

CHARACTERIZATION OF WOODY SPECIES DISTRIBUTION IN RIPARIAN FORESTS OF LOWER MICHIGAN, USA USING MAP-BASED MODELS

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Abstract: The goal of this study was to identify and characterize the range of variation in riparian forests across Lower Michigan, USA as a basis for assessing the utility of map-based information in the characterization of riparian environments. We obtained a regional sample of riparian forests and valley-bottom physiography from 94 locations throughout Lower Michigan and distinguished seven major riparian forest types using hierarchical clustering and NMDS ordination. NMDS ordination distances accounted for more than 70% of the distances in species space and achieved excellent discrimination among riparian types. We then evaluated a set of map-based variables indicative of regional climate, catchment hydrology, and valley character relative to ordination axes and interpretations of the autecology of principal tree species from each forest group. Map-based predictors accounted for 83% of the variation in sample scores along NMDS Axis 1 and explained 42% of the variation in Axis 2. Species and riparian types varied along two principal gradients, one associated with climate and geology along a north-south gradient, the second associated with flood duration and power. Map-based interpretations of regional climate and hydroperiod dynamics agreed closely with species-based interpretations of riparian character, although in certain cases, a similar biotic response arose from apparently distinct hydrogeomorphic contexts. Such dynamic patterns underscore the need for better and more explicit linkages between the controls of riparian hydrology and more proximal physical cues on biotic communities in order to understand the drivers of spatial variation in riparian ecosystem structure and composition.

Key Words: riparian areas, GIS, modeling, wetland vegetation

INTRODUCTION

Riparian areas have been recognized for their importance in the maintenance of biodiversity, stream integrity, wildlife habitat, and movement corridors (Gregory et al. 1991). As ecotones between land and water, streamside riparian areas show spatio-temporal heterogeneity associated with fluvial processes. As such, riparian areas are diverse in terms of both species and ecosystem richness relative to uplands (Lapin and Barnes 1995, Tabacchi et al. 1996). Lateral patterns in bottomland vegetation have been variously attributed to similar patterns in sediment erosion and deposition (Harris 1987), soil particle size and moisture status (Frye and Quinn 1979), and fluvial landforms (Hupp and Osterkamp 1985). These gradients appear to reflect various combinations of soil wetting and anaerobic conditions from an annual flood regime, as well

as the capacity of overbank flows to entrain sediment, transport propagules, damage stems, or uproot existing vegetation (Lindsey et al. 1961, Junk et al. 1989). Such observations suggest that, at a given location along a river, the size and shape of various fluvial landforms controls the frequency, duration, or intensity of inundation experienced by floodplain vegetation. In other words, the product of local physiography and its interaction with a river system expressly determines the character of a given riparian area.

Longitudinal patterns of riparian plant diversity parallel to river flow (Tabacchi et al. 1996) have been attributed to down-valley patterns of fluvial landforms (Hupp 1982, Baker and Barnes 1998), stream size (Bendix 1994, Nilsson et al. 1994), and human alteration of longitudinal flow continuity (Ward and Stanford 1995). A number of studies have also linked lon-

gitudinal forest patterns with spatial patterns of flooding, and patterns of natural disturbance associated with high flows and anaerobic soils (Tabacchi et al. 1996, Bendix and Hupp 2000). Other researchers have observed even broader-scale variation associated with climate, physiography, or hydrology (Baker 1989, Crow et al. 2000). The causal mechanisms driving riparian variation are difficult to summarize, but it seems clear that patterns of riparian vegetation can occur as the result of a complex suite of interacting factors operating at multiple spatial and temporal scales.

Although descriptions of riparian areas have progressed in detail and extent, understanding the causes and consequences of riparian diversity at many spatial scales across broad landscapes remains a challenge for researchers and managers alike. Thus far, "hydrogeomorphic" approaches relating riparian vegetation to hydrologic and/or geomorphic conditions have required site-specific assessment and/or expert interpretation (Harris and Olsen 1997, Hauer and Smith 1998, Cole and Brooks 2000). More recently, researchers have begun to recognize the potential for approaches that make use of remote, map-based estimates of hydrogeomorphic character (Bendix 1994, Baker et al. 2001) or hydrologic processes (e.g., Russell et al. 1997) to characterize riparian zones. Nevertheless, there remains a substantial need for analyses that support the conservation and restoration of riparian areas (Nilsson and Grelsson 1995, O'Neill et al. 1997).

