-lying floodplain areas were likely dominated by early-successional flood tolerant cottonwoods (*Populus deltoides*) and black willows (*Salix nigra*), while midsuccessional species such as American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*) and sycamore (*Plantanus occidentalis*) were found at slightly higher elevations. High terraces consisted of late-successional oak communities. Following lock and dam construction, water levels throughout the UMR rose significantly, especially at low discharges, and more of the floodplain is correspondingly wetter. Much of the floodplain is now dominated by flood tolerant species such as silver maple (*A. saccharinum*) (Yin et al., 1997; Knutson and Klaas, 1998).

2.2. Sampling methodology

Between 2006 and 2008, personnel from the US Army Corps of Engineers (USACE) identified 121 sites for permanent forest monitoring (Fig. 1). Sites were selected to the extent possible to span the entire length of individual navigation pools, from just below a lock and dam to just above the next lock and dam. Within each pool local managers attempted to pair five forest stands of relatively low species richness with five stands of higher species richness based on previous forest inventory data. Although some sites initially assumed to be high diversity stands turned out to contain only a few species when encountered in the field, this procedure resulted in sites that spanned a wide range of elevations and plant species compositions. Sites were selected to avoid major anthropogenic disturbances such as development and agriculture. Patch edges were avoided by establishing plots a minimum of 50 m into the forest interior. GPS locations were recorded at each site, along with the river mile, to the nearest 1/10th of a mile. Site elevations

Table 1
Hypotheses for the response of Upper Mississippi River (UMR) floodplain vegetation and soils to increasing flood duration.

	Response	Vegetation	Soils	Implication for site selection
H_0 Eq. (1)	Random	Random composition of flood-tolerant species	Randomly varying	Flooding controls vegetation and soils stochastically. Little potential to identify sites with high capacity for nutrient processing or biodiversity based on topography
H_1 Eq. (2)	Linear	More flood-tolerant species at lower elevation sites that flood for longer durations	More fine-grained sediments at lower elevation sites that flood for longer durations	Vegetation and soils each segregate according to topography. Sites with high capacity for nutrient processing or biodiversity can be mapped as a continuous function of elevation
$H_{2,1}$ Eq. (3)	Threshold	Linear decline in the abundance of non-flood tolerant species from short to moderate flood durations, followed by uniformly high abundance of flood tolerant species beyond some threshold flood duration	Decreasing amounts of coarse-grained sediments from short to moderate flood durations, followed by uniformly fine-grained sediments at flood durations beyond some threshold	Vegetation and soils each segregate according to topography. The occurrence of sites with high capacity for nutrient processing or biodiversity can be mapped as a continuous function of topography, until some elevation, below which, site selection no longer depends on flood duration
$H_{2,2}$ Eq. (4)	Threshold	Random distribution of plant species from short to moderate flood durations, followed by a linear decline in non-flood tolerant species beyond some threshold flood duration	Random distribution of soil texture from short to moderate flood durations, followed by a linear decline in coarse-grained sediments beyond some threshold flood duration	Vegetation and soils each segregate according to topography. The occurrence of sites with high capacity for nutrient processing or biodiversity does not depend on topography, until some elevation, below which, site selection can be mapped as a continuous function of topography

Equations are given in text. Comparison among models was conducted using AIC weights.

at four corner points per plot were determined using standard surveying equipment. The vertical difference between the sample plots and the nearest water surface elevation of the UMR was determined in the field and later used to estimate the elevation of each corner post in meters above sea level (MASL).

Each sample plot measured 404.6 m^2. Within each sample plot, three 40.62 m^2 subplots were established. A single soil sample was taken from the center of each subplot using a standard soil core sampler to a depth of 30 cm. The three soil samples were combined, air dried and shipped to the University of Missouri Soil Testing Laboratory for analysis of percentage sand, silt, clay, pH, percentage organic matter by loss on ignition and extractable phosphorous, calcium, magnesium and potassium. The relative dominance and health of each species were assessed by visual inspection and the diameter at breast height (DBH) of each overstory tree greater than 13 cm in diameter was measured within each sample plot. Similar measurements were made on understory trees (<13 cm diameter) in the three subplots. For the overstory trees, DBH was converted to basal area and then relative abundance and relative basal area were summed to estimate importance values for each species. For the understory trees, the relative abundance of each species was calculated.

Annual flood duration was calculated as the mean number of days during the growing season (April 1–Sept 30, 180 days maximum) that the ground elevation of sample sites was flooded by comparing site elevation with daily river stage for the past 30 years. To estimate river stage at each 1/10th of a river mile, linear interpolation of the daily river stage was used for gauges just below and just above each dam. Daily river stage was extracted from a database developed by Ickes et al. (2007). Growing season flood duration values were then averaged across the years 1974–2004.

2.3. Data analysis

Multivariate data reduction was used to examine both the vegetation and soils data from the 121 sample locations. Three independent Principal Component Analyses (PCA) were conducted on the soils data, the understory tree data and the overstory tree data with varimax rotation. Rotated factor scores were used to evaluate loadings of individual soil variables and tree species abundance or importance values. To avoid bias due to the occurrence of rare species, each overstory species that was present on >15% of the sampling plots and for which we observed at least 50 individuals was considered according to species. All other, less common species, were grouped into a single category of ‘other’ species. Far fewer understory individuals were encountered in the field and we therefore restricted our analysis to the three most common species and one additional category of ‘all other species’. Scores for the first, second and third principal components for both plant and soil variables were retained as measures of plant species composition and soil texture and fertility. Total basal area of overstory trees and the density of understory trees were also retained as surrogate measures of total above ground biomass. Finally, Shannon’s diversity indices (Shannon and Weaver, 1962) were calculated from the data for all species and used as measures of diversity.

