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Article

Vegetation composition, nutrient, and sediment dynamics along a floodplain landscape

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With 5 figures and 2 tables

Abstract: Forested floodplains are important landscape features for retaining river nutrients and sediment loads but there is uncertainty in how vegetation influences nutrient and sediment retention. In order to understand the role of vegetation in nutrient and sediment trapping, we quantified species composition and the uptake of nutrients in plant material relative to landscape position and ecosystem attributes in an urban, Piedmont watershed in Virginia, USA. We investigated in situ interactions among vegetative composition, abundance, carbon (C), nitrogen (N) and phosphorus (P) fluxes and ecosystem attributes such as water level, shading, soil nutrient mineralization, and sediment deposition. This study revealed strong associations between vegetation and nutrient and sediment cycling processes at the plot scale and in the longitudinal dimension, but there were few strong patterns between these aspects at the scale of geomorphic features (levee, backswamp, and toe-slope). Patterns reflected the nature of the valley setting rather than a simple downstream continuum. Plant nutrient uptake and sediment trapping were greatest at downstream sites with the widest floodplain and lowest gradient where the hydrologic connection between the floodplain and stream is greater. Sediment trapping increased in association with higher herbaceous plant coverage and lower tree canopy density that, in turn, was associated with a more water tolerant tree community found in the lower watershed but not at the most downstream site in the watershed. Despite urbanization effects on the hydrology, this floodplain functioned as an efficient nutrient trap. N and P flux rates of herbaceous biomass and total litterfall more than accounted for the N and P mineralization flux rate, indicating that vegetation incorporated nearly all mineralized nutrients into biomass.

Keywords: Piedmont, riparian vegetation, litterfall, plant composition, nutrient cycling, River Ecosystem Synthesis

Introduction

Floodplains are important landscape features for retaining river nutrients and sediment loads transported from overbank flooding (Craft and Casey 2000, Olde Venterink et al. 2006, Hupp et al. 2008, Noe & Hupp 2009). Research on floodplains is increasing in response to the demand to restore riparian connectivity of river flow and riparian nutrient and sediment trapping. Vegetation plays an important role in floodplain functions such as nutrient cycling (Pinay et al. 1995, Prescott 2002, Hefting et al. 2005) and sediment trapping (Hupp 1992, Gonzalez 2010, Jolley et al. 2010, Hession & Curran 2013). However, there are changes in the functioning of floodplains along the floodplain landscape that need further investigation to improve our predictions of floodplain functions and restoration effects in various geographic regions (Brinson 1993).

Floodplain nutrient dynamics and vegetation characteristics are expected to change longitudinally with distance downstream as river discharge and floodplain inundation and width increase (Brinson 1993, Spink et al. 1998, Rheinhardt et al. 2013, Bruno et al. 2014) and later-

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ally as topography and inundation varies across the floodplain (Junk et al. 1989, Hupp 2000, Wassen et al. 2002, Noe et al. 2013). There are many general conceptual frameworks for understanding patterns of nutrient cycling and biocomplexity along a river system. For example, the River Continuum Concept describes the structure and function of communities along a river system as a predictable continuum (Vannote et al. 1980). Contrasting with this view, the River Ecosystem Synthesis perspective predicts that longitudinal position is less important than other hydrogeomorphic features of a valley scape in governing ecosystem structure and function (Thorpe et al. 2006).

Ecosystem attributes such as water level, shading, soil mineralization, sediment deposition and hydraulic conditions interact to affect vegetation and nutrient cycling in floodplains. Floodplains with very high sedimentation rates may induce stress which could result in lower concentrations of plant nutrients and more efficient use of nutrients (Jolley et al. 2010). Wetness gradients may influence vegetation nutrient dynamics such that dryer sites have lower litterfall N content than wetter sites with longer periods of soil saturation on deciduous forested floodplains in the southeast USA (Clawson et al. 2001). This indicates that the trees at the driest sites maybe more efficient in internal translocation of N (Clawson et al. 2001). Vegetation biomass varies with soil mineralization on riparian peatlands (Wassen et al. 2002) and with wetness in montane meadows (Dwire et al. 2004). Herbaceous biomass increases when timber harvesting reduces overstory density, increasing light availability, and tree thinning is a mechanism to increase herbaceous vegetation for the purpose of trapping sediment on forested bottomland floodplains (Aust et al. 2012). However, there is a lack of information about productivity and nutrient cycling or the role of vegetation in sediment trapping and nutrient dynamics in Piedmont regions.

Vegetation composition in forested floodplains is indicative of prevailing hydro-geomorphic condition (Hupp & Osterkamp 1985, Bendix & Hupp 2000, Diaz & Cabido 2001, Hupp & Bornette 2003). Vegetation composition varies across hydrogeomorphic gradients; laterally between the channel and the upland (Hupp 2000, Wassen et al. 2002, Auble et al. 2005) and longitudinally in riparian wetlands systems from headwaters to large river floodplains (Hupp & Osterkamp 1985, Rheinhardt et al 2013). Local species composition variation is complicated by many environmental factors including the amount of the water, soil fertility, and disturbance, which directly influence plant productivity and diversity as well as ecosystem processes; therefore species composition is both a variable responding to the environment and a factor influencing ecosystem functioning (Diaz & Cabido 2001). Tree species with fast growing roots are found in areas affected by high sedimentation rates (for example, *Salix* and *Platanus,* as well as *Betula, Acer,* and *Populus* spp., in the southeast USA, Hupp & Bornette 2003). Establishment of pioneer species of plants suitable to withstand flooding and high sedimentation increases hydraulic roughness leading to modifications that favor recruitment of later, more stable-site species (Hupp 1992, Friedman et al. 1996). Floodplain environmental gradients and species composition depend on the setting. It is unclear, however, whether gradients or hydrogeomorphic patches in Piedmont floodplains of medium sized watersheds are large enough to support vegetative differentiation along lateral and/or longitudinal dimensions relative to other settings.

We focus here on the role of vegetation in an urban Piedmont floodplain ecosystem. Our goals were to 1) characterize patterns in the species composition and the uptake of nutrients in plant material relative to landscape position along longitudinal and lateral dimensions of the floodplain 2) identify linkages among vegetation production or nutrient cycling and ecosystem attributes (water depth, shading, nutrient mineralization, and sedimentation) and; 3) determine if species composition varied with ecosystem attributes.

Study area

The study area is in the temperate, forested, floodplain of Difficult Run, a 23 km long stream in Fairfax County, Virginia, USA (Fig. 1). It is within a developed watershed (urban and suburban development with 16% impervious cover) in the Piedmont Physiographic Province of the Chesapeake Bay watershed. Difficult Run is typical of many if not most Piedmont streams that have been affected by historic high sediment deposition in response to colonial agriculture practices leaving behind a large legacy deposit on the modern floodplain (Hupp et al. 2013). This results in an elevated and more uniform topography on the floodplain relative to a pristine riverine system.

The mean annual discharge near the mouth of the 151 km^2 watershed is 1.76 m^3 s^{-1} (US Geological Survey 2007). The floodplain is regularly inundated with short duration floods (Hupp et al. 2013). The annual mean hydroperiod is 0.5 days on the levee and toe-slope and 45 days on the backswamp features (Noe et al. 2013). Discharge records show a distinct shift in discharge patterns that may be related to increased imperviousness during urbanization; the floodplain at site 3 has been inundated 4 times per year on average since urbanization began in 1965, and once per year prior to that (Hupp et al. 2013) but baseflow discharge at the mouth of the watershed has decreased over time (Batson et al. 2015).