The purpose of this study was to describe the range of riparian forest variation throughout Lower Michigan, USA. Specifically, our objectives were (1) to identify a number of distinct forest assemblages, (2) to interpret the characteristic site conditions of each assemblage using the autecology of predominant tree species, and (3) to evaluate the potential for mapped information both to predict these conditions and further characterize the geographic and hydrologic context of forest samples. The primary goal was to characterize the nature of environmental variation in riparian areas throughout Lower Michigan. A secondary goal was to identify and assess the ability of map-based indices to account for the observed variation. If geographic summaries of primary spatial data (as well as derived indices) accounted for substantial proportions of the observed variation in riparian forests, and map-based interpretations corroborated autecological evidence of environmental conditions, then mapped information might reasonably be expected to facilitate description and assessment of riparian variation throughout Lower Michigan.

METHODS

Study Area

The Lower Peninsula of Michigan includes a diversity of landscapes resulting from glacial drift (end mo-

raines, till plains, and ice-contact terrain), pro-glacial deposits (outwash and lacustrine plains), and glaciofluvial valleys (Farrand and Bell 1982). This variable geology is complemented by ecologically relevant climatic gradients from north to south and from east to west, particularly in the northern Lower Peninsula (Albert et al. 1986). These landscape features underlie a patchwork of land use/land cover across approximately 20 major river basins and result in a broad range of catchment and local-scale climatic and hydrologic conditions.

After site reconnaissance of more than 300 river reaches, 94 sampling transects were established on the basis of the following criteria: geographic dispersion across Lower Michigan, local geologic/geomorphic setting (glacial outwash, end moraine, till plain, proglacial lakeplain), and stream size (1st to 5th order). We endeavored to acquire numbers of samples approximately proportional to each combination of location criteria within the landscape. In addition, sample sites were required to contain a mature forest canopy without obvious signs of recent (10–20 yrs) anthropogenic disturbance. Forest sampling was also restricted to river reaches without any obvious recent geomorphic alteration due to anthropogenic channel modifications or peaking from hydropower dams because such modifications may have affected both riparian vegetation and the physical habitat template of the riparian zone.

Field Sampling

At each sampling location, our purpose was to generate a description of forest composition and geomorphology across the entire aquatic-terrestrial gradient. Transects were located to encompass as much of the valley bottom width as possible from the river to the upland (or glaciofluvial terrace). A surveying laser (Laser Atlanta, Inc.) equipped with both a clinometer and a compass was used to measure the relative extent and elevation of fluvial landforms and plant assemblages (Figure 1). In general, clear changes in plant assemblage structure and/or composition were easily distinguished laterally (perpendicular to river flow) on a single fluvial landform or between fluvial landforms (*sensu* Baker and Barnes 1998). We employed stratified, random, prism-point sampling in each distinct forest assemblage along the transect using three 10 Basal Area Factor (BAF) prism points (Figure 1) located at least 30 m from one another. Tree stems included in each plot were identified to species following the nomenclature of Voss (1972, 1985, 1996).

Transects were characterized and located within regional ecosystem units and major river basins using an ArcView 3.0 (Environmental Systems Research Institute, Inc.) geographic information system (GIS), field

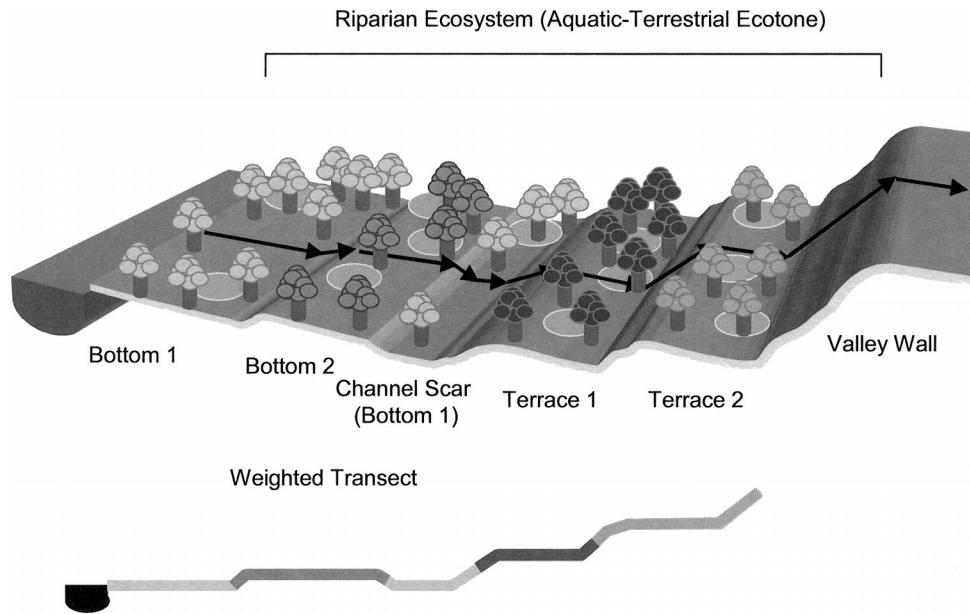


Figure 1. Idealized river valley showing a transect pathway through four distinct forest assemblages and sample plot locations used to generate weighted composition estimates for each transect.