Next, we ruled out the possibility that our response variables displayed longitudinal patterns by plotting them against river mile and fitting increasingly higher order polynomial models to the data. Three models were then fit to bivariate relationships between ‘days flooded’ and our response variables: random (H_0, Eq. (1)), linear (H_1, Eq. (2)) and threshold (H_2, Eqs. (3) and (4)).

$$H_0 : y = \beta_0 + \varepsilon \tag{1}$$

where β_0 is the mean which displays no significant change in response to increasing flood duration. We predicted that the plant community of the UMR is composed of highly flood tolerant species, regardless of elevation; and that soil texture and fertility are uniformly fine grained and relatively high respectively (Table 1).

$$H_1 : y = \beta_0 + \beta_1 x + \varepsilon \tag{2}$$

Eq. (2) is a linear model that characterizes linear changes in y (vegetation or soils) with increasing flood duration (x), were β_0 is the y-intercept and β_1 is the slope. Eq. (2) predicts that soil texture will become increasingly finer grained, with higher amounts of organic matter, the longer sites are flooded, reflecting the sorting of sediments by grain size. It also predicts that the plant community will become increasingly dominated by more flood tolerant plant species the longer sites are flooded.

$$H_{2,1} : y = \begin{cases} y = \beta_0 + \beta_1 x + \varepsilon & , x \le X_1 \\ y = \beta_0 + \varepsilon & , x > X_1 \end{cases} \tag{3}$$

or

$$H_{2,2} : y = \begin{cases} y = \beta_0 + \varepsilon & x, \leq X_1 \\ y = \beta_0 + \beta_1 x + \varepsilon & x, > X_1 \end{cases} \tag{4}$$

The second alternative hypothesis was that the vegetation and soils of the UMR floodplain display threshold responses to increasing flood duration. Threshold responses could occur in two different ways ($H_{2,1}$, Eq. (3) or $H_{2,2}$ Eq. (4)). Eq. (3) is a two segment linear model that characterizes a linear change in y (vegetation and/or soils) with x (flood duration), to a threshold flood duration (X_1), followed by no subsequent change in vegetation or soils with increasing flood duration beyond X_1. Eq. (4) is also a two segment linear model, but it characterizes no change in vegetation and/or soils (y) with increasing flood duration (x) to a threshold flood duration (X_1), followed by a linear change in vegetation or soils across flood durations lasting longer than X_1. We predicted that the vegetation and soils across our sites would display the greatest changes from short to moderate flood durations, with little additional change attributable to further increases in flood duration. This finding would suggest progressively stronger physiological control over the plant community as flood duration increases, to a point at which the community is dominated by only a few highly flood tolerant species, with no further changes in species composition occurring at even longer durations.

Eqs. (1) and (2), and either Eqs. (3), (4) (after examining the biplots visually) were fit to the data and the best model was selected using AIC weights. AIC weights can be thought of as "probabilities" that the estimated model r is the best model for the data, given the set of models considered (Burnham and Anderson, 1998). Finally, we used residual regression to determine whether soils measurements could explain a significant amount of the variance in plant measurements after accounting for the influence of flood duration. We carried out all data analyses in R version 2.7.1 (R Development Core Team, 2008).

2.4. Mapping flood duration

Support for H_1 or H_2 would suggest that landscape distributions of flood duration could be used as a first approximation for landscape distributions of forest plant species composition and soil texture and fertility, surrogate measures for biodiversity and denitrification. We therefore created maps of the distribution of mean growing season flood duration using a continuous elevation surface developed using LIDAR (light detecting and ranging) by the Long Term Resources Monitoring Program. The mean number of days during the growing season (April 1–Sept 30, 180 days) from 1974–2004 that each elevation (0.5 foot increments) at each river mile (1/10th mile increments) was flooded was calculated using the database developed by Ickes et al. (2007). We then mapped these flood durations in ArcGIS 10 (ESRI, 2011) using 10 m pixels.

3. Results

3.1. Soil and vegetation measurements

A wide variety of soil textures and fertilities were encountered across the sample sites. Sand content ranged from 0% to 97.5%, extractable phosphorous ranged from 18 ppm to 240 ppm, and percentage organic matter ranged from 0.8% to 18.5%. Multivariate analysis revealed negative correlations among sand (PC1 loading of 0.514) and silt (PC1 loading of −0.504) and to a lesser extent clay (PC1 loading of −0.397) and this axis explained 64.7% of the total variance among sample sites (Table 2). Hence PC1 is primarily a gradient of soil texture, with more negative values corresponding to sites with more fine grained sediments and positive values corresponding to sites with coarser grained sediments. Further, pH, organic matter, Ca, Mg and K all had weak negative correlations with sand, suggesting that sandier sites were also less fertile than silt/clay sites.

Table 2
Loadings from Principal Components Analysis of floodplain soils.

Variable	PC1 (64.7%)	PC2 (10.2%)	PC3 (8.2%)
pH	−0.132	0.133	0.017
OM	−0.164	−0.233	0.125
P	0.012	**0.562**	−0.459
Ca	−0.426	−0.101	−0.306
Mg	−0.291	−0.4	−0.288
K	−0.116	0.227	−0.606
Sand	**0.514**	−0.161	−0.217
Silt	**−0.504**	0.461	0.401
Clay	−0.397	−0.389	−0.145

Loadings with an absolute value >0.5 are in bold. The percentage of variation explained by components 1–3 are given in parentheses. PC1 for the soils data was a gradient of soil texture and fertility, with coarser grained soils and lower fertility found at sites having more positive scores and finer grained sediments with higher fertility at sites with more negative scores.