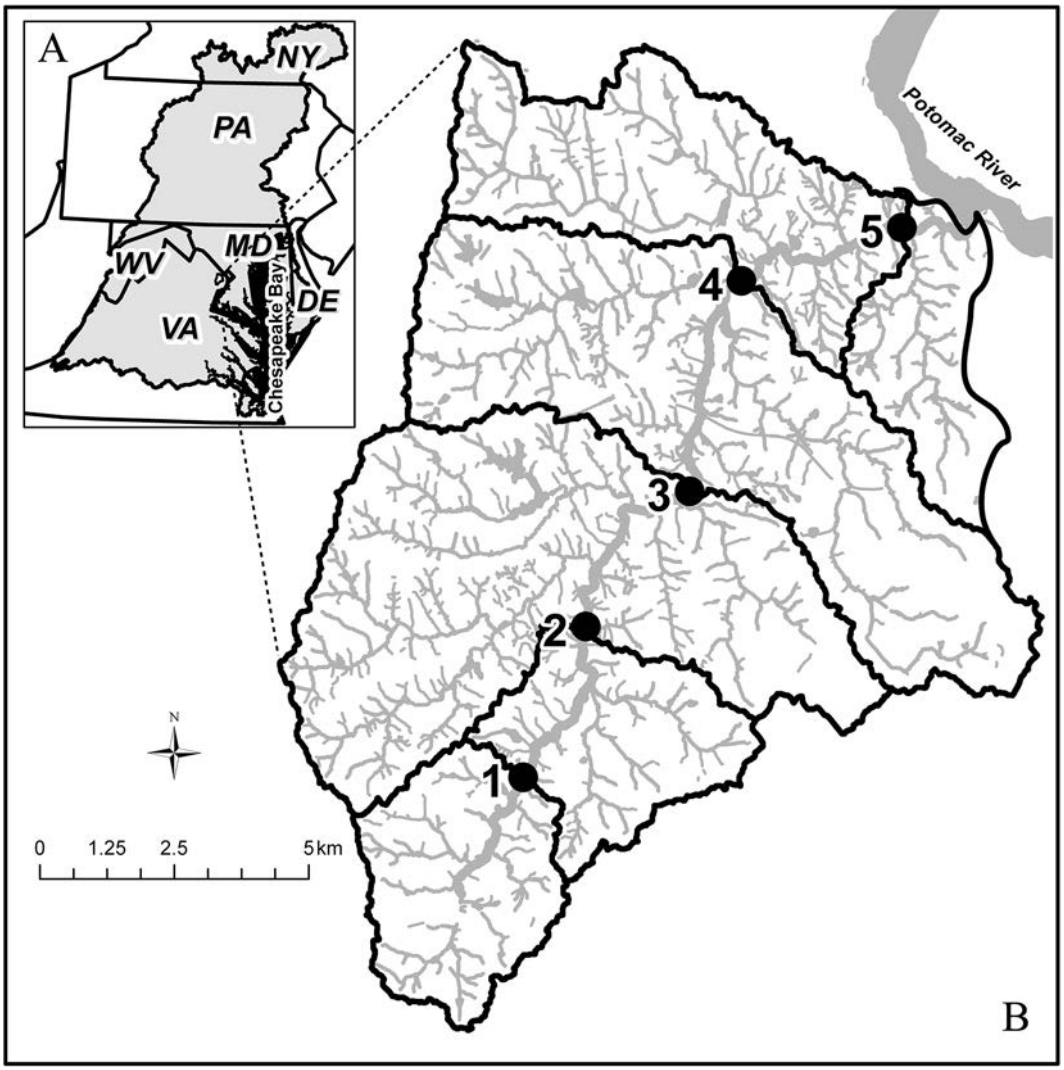
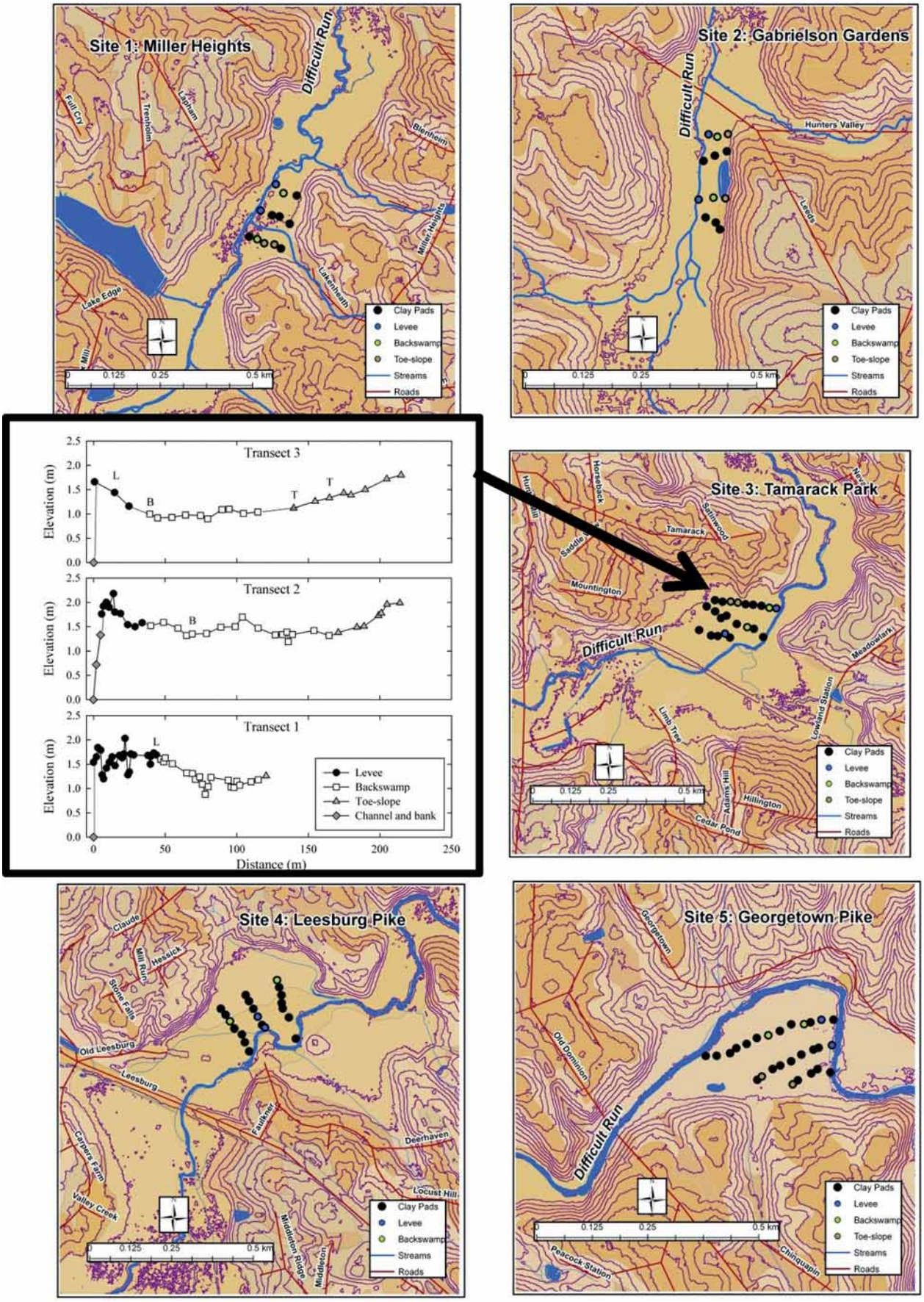


Fig. 1. A) Map showing the location of the Difficult Run watershed in the Chesapeake Bay watershed, USA. B) Map of the Difficult Run watershed showing the locations and catchment areas of sites 1 through 5. Site 5 is 0.6 km upstream of a gorge.