The understory tree community was poorly developed; a total of only 277 individual trees were found across all 121 sites. The density of understory trees ranged from 82 stems/ha to 900 stems/ha and averaged 248 stems/ha. The understory contained more species (38) than the overstory (26), but most understory species were very rare (Table 3). *F. pennsylvanica* was the most abundant species in the understory (126.1/ha) followed by *A. saccharinum* (91.5/ha) and *U. americana* (52.9/ha) (Table 3). Overstory tree densities ranged from 49.43 trees/ha to 1112 trees/ha and averaged 434.8 trees/ha. Total basal area of the overstory ranged from 4.5 m^2/ha to 75 m^2/ha and averaged 31.9 m^2/ha. There were 26 species and 2126 individual overstory trees present in the 121 sampling plots. *A. saccharinum* was the most abundant overstory species with a density of 218.2/ha, followed by *F. pennsylvanica* (61.7/ha) and *U. americana* (35.5/ha) (Table 3). *A. saccharinum* was found at 83% of sample sites and *F. pennsylvanica* was found at 56% of sample sites.

Multivariate analysis of the understory tree community revealed a strong negative relationship between sites dominated by *A. saccharinum* (PC1 loading of −0.528) and sites with species from the 'other' category (PC1 loading of 0.817). The second and third most abundance species also had weak negative correlations with other species (*F. pennsylvanica*, PC1 loading of −0.222, and *U. americana*, PC1 loading of −0.067). PC1 explained 50.9% of the total variance among sample sites (Table 4). The understory PC1 therefore represents increasing abundance of any species other than the three most common species. PC2 explained 32.9% of the remaining variance among sampling sites and it was an axis of *A. saccharinum* (PC2 loading of −0.604) to *F. pennsylvanica* (PC2 loading of 0.776) (Fig. 2, Table 4). Visual inspection of the biplot in Fig. 2 suggests little association between flood duration (symbol size) and the position of sites along either PC1 or PC2.

In the overstory, *A. saccharinum* (PC1 loading of −0.875) was weakly negatively correlated with *F. pennsylvanica* (0.165), *U. americana* (PC1 loading of 0.088) and more strongly negatively correlated with all other species (PC1 loading of 0.432). PC1 explained 54.4% of the total variance among sample sites (Fig. 2, Table 4). Hence, PC1 for the overstory trees was a measure of the abundance of *A. saccharinum* and any site with a negative PC1 score was likely to be dominated by *A. saccharinum*. Along the second principal component, *A. saccharinum* (PC2 loading of 0.253) was positively correlated with the species grouped into the 'other' category (0.786) and negatively correlated with the remaining species (Fig. 2, Table 4). PC2 accounted for 17.8% of the total variance among sample sites. Visual inspection of the biplot in Fig. 2 suggests a strong association between flood duration (symbol size)

Table 3
The densities of most common understory and overstory tree species detected in all sample plots, listed in order of the abundance of overstory species.

Scientific Name	Abbreviation	Common name	Overstory density (#/ha)	Understory density (#/ha)	Flood tolerance
Acer saccharinum	ACSA2	Silver maple	218.2	91.5	1,2
Fraxinus pennsylvanica	FRPE	Green ash	61.7	126.1	1,2
Ulmus americana	ULAM	American elm	35.5	52.9	2,3
Betula nigra	BENI	River birch	21.4	32.5	2,3
Populus deltoides	PODE3	Eastern cottonwood	19.4	0.0	2
Acer negundo	ACNE12	Boxelder	13.7	14.2	1,2
Quercus bicolor	QUBI	Swamp white oak	11.0	26.4	3
Robinia pseudoacacia	ROPS	Black locust	10.6	6.1	4
Quercus rubra	QURU	Northern red oak	9.2	10.2	4
Celtis occidentalis	CEOC	Common hackberry	5.1	20.3	4
Fraxinus nigra	FRNI	Black ash	4.1	8.1	4
Quercus velutina	QUVE	Black oak	3.9	4.1	4
Populus tremuloides	POTR5	Quaking aspen	3.5	8.1	4
Salix nigra	SANI	Black willow	2.9	6.1	1
Salix spp.	SALIX	Willow	2.5	4.1	1
Tilia americana	TIAM	American basswood	1.6	2.0	2,3
	UNK	Unknown	1.6	0.0	
Pinus resinosa	PIRE	Red pine	1.2	0.0	4
Quercus spp.	QUERC	Oak	0.4	0.0	3,4
Juglans nigra	JUNI	Black walnut	0.8	0.0	4
Carya cordiformis	CACO15	Bitternut hickory	0.8	6.1	4
Morus rubra	MORU2	Red mulberry	0.8	0.0	4
Prunus serotina	PRSE2	Black cherry	0.8	4.1	2
Gleditsia triacanthos	GLTR	Honey locust	0.8	0.0	1,2
Rhamnus cathartica	RHCA3	Common buckthorn	0.4	16.3	2,3
Morus alba	MOAL	White mulberry	0.4	0.0	4

Flood tolerance values are from Whitlow and Harris (1979). 1 = highly flood tolerant, 2 = moderately flood tolerant, 3 = less flood tolerant species and 4 = species that are not flood tolerant.

and the position of sites along the PC1 axis. Sites dominated by species other than *A. saccharinum* (positive PC1 scores) tended to be situated on higher elevations, which experienced shorter flood durations (smaller symbol sizes).

3.2. Soil and vegetation relationships with flood duration

No significant associations were found between either soils or plant measurements and longitudinal position (river mile) ($P > 0.05$), suggesting that this 320 km river reach likely falls within a single physiographic region with respect to both geomorphology and the forest community. Statistical tests were therefore carried out on the data from all sites collectively. Statistical associations between flood duration and measures of soil texture, fertility and plant community composition and diversity were either random or fit the threshold model (Eq. (3)) (Table 5). Threshold relationships were found between flood duration and the first principal component of the soils data as well as percent organic matter (Fig. 3, Table 5). Soil texture became increasingly finer grained (negative PC1 score) with increasing flood duration to a threshold at 69.8 (+/−6.4 SE) days inundated. Beyond that threshold, soils were exclusively silt/clay (>65% and negative PC1 scores) and displayed no further changes with increasing flood duration (Fig. 3). Substantial variation existed around the regression line from 0 days to 69.8 days of flooding, suggesting that although short flood durations tend to correspond with sandier soils, a relatively wide range of soil textures and fertilities can be found at sites that flood for less than 69.8 days (∼40% of the growing season). Percent organic matter increased from 0 days to 52 (+/− 11.9 SE) days flooded, but was consistently >5% and remained unchanged with further increases in flood duration (Fig. 3, Table 5).

The scores of all three principal components for the understory tree community were randomly associated with flood duration (Fig. 4, Table 5), confirming the lack of association visible in the biplot in Fig. 2. However, the diversity of the understory tree community declined significantly from 0 days to 41.3 (+/−10.8 SE) days flooded, followed by no further changes in diversity across longer flood durations (Fig. 4, Table 5). As for the soils data, understory tree diversity varied considerably across sites that flooded for less than 41.3 days. Grouping the understory sites by flood

Table 4
Loadings from Principal Components Analysis of the understory (a) and overstory (b) tree communities.

(A) Understory Trees	PC1 (50.9%)	PC2 (32.9%)	PC3 (16.2%)	(B) Overstory Trees	PC1 (54.4%)	PC2 (17.8%)	PC3 (9.9%)
Acer saccharinum	−**0.528**	**-0.604**	−0.326	*Acer saccharinum*	−**0.875**	0.253	0.126
Fraxinus pennsylvanica	−0.222	**0.776**	0.313	*Fraxinus pennsylvanica*	0.165	−0.453	**0.765**
Ulmus americana	−0.067	0.007	−**0.863**	*Ulmus americana*	0.088	−0.212	−0.293
Other	**0.817**	−0.179	0.225	Betula nigra	0.064	−0.013	−0.042
				Populus deltoides	0.041	−0.147	−0.202
				Acer negundo	0.085	−0.214	−0.499
				Other	0.432	**0.786**	0.146

Loadings with an absolute value >0.5 are in bold and the percentage of variation explained by components 1–3 are given in parentheses. PC1 for the understory community was a gradient of the three most common species (*A. saccharinum*, *F. pennsylvanica*, *U. americana*) which had negative PC1 loadings and all other species, which had a loading of 0.817. PC1 for the overstory community was a gradient of *A. saccharinum* (−0.875) to all other species (positive loadings).