Method

Five floodplain sites were selected along the longitudinal dimension of the mainstem of Difficult Run (4th through 5th orders) from near the headwaters to the gorge above the mouth of the watershed (Fig. 1; Noe et al. 2013). Site locations were chosen at 3 to 4 km intervals to span the watershed, had typical geomorphology and vegetation, and were publicly owned and managed for natural resource protection (Fairfax County Park Authority). All sites were forested, located on one side of the river, and included three lateral dimension geomorphic features: a relatively high elevation natural levee adjacent to the channel; low elevation backswamp; and high elevation toe-slope (Fig. 2). The toe-slope was adjacent to the uplands, except at Site 4 where an accessible toe-slope feature was lacking. The five sites varied in stream gradient (ranging from 0.0018 to 0.0050), floodplain width (ranging from 52 to 162 m) and sampled length (ranging from 125 to 200 m). Stream gradient and floodplain width at the two uppermost sites were relatively steep and narrow, the middle two sites were flat and wide, and the most downstream site (above the gorge) was steep and wide (Hupp et al. 2013). Each site had three transects oriented perpendicular to the channel that began on the levee near the river and ended at the transition from toe-slope to uplands (lateral dimension). Transects were spaced about 50 m apart. Elevation was measured at approximately 10 to 25 m intervals along each transect and classified into one of the three geomorphic features based on site hydro-


Site 1: Miller Heights
Difficult Run
Full Cry
Trenholm
Lapham
Blenheim
Miller Heights
Lakenheath
Lake Edge
Clay Pads
Levee
Backswamp
Toe-slope
Streams
Roads
0 0.125 0.25 0.5 km
Site 2: Gabrielson Gardens
Difficult Run
Hunters Valley
Leeds
Clay Pads
Levee
Backswamp
Toe-slope
Streams
Roads
0 0.125 0.25 0.5 km
Transect 3
Transect 2
Transect 1
Elevation (m)
Distance (m)
L
B
T
Levee
Backswamp
Toe-slope
Channel and bank
Site 3: Tamarack Park
Horseback
Tamarack
Satinwood
Saddle
Mountington
Difficult Run
Meadowlark
Limb Tree
Lowland Station
Adams Hill
Hillington
Cedar Pond
Clay Pads
Levee
Backswamp
Toe-slope
Streams
Roads
0 0.125 0.25 0.5 km
Site 4: Leesburg Pike
Claude
Mill Run
Hessick
Stone Falls
Old Leesburg
Leesburg
Faulkner
Deerhaven
Carpers Farm
Valley Creek
Locust Hill
Middleton Ridge
Middleton
Clay Pads
Levee
Backswamp
Streams
Roads
0 0.125 0.25 0.5 km
Site 5: Georgetown Pike
Georgetown
Old Dominion
Difficult Run
Peacock Station
Chinquapin
Clay Pads
Levee
Backswamp
Toe-slope
Streams
Roads
0 0.125 0.25 0.5 km

geomorphic interpretation and relative elevation (see Hupp et al. 2013). From among the three transects within a site, two plots (termed focal plots) in each geomorphic feature were randomly chosen for measurement of soil N and P mineralization, sedimentation, and vegetation (n = 28 for the entire study area, Fig. 2). The number of plots at each of five sites along the longitudinal dimension was six, except site 4 (lacking toe-slope), where n = 4. The number of plots representing the three geomorphic features along the lateral dimension was ten, except the toe-slope, where n = 8.

Vegetation measurements

Tree, shrub, and herbaceous characteristics were measured at each focal point by using a 20 * 20 m plot (400 m^2) in midsummer 2008. In the 400 m^2 plot we identified, counted and measured diameter at breast height (DBH) of all trees (tree defined as those with diameter > = 2.5 cm at breast height (1.3 m). We randomly chose one quadrant (100 m^2) of the 400 m^2 plot, and identified and counted the tall shrub species (defined as those with diameter < 2.5 cm at breast height). We also identified herb and short shrub species and estimated proportional herb and short shrub species coverage (0 to 100%, at 1% increments). This included vines and any short (< breast height) woody species, such as tree seedlings, that occurred in the 100 m^2 quadrant. Multiple layers of short shrub and herb plant cover occurred in some plots, resulting in a cumulative coverage of herb and short shrub species greater than the area sampled, or in other words, a ratio of herb and short shrub cover: total area greater than 1.

Tree density, diameter, and basal area for all species combined and individual species, total number of species (richness), and Shannon-Weiner diversity (based on proportional species density of trees, or coverage of herb and short shrubs) were calculated for each plot. Importance values for each species across all plots were calculated by averaging three indicators of importance for trees (Rheinhardt, 1992), relative occurrence (occurrence of $species_i$ / ∑ occurrence of all species) * 100, relative basal area (BA of $species_i$ / ∑ BA of all species) * 100, and relative density of tree species (density of $species_i$ / ∑ density of all species) * 100. Nomenclature used for identifying the plants follows that of Radford et al. (1968) and Gleason & Cronquist (1991) while the identification and categorization of introduced or exotics species followed Miller et al. (2010), Leicht-Young et al. (2007), and the online source, USDA, NRCS (2012). Regional indicators of wetland status for trees are included that express the estimated probability (likelihood) of a species occurring in wetlands versus non-wetlands in the northeast region USA and follows USDA, NRCS (2012). The plant species indicators are as follows: FACW is facultative wetland and indicates it usually occurs in wetlands (estimated probability 67%–99%), but occasionally found in non-wetlands; FAC is facultative and indicates it is equally likely to occur in wetlands or non-wetlands (estimated probability 34%–66%). FACU is facultative upland and indicates it usually occurs in non-wetlands (estimated probability 67%–99%), but occasionally found on wetlands (estimated probability 1%–33%). The wetland indicator status of each species was retrieved (USDA, NRCS (2012) and wetland species were considered those categorized as facultative wet or obligate wet for the Eastern Piedmont region while facultative and facultative upland species were categorized as upland species for this analysis as OBL and FACW are the most reliable indicators of the presence of a wetland (Tiner 1999). For the purposes of this study, the taxa, *Carex* spp., were identified as wetland indicator taxa, although we did not identify the genus *Carex* to species. Therefore the proportion of wetland indicators herbs at sites with an abundance of *Carex* spp. may overestimate the sites' wetness.

Vegetative nutrient flux

Litterfall nutrient fluxes were calculated from biomass production at each plot measured by using duplicate litterfall traps (elevation 1.2 m above soil surface, surface area 0.3 m^2 with a mesh net 0.6 m deep) with monthly collections (September 2008 to August 2009). Herb biomass was quantified at each plot with triplicate standing crop plots (1 m^2) collected during the period (1 July to 10 August 2009) of peak herbaceous biomass. The herb biomass plots were located randomly in three of the four cardinal directions at 2m distance from the center of the focal plot. All above-ground herbaceous plant material was clipped, and the biomass samples were oven dried, weighed, and then ground in a Wiley Mill to pass a 40 mesh screen for nutrient analysis. Monthly litterfall samples were collected, dried and sorted into 5 groups (leaf parts, reproductive parts, fine woody debris (< 2 mm), coarse woody

Fig. 2. Maps showing Sites 1 to 5. Solid circles colored black show elevation measurements at clay pads, while circles colored blue, green, and brown show focal plots at the levee, backswamp, and toe-slope, respectively. Inset showing floodplain soil elevation relative to river surface water versus distance from the stream for the three transects at Site 3; the different geomorphic features are shown by different symbols, with the location of the type of focal plot shown by letters above the symbols (L levee; B backswamp; T toe-slope).

debris (≥ 2 mm), and other debris (unidentifiable, lichens, frass, etc.). After sorting, samples were weighed then ground for nutrient analysis. Mass was not always sufficient for litter nutrient analysis of individual litter groups by plot by month. We determined nutrient concentration by compositing the mass for one to 12 months, depending on the components. For example, leaf material was composited into four groups; group 1was September, group 2 was October, group 3 was November to February (winter), and group 4 was March to August (spring to summer). Reproductive material in litter was composited into two groups; September to February (fall to winter) and March to August. Course woody litter was not analyzed while fine woody and other debris was composited into one group for the entire period, September to August. The ground litterfall and herbaceous samples were analyzed for total carbon and nitrogen (TC and TN); using a CHN elemental analyzer; Thermo Electron, Milan, Italy), and for TP using microwave-assisted acid digestion (CEM, Matthews, North Carolina USA) and analysis on a ICP-OES (Perkin-Elmer, Waltham, Massachusetts USA). Elemental nutrient concentrations for each litterfall component were multiplied by mass to calculate monthly nutrient standing stock and summed to determine annual litter nutrient fluxes at each plot. Elemental nutrient values for the herbs were also multiplied by herb biomass to calculate annual herb nutrient fluxes at each plot. Stoichiometric C:N, C:P, and N:P ratios in litterfall and herbs were calculated on a molar basis.

Other plot parameters

Rates of annual net N and P mineralization in surficial soil (0–5 cm) were measured in each plot by using sequential monthly incubations of modified resin cores (Noe et al. 2013) for one year beginning in September 2008. Modified resin cores (Noe 2011) use relatively open incubations of intact wetland soil to measure in situ net rates of soil ammonification, nitrification, and P mineralization. Only the cumulative annual net areal N and P mineralization will be referred to here (source is Noe et al. 2013).

Net sedimentation rate (g m^{-2} yr^{-1}) at each plot was measured by coring the depth of sediment over a feldspar clay marker horizon (net deposition) at each focal plot that accumulated from 17–27 June 2008 for 2.5 to 3.1 years, depending on the site (Noe, unpublished data). For each core, bulk density was estimated from the dry weight of the soil and the volume of the soil, and the organic fraction of the sample was determined by loss-on-ignition (400°C for 16 hours, Nelson & Sommers 1996). Net sediment accretion rate (mm yr^{-1}) at each plot was measured from the change in the depth of sediment over the feldspar clay marker horizon (deposition) or the exposed length of a buried chain (erosion) from June 2008 to June 2009 (Noe et al. 2013).

Additional environmental parameters included overstory density and water level. Overstory density of the tree canopy cover at the focal point was measured monthly with replicate densiometer measurements (n = 4, in the four cardinal directions) from September 2008 to August 2009. The mean annual overstory density was calculated. Long term water level was based on water levels recorded every 15 min beginning in November 2008 until August 2011. A pressure transducer (Esterline Pressure Systems, Hampton, Virginia USA) was installed in a screened, PVC pipe adjacent to the lowest elevation plot at each site. Water elevation relative to the soil surface of each plot was calculated from the transducer water elevation reading, depth of the transducer below the soil surface, and of elevation difference of the soil surface at each plot relative to the well. Soil surface elevation was derived from detailed surveying of each site.

Statistical analysis

Univariate analyses: The influence of longitudinal position (site) and lateral position (geomorphic feature; levee, backswamp, or toe-slope) on selected parameters, including annual litterfall and herbaceous nutrient concentration and fluxes and tree and herbaceous community characteristics for the focal plots (Table 1), were tested by using analysis of variance (ANOVA) and Tukey's post hoc HSD test. Pearson product moment correlation analysis was performed between the herb and litterfall flux, mass, or nutrient concentration and the environmental variables, overstory density, long term water level, soil N and P mineralization rates, and organic sedimentation rates for the focal plots. These variables represent light flux, wetness, and soil fertility or sedimentation attributes. Data were optimized for parametric analyses; each parameter was tested for normality and transformed if necessary. Results were considered significant if probabilities were ≤ 0.05. Univariate analyses were done in the program TIBCO Spotfire S+ (Somerville, Massachusetts).

Multivariate analyses: We examined the differences in species composition along lateral (levee, backswamp, toe-slope) and longitudinal dimensions (site 1 to site 5). The software, Primer-E Ltd (Plymouth, England) was used for all multivariate analyses. This analysis was done separately for each of the three types of vegetation strata, tree, herb and short shrub, and tall shrub where the variables were species and the samples were the focal plots. The species assemblage data were used to construct a Bray-Curtis similarity matrix, which was subjected to non-metric multidimensional scaling (nMDS) ordination

Table 1. Selected vegetation characteristics showing means and significant differences longitudinally and/or laterally (2 way ANOVA) * is p = 0.05 to 0.01;** is p < 0.01 to 0.001; *** is p < 0.001. N = 28 (except herbaceous P flux is n = 27), Geo is geomorphic feature.

Variable	All plots mean	All plots SE	Site 1	Site 2	Site 3	Site 4	Site 5	Lateral (Geomorphic feature)	Longitudinal (Site)	Site*Geo
Litter flux (g m^{-2} yr^{-1})	489.13	19.06	554.25	449.56	473.84	451.98	503.62			
Litter C flux (g-C m^{-2} yr^{-1})	229.11	8.83	258.51	208.58	225.45	212.91	234.71			
Litter N flux (g-N m^{-2} yr^{-1})	6.38	0.32	6.01	4.42	7.17	7.19	7.39		***	*
Litter P flux (g-P m^{-2} yr^{-1})	0.57	0.03	0.57	0.41	0.59	0.65	0.64		*	
Leaf C flux (g-C m^{-2} yr^{-1})	162.45	6.42	182.83	146.37	171.19	156.90	153.13			
Leaf N flux (g-N m^{-2} yr^{-1})	4.41	0.25	4.33	3.07	5.29	4.99	4.56		*	
Leaf P flux (g-P m^{-2} yr^{-1})	0.40	0.02	0.43	0.32	0.44	0.44	0.41			
Leaf C (%)	46.67	0.18	46.39	46.03	47.61	47.06	46.38			
Leaf N (%)	1.27	0.05	1.10	0.97	1.47	1.50	1.38		**	
Leaf P (%)	0.12	0.004	0.11	0.10	0.12	0.13	0.12			
Leaf C:N ratio	44.88	1.85	49.37	56.56	38.15	38.97	39.39		**	
Herb (g m^{-2} yr^{-1})	35.91	7.68	13.46	10.35	76.30	77.00	16.15		*	
Herb C flux (g-C m^{-2} yr^{-1})	14.11	3.06	5.50	3.87	30.50	29.95	6.01		*	
Herb N flux (g-N m^{-2} yr^{-1})	0.69	0.13	0.29	0.21	1.46	1.37	0.36		**	
Herb P flux (g-P m^{-2} yr^{-1})	0.07	0.01	0.03	0.02	0.15	0.14	0.03		*	
Herb C (%)	38.68	0.66	39.84	37.98	39.57	38.90	37.19			
Herb N (%)	2.09	0.07	2.21	2.02	2.01	1.90	2.26			
Herb P (%)	0.20	0.007	0.22	0.18	0.19	0.18	0.19			
Herb C:N ratio	22.09	0.70	21.34	22.45	23.16	24.75	19.63			
Litter+herb C flux (g-C m^{-2} yr^{-1})	243.22	8.68	264.01	212.44	255.95	242.86	240.72			
Litter+herb N flux (g-N m^{-2} yr^{-1})	7.07	0.39	6.30	4.63	8.63	8.56	7.75		**	
Litter+herb P flux (g-P m^{-2} yr^{-1})	0.64	0.03	0.60	0.43	0.74	0.79	0.68		**	
Tree diversity index	1.31	0.09	1.64	1.18	1.03	1.04	1.56		*	*
Tree richness	5.54	0.44	7.17	4.67	4.00	4.00	7.33		*	*
Mean overstory density (%)	53.40	1.13	53.11	57.74	51.31	49.41	54.10			
Tree BA (m^{-2}/ha)	33.67	3.10	39.14	36.24	30.67	23.69	35.30			
Tree density (stems/ha)	548.21	46.70	662.50	583.33	429.17	418.75	604.17			
Short shrub and herb exotics (%)	50.87	0.09	68.93	54.22	34.82	36.50	55.07			
Short shrub and herb diversity index	1.61	0.10	1.26	1.56	1.44	1.83	2.00			
Short shrub and herb richness	20.21	0.98	20.00	21.83	17.33	16.50	24.17			
Ratio short shrub and herb total cover : total area	1.02	0.09	0.87	0.61	1.05	1.56	1.20		*	