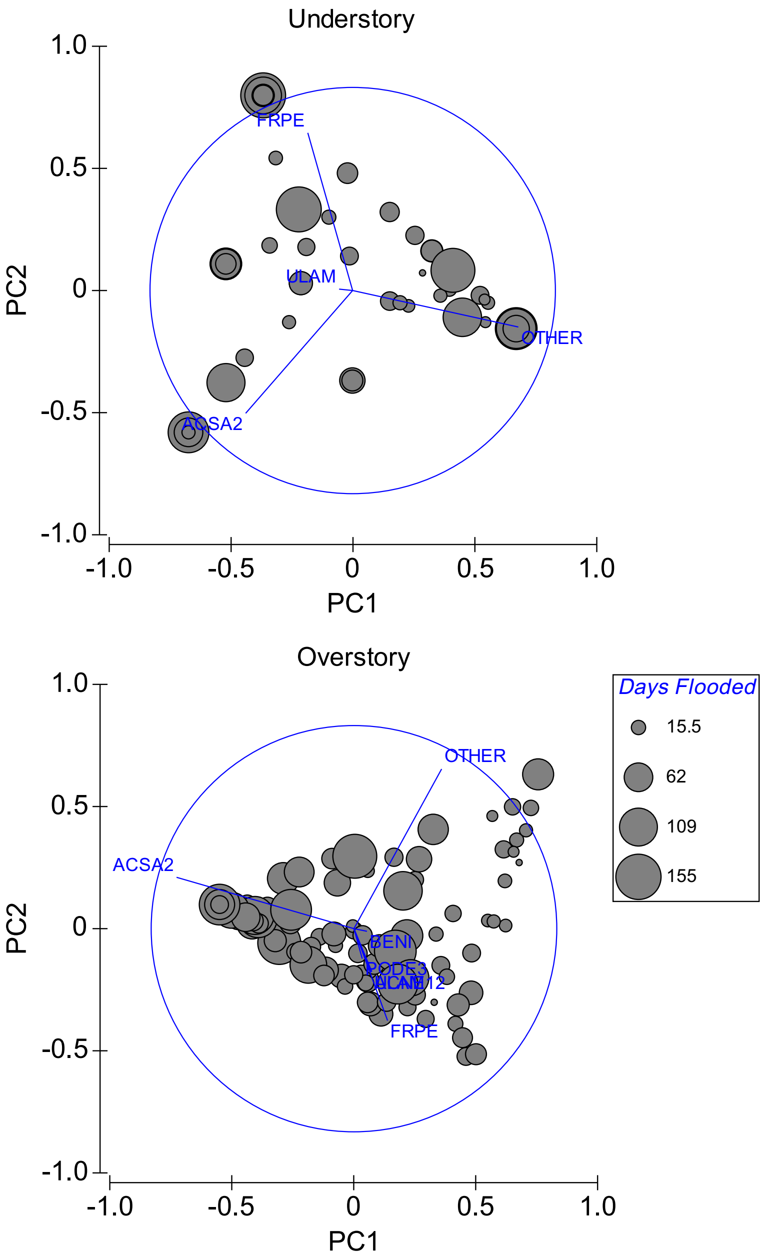

Fig. 2. Biplots of the understory and overstory tree community. Vectors represent increasing abundance of particular species (see Table 3 for abbreviations). The closer each data point is to the end of each vector, the more dominated it is by the species represented by the vector. Each site is represented by circles which are scaled to flood duration. For overstory trees, note the association between short flood durations (smaller circles) and all species besides *A. saccharinum* (ASCA2).

duration classes revealed an increase in the proportional abundance of *A. saccharinum* with increasing flood duration up to approximately 60 growing season days and a general decline in the proportional abundance of species in the 'other' category (Fig. 5).

A threshold relationship was found between flood duration and PC1 for the overstory trees (Fig. 4, Table 5). PC1 decreased strongly from 0 days to 55.2 (+/−9.1 SE) days flooded, after which point PC1 was typically negative. This indicates that sites that flood for longer than 55.2 days (~30% of the growing season) tend to be dominated by *A. saccharinum* (negative PC1). Further, the diversity of overstory species declined from 0 days to 64.0 (+/−8.4 SE) days flooded (~40% of the growing season), after which point diversity estimates were homogeneously low (Fig. 4, Table 5). Grouping the overstory sites by flood duration classes confirmed the strong increase in the proportional abundance of *A. saccharinum* with increasing flood duration up to approximately 50–70 days of the growing season and a strong decline in the proportional abundance of all other species (Fig. 5). Finally, we found no significant relationship between flood duration and the density of understory trees or the basal area of overstory trees ($P > 0.05$), indicating that the main effects of flooding was on species composition as opposed to plant abundance.

Given the low R^2 values of the threshold models shown in Fig 4, and relatively high variance in plant community measures found from 0 to the threshold flood durations (~30–40% of the growing season), we further tested the hypothesis that the soils measurements would explained a significant amount of the variance not accounted for by the linear association with flood duration at sites that flooded for less than the threshold estimates. Soil PC1 was a

Table 5
AIC weights for random, linear and threshold models fit to the variables listed as a function of flood duration.

Data Type	Variable	Random	Linear	Threshold
Soils	PC1	0	0.01	**0.99**
	PC2	**0.59**	0.36	0.05
	PC3	**0.61**	0.37	0.02
	% Organic Matter	0	0.02	**0.98**
Understory trees	Density	**0.88**	0.10	0.02
	PC1	**0.62**	0.33	0.05
	PC2	**0.69**	0.11	0.2
	PC3	**0.77**	0.18	0.05
	Shannon's diversity	0.06	0.04	**0.9**
Overstory Trees	Basal Area	**0.95**	0.04	0.01
	PC1	0	0.10	**0.90**
	PC2	**0.99**	0	0
	PC3	**0.79**	0.18	0.04
	Shannon's diversity	0.03	0.07	**0.9**

AIC weights can be interpreted as the probabilities that any single model is the best model for the data, given the three models considered (Burnham and Anderson, 1998). Weights for the best models are given in bold.

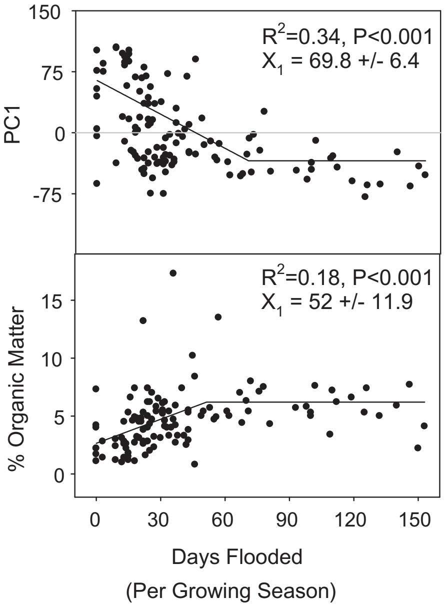

Fig. 3. Scores for PC1 for the soils data, an axis of sand (+) to silt/clay (−), as well as percentage organic matter plotted as functions of flood duration (mean number of days each site was inundated during the growing season over the past 30 years). Regression lines are given for models with the highest AIC weights (Table 5). X_1 is the threshold flood duration (±SE), beyond which point PC1 is consistently negative (silt/clay soils) and organic matter >5%, regardless of further increases in flood duration.

significant predictor of the remaining variance in understory diversity ($R^2 = 0.12$, $P = 0.02$), overstory diversity ($R^2 = 0.15$, $P < 0.001$) and overstory PC1 ($R^2 = 0.16$, $P < 0.001$) after first removing the linear effect of flood duration.

4. Discussion

4.1. Threshold effects of flood duration

The forest vegetation and soils of this stretch of the Upper Mississippi River (UMR) displayed threshold responses to increasing flood duration, measured as the mean number of days during the growing season that each site was flooded over the past 30 years. Studies conducted along other rivers also indicate that flood inundation duration is a key environmental factor shaping the vegetation and soils of floodplains at landscape scales (e.g. Auble et al., 1994; Toner and Keddy, 1997; Pinay et al., 2000). Furthermore, nonlinear, threshold responses frequently occur in wetland and other semiterrestrial systems (Gergel et al., 2002; Groffman et al., 2006). Our results showed that low elevation sites that flood for longer than about 40% of the growing season (~70 days) have homogeneously silt/clay soils with organic matter exceeding 5%, and an overstory tree community composed of >70% *A. saccharinum*. Further, the diversity of both the under and overstory communities was uniformly low in such areas.

Previous studies along the UMR have documented a loss of flood intolerant plant species along the reach studied here (e.g. *Quercus* spp.) and poor generation of understory trees as a result of higher water surface elevations following dam construction (Yin et al., 2009; Knutson and Klaas, 1998; Romano, 2010). Our findings at sites that were annually flooded for longer than 40% of the growing season may reflect such hydrologic modifications. In addition to the hydrologic modifications to this reach, past studies have documented increased deposition of fine textured sediments due to agricultural land use and erosion (Nielsen et al., 1984; Knox, 2006), especially in low-laying areas (Rogala et al., 2003), which likely explains the homogeneous soil types found at the low elevation sites of our study. Sedimentation rates are typically much greater in lower elevation floodplain sites (Hupp and Morris, 1990; Mitsch and Gosselink, 1993). The differences we found in plant community composition between high and low elevation sites are also consistent with effects of sedimentation and enhanced nutrient availability (Ewing, 1996; Wardrop and Brooks, 1998; Adamus et al., 2001; Walls et al., 2005) and it is possible that the altered hydrologic regime of the UMR and the altered land use of the UMR basin have additive effects on the plant communities found at lower floodplain elevations.

In contrast to the homogeneity of floodplain vegetation and soils found at sites that flooded for longer than 40% of the growing season, we detected the greatest amount of change in plant and soil properties with increases in flood duration lasting from 0% to roughly 40% of the growing season. However, across our models, goodness of fit measures (R^2) never exceeded 0.34 and much of the variation in plant and soil measurements not accounted for by the threshold response to flooding occurred at sites experiencing short flood durations. These results indicate that although the vegetation and soils of the UMR are highly predictable at low elevation sites that flood for long durations, a comparatively wider range of ecosystem properties exists at higher elevation sites. Soil PC1 accounted for an additional 12–16% of the variance in the plant measurements at sites that flooded for durations shorter than the thresholds shown in Fig. 4, indicating that soil texture and fertility

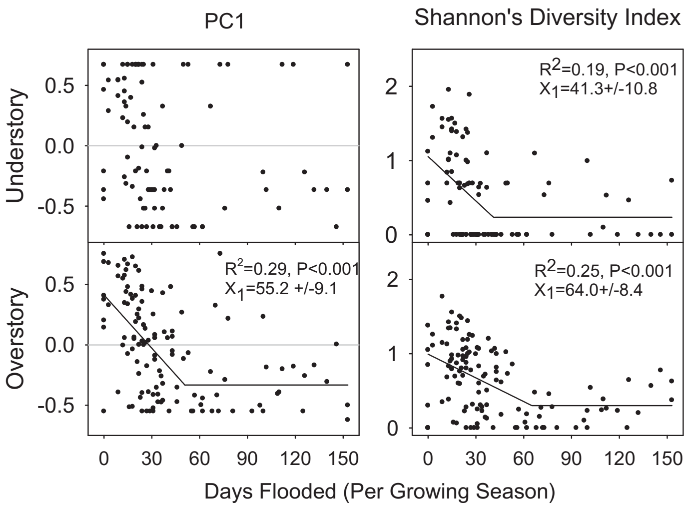

Fig. 4. Scores for understory and overstory PC1 as well as the diversity of understory and overstory trees plotted as functions of flood duration. As in Fig. 3, regression lines are given for models with the highest AIC weights (Table 5) and X_1 denotes the threshold flood duration. Sites dominated by an understory community of *A. saccharinum*, *F. pennsylvanica* and *U. americana* have negative understory PC1 scores while sites dominated by other species have positive scores. Sites dominated by *A. saccharinum* have negative overstory PC1 scores while sites dominated by other species have positive scores.

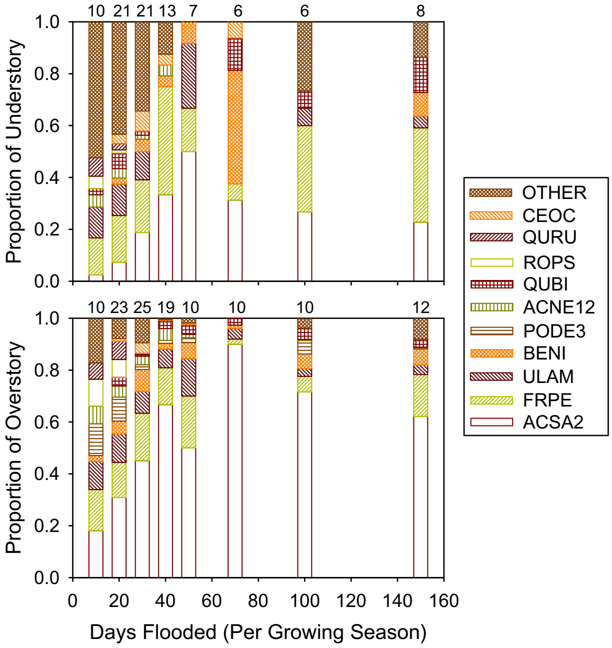

Fig. 5. The proportional abundance of the ten most abundant species (with all other species grouped into a single 'other' category) for sample sites grouped according to flood inundation. Numbers along the top of graphs denote the number of samples within each grouping. Note the strong increase in *A. saccharinum* (ASCA2) with increasing flood inundation in both the understory and overstory. Other abbreviations are defined in Table 3.

explain some of the variance in the plant communities found at higher elevation sites. Nevertheless, anywhere from 50% to 70% of the variance in the plant community at the higher elevation sites appears to be due to factors other than flood duration or soils, suggesting that although short flood durations and sandy soils may be necessary for diverse tree communities, they are not sufficient.