and one-way analysis of similarities (ANOSIM) (Clarke & Warwick 2001) to test that there were no differences among samples grouped by site or geomorphic feature [with a $p < 0.05$ indicating a significant difference in samples for each group]. The magnitudes of the global R-statistic values in the ANOSIM test were used to determine the relative extent that the plant communities differed. Global R values typically range from 1 if there is no overlap to 0 if samples overlap completely. We used similarity of percentages (SIMPER) to determine the relative contribution of the individual species to the dissimilarity between the groups when differences were significant.

To reduce the number of species and thus the size of the matrix of species-composition similarity for individual plots, we analyzed species-specific abundance of only the dominant species for the tree stratum and the dominant herb and short shrub stratum. Dominant species of tree had a relative basal area > 1%, where relative basal area is 100 * basal area of species *i* / sum of basal area all tree species sampled. Dominant species of herbs had a coverage > 25% of the total coverage of herbs and short shrubs in at least one of the plots. The tall shrub stratum was somewhat unique. The tall shrub stratum had few species therefore it was not necessary to reduce the number of species for the analysis of that stratum. Also, while herbs or trees occurred ubiquitously on plots, tall shrubs were frequently absent from plots. We introduced a dummy variable to the Bray-Curtis matrix for the tall shrub stratum taking the value 1 for all sample plots (Clark, Somerfield & Chapman 2006). This forces two samples with no tall shrubs to be 100% similar.

The data for the herb and short shrub stratum included one outlier plot. The plot was covered with dense bamboo. The plot was excluded from the multivariate analyses of herbs and short shrubs because it was completely dissimilar to other plots.

The Bio-Env procedure (BEST) was used to test for relationships among the vegetation strata and environmental variables (N mineralization rate, P mineralization rate, long term water level, sediment accretion rate, and organic sedimentation rate). This analysis was done separately for the dominant tree, dominant herb and short shrub, or tall shrub strata.

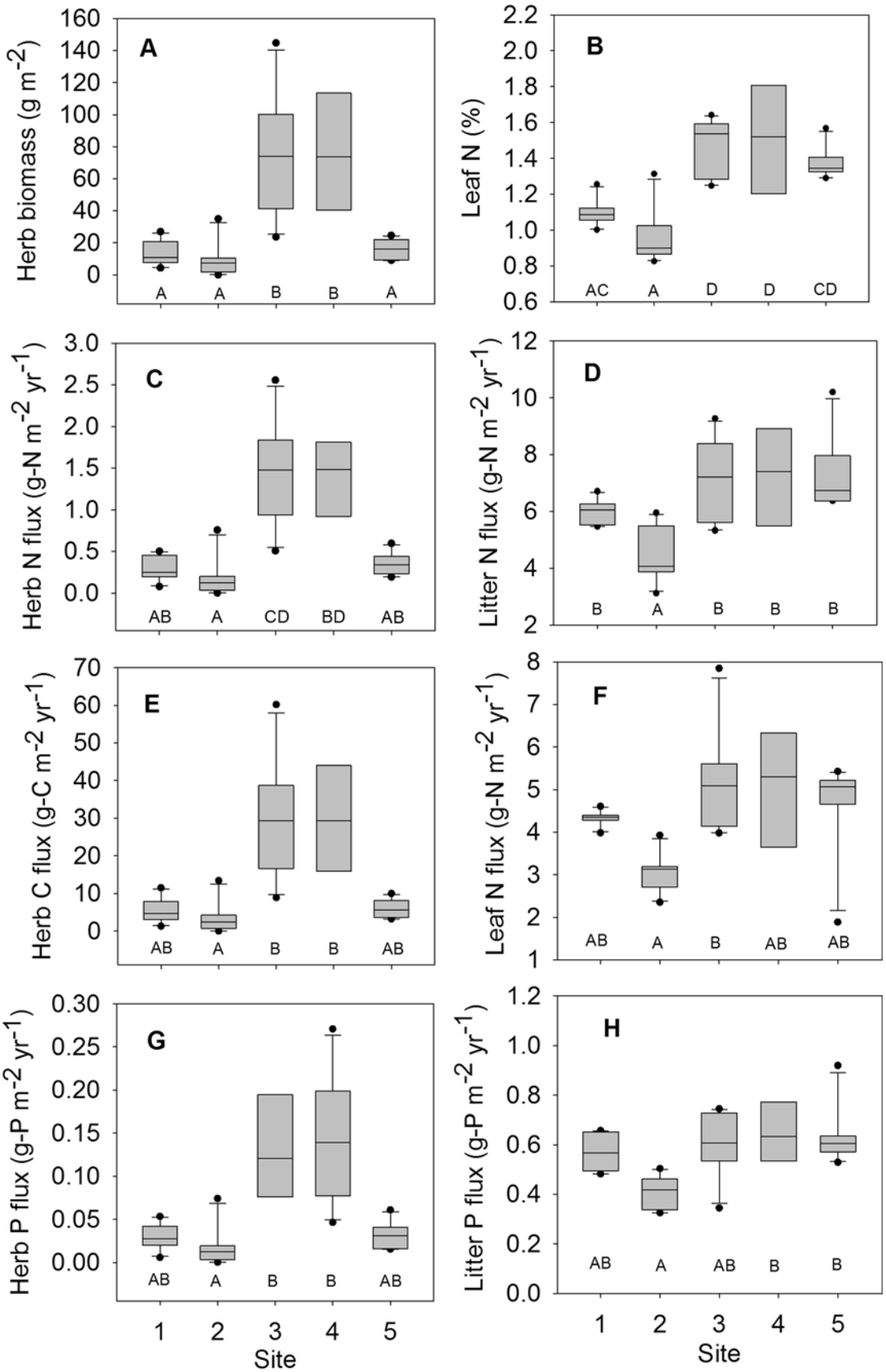
Results

Vegetation longitudinal and lateral patterns

Annual vegetation flux rates and nutrient content: We examined the differences in vegetation flux rates and nutrient content along lateral (levee, backswamp, toe-slope) and longitudinal dimensions (site 1 to site 5). The majority of vegetation nutrient flux rates were similar among lateral geomorphic features but many of these rates differed significantly by longitudinal site (Table 1, Fig. 3). Herbaceous biomass production differed by site and the production at sites 3 and 4 was double that at other sites (Fig. 3A). The herb % C, % N, and % P and the leaf % C and % P and leaf mass production rate were homogeneous among sites. However, the leaf % N differed by site and was greater at the three most downstream sites than at the upper sites (Fig. 3B). Nutrient flux is calculated by using both elemental nutrient concentration and productivity of the vegetation. The wide variation in herb biomass (Fig. 3A) and leaf % N (Fig. 3B) along the longitudinal dimension largely governed the vegetation nutrient flux patterns. The influence of the herb biomass can be seen in the patterns of the herb nutrient flux (Fig. 3C, E, and G). Litterfall N and leaf N flux patterns (Fig. 3D and F) were driven by patterns in the leaf N (%) as the litter mass did not differ among sites (Table 1). In addition, total litterfall C:N and C:P, as well as leaf C:N, differed by site and decreased somewhat at the downstream most sites but were homogenous on the lateral gradient. Litter, leaf, and herb N:P, leaf and herb C:P, and herb C:N did not vary significantly by site (and did not differ on the lateral gradient). While the variation in litterfall N flux differed by site (Fig. 3D), this flux was also dependent on geomorphic feature. The litterfall N flux was greatest at sites 3, 4, and 5 on levee features. Other flux rates that differed by site included herbaceous P flux (Fig. 3G), and litterfall P flux (Fig. 3H), like most parameters, these were lowest at site 2 (Table 1). Total vegetative flux of N and P (litterfall and herb) also differed among sites and was lowest at site 2.