One explanation for the wide range of plant and soil measures found at higher elevation sites is that no single measure of flooding can account for all aspects of water-related effects on wetland vegetation and soil distributions (Mitsch and Gosselink, 1993). Inundation duration is an useful predictor because it tends to be correlated with a suite of other environmental variables, such as: flood frequency, the duration of anoxia that roots experience, sediment deposition, soil moisture and depth to groundwater. However, a single, long-lasting flood event, such as the UMR experienced in 1993, could deposit fine textured sediments at some higher elevation sites and contribute to increased variance in the plant community through increased mortality (Yin, 1998).

Another explanation for the variance found in the plant community at higher elevation sites might be the occurrence of multiple other biotic factors in such areas (Dobzhansky, 1950; MacArthur, 1972; Brown et al., 1996). Abiotic factors related to physiological stress and biotic factors related to competition and predation often interact to set limits on species distributions (Brown et al., 1996). However, along environmental gradients, relative control over species distributional patterns may switch from primarily physiological mechanisms to biotic factors. Lower elevations experience longer flood durations than higher elevations, which constitutes greater physiological stress on plant germination and growth due to longer anaerobic conditions (Hosner and Minckler, 1963; Whitlow and Harris, 1979; Mitsch and Gosselink, 1993; Yin, 1998; Burke et al., 2003). Further, areas of high deposition favor more light seeded species (e.g. *Acer* spp.) (Jurik et al., 1994). We would therefore expect greater physiological control over floodplain vegetation at sites lower in elevation, which experience longer flood durations and greater sediment accumulation. The homogeneity among our measurements of floodplain vegetation community composition at sites lower in elevation as compared to higher elevation sites may be a reflection of this phenomenon as only a few extremely flood and sediment tolerant species were found at such sites. In contrast, the wider range of community compositions and diversity estimates at higher elevation sites suggest weaker physiological control and progressively stronger biotic control (e.g. competition, herbivory, etc.), the outcomes of which are more difficult to predict on the basis of landscape position. Our results indicate that there may be a critical point along the elevation gradient of this floodplain reach at which control over vegetation switches from several biotic factors to physiological factors associated with flood duration (e.g. soil moisture, anoxia, sedimentation). Flood durations lasting approximately 40% of the growing season appear to be a quantitative measure of this critical point.

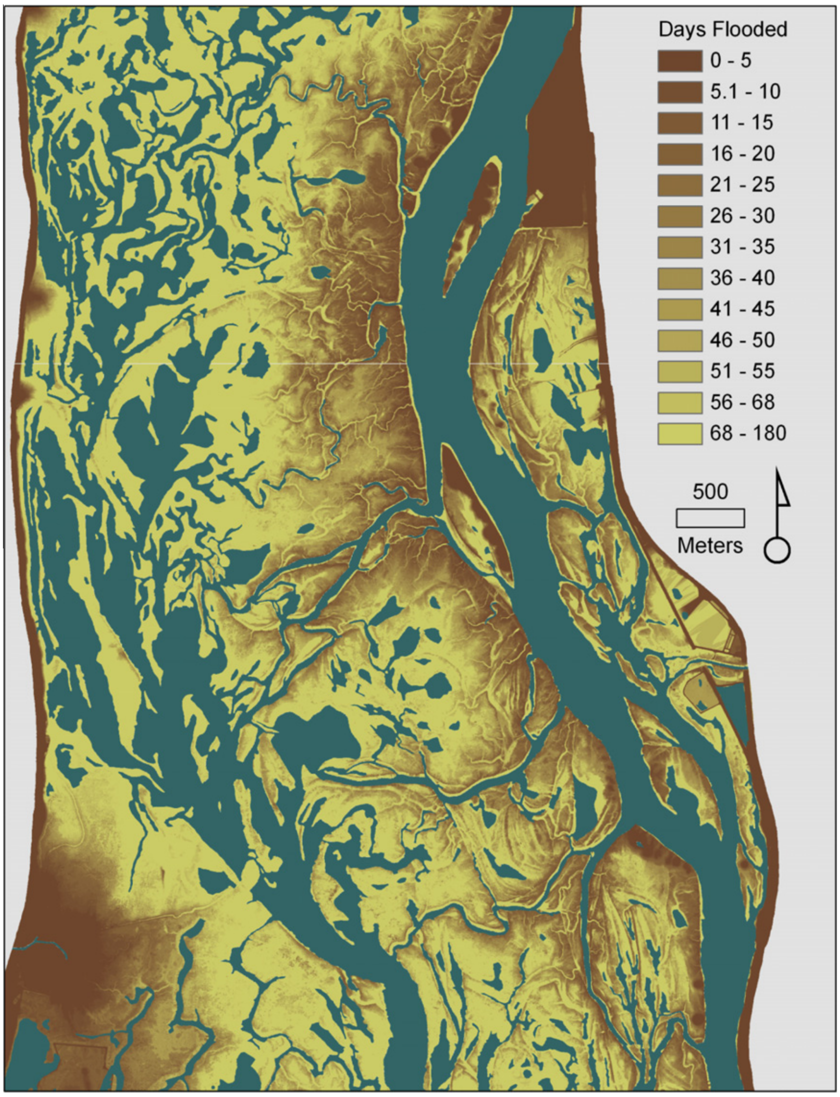

Fig. 6. An example of a map of the spatial distribution of growing season flood duration (0–180 days), for a small portion of the river reach studied here. Higher elevation sites are shown in progressively browner colors, sites positioned at higher elevations are likely to have much sandier soils and a more diverse forest community relative to lower elevation sites. Sites found within the 68–180 days flooded class are likely to have uniformly high silt/clay contents and less diverse forest communities.

4.2. Ecological and management implications

Variation in sediment texture can have important implications for plant species composition (Ewing, 1996; Wardrop and Brooks, 1998; Adamus et al., 2001; Walls et al., 2005). But sediment texture is also a primary factor regulating denitrificaiton and the ability of floodplains to reduce nitrogen delivery to downstream coastal areas (Peterjohn and Correll, 1984; Pinay et al., 2007; Noe and Hupp, 2009). While the duration of flooding directly influences soil nutrient cycling by controlling the duration of oxic and anoxic phases (Ponnamperuma, 1972; Keeney, 1973; Patrick and Tusnem, 1972) soil texture influences nutrient cycling by altering water holding capacity, organic matter content and the C and N present in microbial biomass (Pastor et al., 1984; McClaugherty et al., 1985; Pinay et al., 1995). Interestingly, Pinay et al. (2000) showed that beyond a threshold of 65% silt plus clay, soil denitrification rates in the Garonne River floodplain in France increased linearly with silt plus clay content. Other studies have reported negligible soil denitrification below 60% water holding capacity, which is characteristic of sandier soils (Aulakh and Rennie, 1985; Grundmann and Rolston, 1987). Soils with silt plus clay content greater than 65% have much higher water holding capacities. In our study, beyond the threshold flood duration of 40% of the growing season, silt plus clay was never lower than 45%. These results suggest that landscape distributions of flood duration across the UMR floodplain likely correspond directly with rates of denitrification via control over nitrate delivery, soil texture and oxygen concentrations. This is an important hypothesis to test along this and other floodplain rivers given the huge importance of denitrification for reducing nitrogen transport to downstream coastal areas (Peterjohn and Correll, 1984; Noe and Hupp, 2009).

If it is a goal of resource managers to enhance the capacity of floodplains to provide ecosystem services under both current and potential future hydrologic regimes, then they need know where their efforts are most likely to succeed under a range of hydrologic conditions. In this regard, the occurrence of threshold effects of flood duration provide a potential key to successful management of soil nutrient dynamics and plant community composition in this floodplain. Groffman et al. (2006) pointed out that the process of adaptive management; that is proposing, implementing and re-evaluating solutions to environmental problems is far easier when threshold relationships exist. In such cases, crossing over important ecological thresholds ought to improve the odds of moving ecosystems to the ‘desired state’. Fig. 6 displays a continuous change in growing season flood duration from 0 days to 68 days (the maximum threshold flood duration we observed) from dark brown to light brown, with longer flood durations represented as a single class (the lightest shade of brown) for a small section of the UMR. Our empirical results imply uniform rates of denitrification and species diversity estimates in areas that flood for longer than 68 days of the growing season, suggesting that management outcomes in those areas might ultimately result in highly predictable outcomes. In contrast, the wide range of ecological conditions we found at higher elevation sites that flood less frequently and for shorter durations suggests that management outcomes will be far less predictable there. In such areas, managers will need to account for factors other than flood duration. We hypothesize that such factors are more local in nature and can be managed on a site-by-site basis, but this can be tested through local adaptive management projects. Nevertheless, spatial distributions of flood duration under the current hydrologic regime, such as that shown in Fig. 6, could be compared with similar distributions predicted from model outputs for river discharge and stage under more natural hydrologic regimes (e.g. water level drawdowns) as well as potential changes in discharge and stage due to climate induced changes to regional precipitation patterns. Of particular importance is how the distribution of the >40% flood inundation duration class changes under such alternative scenarios. Given the correlative nature of our study, we cannot conclude that such changes in flood inundation distributions would produce particular plant and soil properties in the future. Furthermore, it should be pointed out that the threshold flood durations identified here are likely unique to the UMR, given its hydrologic regime and sediment loads. However, this approach offers a simple way for floodplain managers to begin to consider their decisions in a more predictive and spatially explicit manner, now and into the future.

5. Conclusions

Most large rivers have experienced major changes in hydrology and sedimentation over the past century, with concomitant effects on nutrient cycling and biodiversity. To better manage the services that these ecosystems provide, a basic understanding of the role hydrology plays in plant and ecosystem dynamics is needed. Our results suggest that flood durations lasting ~40% of the growing season may constitute a threshold point along the elevation gradient of the Upper Mississippi River floodplain. Sites lower in elevation, which tend to be inundated for longer than 40% of the growing season, had exclusively fine grained sediments with higher percent organic matter and homogeneously low estimates of species diversity. Such sites were dominated by a single species (*A. saccharinum*), which made up greater than 70% of the overstory community. A comparatively more diverse forest community and wider range of species compositions and soil conditions were found at sites inundated for less than 40% of the growing season, suggesting that multiple mechanisms in addition to flooding influence floodplain vegetation and soils at higher elevation sites. Landscape distributions of flood duration provide a first approximation of areas with high potential for successful management of nutrient cycling and biodiversity under the current hydrologic regime and may be useful for examining the potential effects of alternative hydrologic conditions due to management actions (e.g. water level management) or environmental conditions (e.g. climate change impacts to hydrology) on landscape distributions of these important ecosystem services.

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