Vegetation abundance and diversity: Most vegetation descriptors were similar by geomorphic feature but several differed significantly by site (Table 1). Tree diversity and tree richness differed by site and variation among plots within sites was quite high. These indicators of biodiversity also were dependent on geomorphic feature; the greatest tree diversity was at site 1 on a toe-slope feature and the greatest tree richness was at site 5 on a backswamp feature. Herb and short shrub coverage was significantly lower at site 2 than at site 4 but coverage at sites 1, 3 and 5 were not different from any other sites. Overstory density, tree basal area, and tree density were not significantly different among sites although values at sites 3 and 4 were lower than other sites (Table 1).

Fig. 3. Box plots of herbaceous and litter flux rates, and leaf N (%) of sites 1 through 5. Boxes show median and upper and lower quartile (circles are outliers). Boxes sharing the same letter or letters are not significantly different at the 5% level of significance.


A
Herb biomass (g m-2)
160
140
120
100
80
60
40
20
0
A A B B A
B
Leaf N (%)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
AC A D D CD
C
Herb N flux (g-N m-2 yr-1)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
AB A CD BD AB
D
Litter N flux (g-N m-2 yr-1)
12
10
8
6
4
2
B A B B B
E
Herb C flux (g-C m-2 yr-1)
70
60
50
40
30
20
10
0
AB A B B AB
F
Leaf N flux (g-N m-2 yr-1)
8
7
6
5
4
3
2
1
AB A B AB AB
G
Herb P flux (g-P m-2 yr-1)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
AB A B B AB
H
Litter P flux (g-P m-2 yr-1)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
AB A AB B B
1 2 3 4 5
Site
1 2 3 4 5
Site

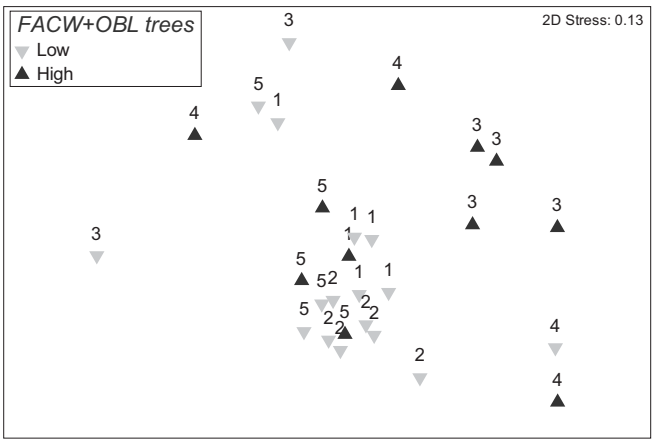


Fig. 4. Two-dimensional nMDS ordination based on a Bray-Curtis similarity matrix showing the difference in the density of the dominant tree species at sites 1 to 5. Numbers are site numbers, symbols shows high or low (above or below average) abundance of wetland indicator tree species, FACW+OBL is facultative wet + obligate wet trees.

Species compositional patterns: An analysis of similarity among species (ANOSIM) was used to reveal difference in relative abundance of species between sites or geomorphic features. Global R values typically range from 1 if there is no overlap to 0 if samples overlap completely. We found the result was the same when we analyzed the full set of species, or just the dominant species, in the tree or herb community. On the lateral gradient, the assemblage of species of dominant trees, dominant herbs and short shrubs, and all tall shrubs were not significantly different (ANOSIM test results, p = 0.40, Global R is 0.009, p = 0.68, Global R is -0.029, and p = 0.77, p = .85, Global R is -0.04, respectively). However, the dominant species in the tree assemblage, the dominant species in the herbaceous assemblage, and the tall shrub assemblage differed by site (p = 0.001, Global R is 0.40, p = 0.001, Global R is 0.34, and p = 0.001, Global R is 0.43, respectively).

Pairwise ANOSIM tests indicated differences in the tree, shrub, and herb composition by site. A simple downstream continuum of species composition similarities was not evident for any of the three strata based on pairwise ANOSIM tests. Tree assemblages at adjacent sites 1 and 2, 2 and 3, and 4 and 5 were significantly different from one another. Sites 3 and 4 were not significantly different and were the most similar of all sites (R = .03). The nMDS plot shows site 3 and 4 focal plots have a high abundance of wetland indicator tree species (facultative wet + obligate wet trees), with few exceptions (Fig. 4). *Acer rubrum, Liriodendron tulipifera* and *Carpinus caroliniana* were the most abundant floodplain trees in the study area but, *L. tulipifera* and *C. caroliniana*, two upland species, were rare or absent at site 3 and site 4 where there was a relatively high density of wetland indicator tree species compared to the other sites. In particular, wetland indicator trees, *Salix nigra* were abundant at site 4 and *Fraxinus pensylvanica* and *Quercus palustris* were relatively abundant at sites 3 and 4. The tree composition represents an assemblage that has formed over a time scale of decades, including a period prior to urbanization. The tree assemblage at sites 1 and 2 represent dry, and sites 3 and 4 represent wet conditions. Site 5 may cluster with the relatively dry sites because a gorge is 0.6 km downstream of the site. A gradual increase in gradient toward the gorge draws the water downstream and diminishes the conditions needed for formation of a backwater area or for pooling of water on the floodplain.

The abundance and composition of tall shrub species varied considerably by site. Sites were significantly different with two exceptions. Sites 2 and 3 were not different (R = .08). These sites were similar in that each had a very low richness and abundance of tall shrubs; however, the sites had no shrubs species in common. Sites 4 and 5 were also not different (R = 0.26). Again, these two sites had no shrubs species in common but they were both devoid of *Lindera benzoin*; a species that typified site 1 and 3. Tall shrub species composition at site 1 differed from all other sites and site 1 had an abundance of *L. benzoin*. Tall shrubs were present at all 6 plots at site 1 however, they were absent at half of the 28 plots in the watershed. The exotic species of *Ligustrum* were only present and abundant at site 1 and 5. The two wetland indicator species, *Betula nigra* and *Cephalanthus occidentalis*, were relatively abundant at site 4. The species richness of tall shrubs ranged from one species at sites 3 and 5, to six species at site 4.

The coverage of the dominant short shrub and herb species also varied considerably and pairwise ANOSIM tests showed that all sites differed from one another. The greatest relative abundance of the exotic, *Microstegium vimineum,* was at site 1, while both *M. vimineum,* and the wetland indicator taxa, *Carex* spp. were abundant at site 2. Short shrub and herb species composition at site 3 differed from all other sites. Site 3 had an abundance of *Festuca* spp. and *M. vimineum*. Site 3 and 4 were the most dissimilar of all sites. Site 4 was best described by its abundance of *Rosa multiflora*. *Carex* spp. and the exotics, *Duchesnea indica*, *Celastrus orbiculatus,* and *Ligustrum* spp. were the most abundant at site 5.

Local effect of ecosystem attributes

Nutrient cycling and ecosystem attributes: The local conditions of wetness, shading, and soil fertility were important ecosystem attributes affecting nutrient cycling (Table 2). Several plant fertility and productivity indicators var-

Table 2. Significant (probability ≤ 0.05) Pearson correlations found among plant flux, mass, or nutrient content and overstory density, hydrology, soil nutrient mineralization rates, or organic sedimentation rates (n = 28). Significance indicated as * is p = 0.05 to 0.01;** is p < 0.01 to 0.001; *** is p < 0.001. Herb is non-woody plants, Leaf is just the leaf component of litterfall, litter is all components of the litterfall, and litter + herb is a combination of litter and herb flux.

Variable 1	Variable 2	Correlation coefficient
Leaf C (%)	N mineralization rate (g-N m^{-2} yr^{-1})	0.37*
Leaf N (%)	Organic sedimentation rate (g m^{-2} yr^{-1})	0.44*
Leaf N (%)	Water level (m)	0.38*
Leaf P (%)	Water level (m)	0.38*
Herb N (%)	Water level (m)	-0.42*
Herb biomass (g m^{-2})	Water level (m)	0.38*
Herb biomass (g m^{-2})	Organic sedimentation rate (g m^{-2} yr^{-1})	0.62***
Herb biomass (g m^{-2})	N mineralization rate (g-N m^{-2} yr^{-1})	0.53**
Herb biomass (g m^{-2})	Mean overstory density (%)	-0.63***
Herb N flux (g-N m^{-2} yr^{-1})	Mean overstory density (%)	-0.63***
Herb C flux (g-C m^{-2} yr^{-1})	Mean overstory density (%)	-0.54**
Herb P flux (g-P m^{-2} yr^{-1})	Mean overstory density (%)	-0.55**
Herb N flux (g-N m^{-2} yr^{-1})	N mineralization rate (g-N m^{-2} yr^{-1})	0.46*
Herb N flux (g-N m^{-2} yr^{-1})	Organic sedimentation rate (g m^{-2} yr^{-1})	0.54**
Litter+herb N flux (g-N m^{-2} yr^{-1})	Organic sedimentation rate (g m^{-2} yr^{-1})	0.49**
Litter+herb N flux (g-N m^{-2} yr^{-1})	N mineralization rate (g-N m^{-2} yr^{-1})	0.37*
Litter+herb P flux (g-P m^{-2} yr^{-1})	Long term water level (m)	0.58**
Litter+herb P flux (g-P m^{-2} yr^{-1})	Organic sedimentation rate (g m^{-2} yr^{-1})	0.43*
Litter+herb P flux (g-P m^{-2} yr^{-1})	N mineralization rate (g-N m^{-2} yr^{-1})	0.46*

ied with wetness and shading. Leaf % N and % P, litterfall and herb P flux, and herb biomass increased with shallower groundwater levels, a surrogate for soil wetness (Table 2). Whereas, leaf C:N and herb N % decreased with shallow groundwater levels. Herb biomass and herb N, C, and P flux correlated negatively with mean overstory density, an indicator of shading on the forest floor (Table 2). Many of the plant annual nutrient flux rates as well as the herb biomass increased with soil N mineralization and organic sedimentation (Table 2). The N mineralization rate and organic sedimentation rate were positively correlated with leaf % C, leaf % N, herb biomass, herb N flux as well as combined litter and herb N or litter and herb P flux (Table 2). While there was a correlation between the combined litter and herb N flux and the N mineralization rate, there was no similar correlation between the combined litter and herb P flux and the P mineralization rate (Fig. 5). Notably, combined litter and herb N and P fluxes were similar to or greater than N and P mineralization in surficial (0–5 cm) soils.

Species composition and ecosystem attributes: The Bio-Env procedure (BEST) was used to test for relations between the tree, tall shrub, or herb composition and environmental variables (N mineralization rate, P mineralization rate, long term water level, sediment accretion rate, and organic sedimentation rate) measured at each focal plot. Species composition samples were highly variable and diverse among plots. Notably, neither of the communities of the three strata was correlated to the environmental variables we tested. Thus, species composition similarity among plots was not strongly governed by these local environmental conditions.

Discussion

Landscape scale variation in plant composition and nutrient flux

Lateral and longitudinal dimensions of the floodplain landscape provide a framework to better understand physical and biological processes on floodplains in various regions (Goebel et al 2012, Noe 2013). We did not see a distinct lateral change in vegetation patterns. The three studied lateral features (levee, backswamp, and toe-slope)

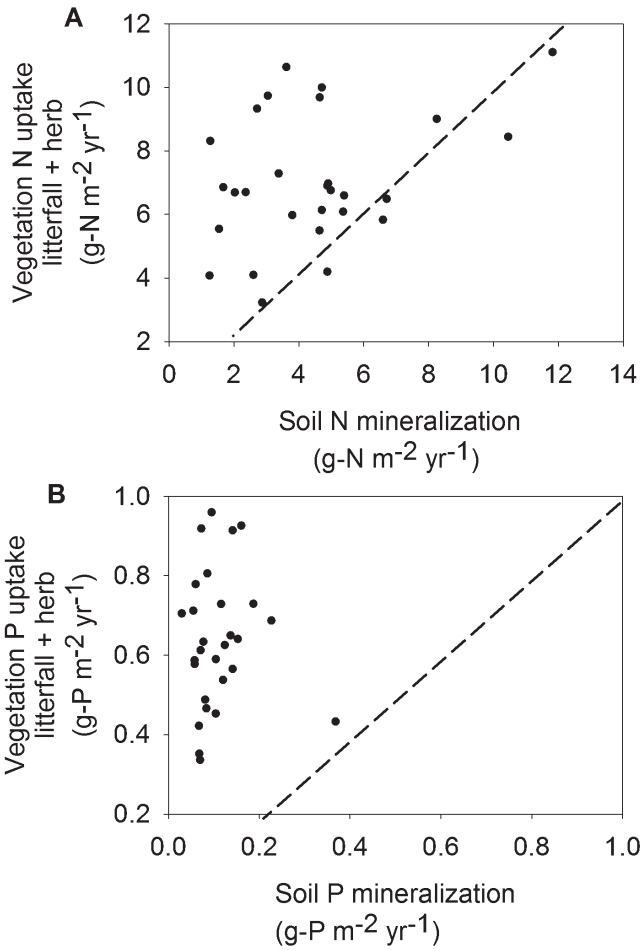


Fig. 5. A) Scatter plots of vegetation N flux (litterfall and herbaceous) versus N mineralization. B) Scatter plots of vegetation P flux (litterfall and herbaceous) versus P mineralization. Plots show 1:1 line.

were not of primary importance in defining plant composition on this Piedmont floodplain in a medium-sized watershed. Lateral changes in vegetation were more distinct at some sites than others on the Difficult Run floodplain but the differences were diminished when features from all sites were combined. In our study the floodplain width was narrow and our focus was on only three geomorphic features. Other studies have shown strong correlation between lateral vegetation patterns, fluvial landforms, and their associated hydrologic processes from the channel to the upland (Hupp & Osterkamp 1985, Hupp 2000, Steiger et al. 2005). Certain woody and herbaceous species have predictable distribution patterns that correspond to fluvial landforms (depositional bar, active channel shelf, floodplain, terrace) that reflect inundation frequency and the susceptibility of plants to damage by destructive floods (Hupp & Osterkamp 1985, Goebel et al. 2012). In the western USA, the vegetation associated with riparian zones is often strikingly different from that of the arid upland (Auble et al. 2005) whereas the dominant trees on the Difficult Run floodplain levee, backswamp, and toe-slope features were also common on Piedmont uplands (Groffman et al. 2006, Brush et al. 1980).

As with species composition, we found rates of vegetation nutrient flux were almost all homogeneous along the lateral gradient, except that litterfall N flux was high on the levee features of the lower 3 sites. In contrast, proximity to the channel was found to influence vegetation nutrient flux in other studies on both wet (but less fluvial) and arid floodplains. Sedge communities on riparian peatlands changed in composition and soil N, vegetation biomass, and N flux rates increased nearest the channel where flood duration was greatest (Wassen et al. 2002). Gonzales (2010) found highest litterfall rates and stem densities nearest the channel in a P limited forested floodplain in Spain, where patterns in litterfall were also correlated with higher soil total P that increased with proximity to the channel.

Longitudinal patterns on the Difficult Run floodplain landscape were governed by the hydrogeomorphology resulting from the valley setting rather than a simple downstream continuum. Tree diversity, tree communities as well as herb biomass and some nutrient flux rates differed along the longitudinal dimension. We found the greatest diversity and richness of trees at site 5 where the relatively steep stream gradient at this site just above a gorge potentially allowed for more high energy floods than the flatter gradient at site 3 where diversity indicators were lowest; a similar result was observed in the Valley and Ridge Province (Hupp & Osterkamp 1985). Some of the pattern in tree species composition by site was linked to wetland indicator species abundance; there was a relatively high density of wetland indicator trees at sites 3 and 4 (Fig. 4), and site 4 had greater than 40% abundance of wetland indicator tree species. While differences in abundance of wetland indicator trees were relatively evident along the longitudinal dimension, abundance of wetland species of tall shrubs or herbs and short shrubs was low (< 40%) at any site and variable among sites. Similarities in tree assemblages appear to be driven by valley-setting scale variables like floodplain width and stream gradient.

The vegetation nutrient flux rates, like tree community patterns, varied along the longitudinal dimension. Vegetation nutrient fluxes generally increased from the headwater to the mouth of the stream where the water-table depth was closer to the surface and there is more hydrologic connection with the floodplains so that fluvial inputs are greater. Litterfall mass did not vary along the longitudinal dimension but herb biomass and herb nutrient flux as well as leaf litter N (%) peaked at sites 3 and 4 (Fig 3A, C, D, E, and G),

sites with the widest floodplain and lowest stream gradient. Our findings are in agreement with others who found differences in plant communities (Naiman et al. 2005, Goebel et al. 2012) and concentration of nutrients in vegetation (Clawson et al. 2001, Gonzalez et al. 2010) varied with hydrology and topographic gradient. The longitudinal gradient can be a good surrogate for change in topography that correlates with fluvial processes, but the pattern may be interrupted if a geological feature (bedrock) causes a shift from gentle to steep gradient and a constriction in floodplain width that influences a change in the stream energy, vegetation type, and sediment trapping efficiency (Hupp 1982, Hupp & Osterkamp 1985, Bendix & Hupp 2000, Hupp et al. 2013, Schenk et al. 2013).

Local factors governing nutrient cycling

Hydrology, nutrient mineralization, and sedimentation influenced vegetative nutrient cycling at the local scale. Variations in herb and litterfall flux rates correlated positively to N mineralization rate, and organic sedimentation rate. High herb biomass and litterfall leaf N and P flux rates also correlated with high groundwater levels (wetness). Others have also reported concentrations of N and P (and nutrient resorption proficiency) of senescing tree leaves followed inundation gradients, with high concentrations at wet locations or high flood durations (Clawson et al. 2001, Gonzalez et al. 2010). This indicates floodplain trees in wet locations in Difficult Run are less efficient in recycling the nutrients from the leaves to long term nutrient storage in wood and roots of the tree before leaf fall, most likely due to greater nutrient availability to plants in wet locations with greater fluvial nutrient inputs. Thus, under wet conditions trees release more of their nutrients back to the Difficult Run floodplain potentially fueling herbaceous productivity in locations where light was not limiting.

Additionally, when both herb and litterfall N flux were combined, the vegetation N flux rate was correlated with the N mineralization (but the vegetation P flux rate was not correlated with P mineralization; Fig. 5). These findings are consistent with results from a very different landscape, a Western European, eutrophic, lowland river floodplain in a peatland, where plant N and biomass increased with N release rates from the peat (Wassen et al. 2002). Herbaceous production also was positively correlated with the turnover rate of soil N via mineralization, although the cause and effect was not clear (Noe et al. 2013).

Local factors and species composition

Multidimensional analysis allowed us to evaluate patterns in the plant assemblages with respect to ecosystem attributes. Species composition on the narrow (< 0.2 km), relatively dry floodplain along Difficult Run was not distinctly related to any ecosystem attributes we tested (N mineralization rate, P mineralization rate, long term water level, sediment accretion rate or organic sedimentation rate) at the local scale. In contrast, Wassen et al. (2002) found N availability closely corresponded with a distinct transition in the sedge community composition along the gentle rise in elevation from the river to the valley margin of the 1 km wide riparian peatland. Gonzales et al. (2010) noted species composition varied with sedimentation on a disturbed floodplain where sedimentation rate was an order of magnitude greater than that found in our Piedmont location. The lack of correlation between the diverse species composition and ecosystem attributes at the local scale in the Piedmont landscape may reflect a lack of strong gradients in important habitat variables. The range of water level depths and sedimentation rates in Difficult Run was narrow compared to these other studies.

Conclusion

We measured a wide range of chemical, physical and biological variables to ascertain patterns in nutrient cycling, and the influence of geomorphic position and vegetation on these patterns in the floodplain of a 152 km^2 catchment in a temperate Piedmont region. The N concentration in leaf litter on the Difficult Run floodplain was greater than swamps and floodplains in relatively wide low gradient systems in Coastal Plain sites in the Southeastern USA (Brinson et al. 1980, Clawson et al. 2001) and N and P concentrations were greater than arid floodplains in Spain (González 2012). Plant community composition and vegetation nutrient flux rates differed along the longitudinal dimension in a manner consistent with the River Ecosystem Synthesis concept (Thorpe et al. 2006). Specifically, tree species composition and vegetation nutrient flux patterns were associated with distance downstream, although these patterns appeared to reflect variation in the floodplain width and the stream gradient rather than a simple downstream continuum. Plant nutrient uptake and sediment trapping were greatest at sites in the relatively low gradient and wide portion of the watershed where the hydrologic connection between the floodplain and stream is high. Sediment trapping increased with distance downstream in association with high herbaceous plant coverage and a water tolerant tree community found in association with wide and low gradient sites. However, the pattern discontinued at the most downstream site where the stream gradient increased slightly and the stream water was drawn into the gorge downstream.

Nutrient retention by vegetation was an important component of the floodplain nutrient budget on the Difficult Run floodplain. Average N and P flux rates of herbaceous biomass and total litterfall more than accounted for the surficial soil N and P mineralization flux rate, indicating that vegetation incorporated nearly all mineralized nutrients in surficial soil into biomass. Vegetative uptake exceeding soil mineralization of N and P in the top 5 cm of soil suggests that plant roots are also able to obtain nutrients from deeper in the soil profile. The efficiency of nutrient cycling in the urban floodplain of Difficult Run may be due to the relatively low rates of N and P mineralization compared to wetlands in landscapes with greater nutrient loading (Noe et al. 2013). Plants directly uptake nutrients and indirectly effect N removal from the system by stimulating the microbial denitrification process via the supply of organic carbon in plant litter (Hefting et al. 2005). Nutrient uptake by plants potentially remains in the system only for a short time until plants senesce and inorganic nutrients are later released by mineralization. However, if the mineralization rate and the uptake rate are equivalent the N and P is continually recycled and is immobilized for a long period such as we found in the floodplain of Difficult Run. Our findings confirm the widely held perception that the biogeochemistry of vegetative N and P cycling is sensitive to valley setting and spatial variation in floodplain hydrogeomorphology and ecosystem attributes. This study is consistent with other studies showing the value of urban floodplains to water quality and the importance of vegetation in N and P cycling and retention.

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