measures, and a set of 25 map-derived variables representing landscape variation at multiple spatial scales (Table 1). Three variables (#1–3 in Table 1) characterized regional climatic variation among samples. We expected these variables to have a direct effect on riparian trees as well as an indirect effect on riparian areas via the regional water balance, whereas the remaining variables described physical factors influencing riparian hydroperiods. Twelve variables (#4–15 in Table 1) captured various aspects of catchment physiognomy that were expected to influence the response of catchments to seasonal water excess and storm events. We used a 1:24000, 30-meter digital elevation model (DEM) to characterize catchment and valley topography. Catchment boundaries were delineated using the DEM and digital sub-basin maps. Additional descriptive variables were generated using summaries of various digital maps including surficial geology (Farrand and Bell 1982), land cover/land use based on 1978 aerial photography (Michigan Resource Information System, Department of Land and Mineral Services, Lansing), and soil (STATSGO, NRCS). A water-table-depth map (#17) was generated using an inverse-distance-weighted interpolation from the elevation of hydrographic features (Baker et al. 2001), and a map-based index of potential groundwater flux (#15–16) was generated using hydraulic conductivity inferred from surficial geology and the DEM (Baker et al. 2003). Rather than mapping actual water tables or water movement, these maps were used as indices of the relative wetness originating from subsurface sources.

We expected greater flood frequencies in catchments characterized by higher drainage density (#11) and run-off potential (#12). High drainage density and runoff potential increase the susceptibility of a river system to disturbance by decreasing trans-catchment travel time (#14) and increasing the magnitude of peak flows (#13) following precipitation (Bedient and Huber 1989). Rather than increasing travel time, greater slopes (#9) arising from coarse Quaternary deposits are correlated with increased ground-water potential (#15) in Lower Michigan (Baker et al. 2003). We expected catchments with fewer channels and greater ground-water potential to have more stable streams that were less subject to hydrologic disturbance.

Eight local variables focused on hydrologic or hydraulic constraints imposed by valley physiography (#16–23 in Table 1). For a given catchment, floodplains characterized by steep, narrow valleys should exert greater shear forces (#22) on riparian vegetation because channel gradient (#18) and valley width (#20) are closely related to both unit shear and power (#21) (Bendix and Hupp 2000), which may be an important determinant of riparian vegetation (Bendix 1994). We used floodplain elevation (#23) as a surrogate for the pattern of fluvial landforms because it characterizes the morphology of valley bottoms and the expression of flood events, which in turn strongly influence patterns of riparian vegetation at a given site (Baker and Barnes 1998, Bendix and Hupp 2000). The remaining variables in Table 1 (#16–17, 24–25) were included as predictors, or the observed result, of local site wetness.

Table 1. Environmental variables measured or estimated for each sampling location.

Code	Description	Indication
1 avtmp	ecoregional mean annual temperature in °C (Albert et al. 1986)	climatic effect on trees
2 totp	mean annual precipitation interpolated from NOAA rain gauge data in cm	regional wetness
3 p/pet	ratio of mean annual precipitation to potential evapotranspiration (Albert et al. 1986)	regional wetness
4 carea	catchment area estimated from digital maps in km ²	size effects
5 shdlen	catchment length estimated from digital maps in m	transport distance
6 elong	ratio of catchment length to circle of same area (Baker 1989)	transport distance
7 relief	catchment relief (max–min elevation) in m (Baker 1989)	transport gradient
8 relrat	catchment relief over length (Baker 1989)	transport gradient
9 shdslp	mean pixellate slope for catchment calculated in %	transport gradient
10 strmlen	total length of stream channel within catchment in m	flow attenuation
11 cdens	channel density calculated by length of stream per unit catchment area	runoff generation
12 scs	SCS curve numbers derived from landcover and soils (Bedient and Huber 1989)	runoff generation
13 qpeak	SCS peak flow estimate in cfs (Bedient and Huber 1989)	size effects
14 lag/area	SCS lag time in hrs per unit catchment area	surface transport
15 shdgdw	mean of catchment potential subsurface flux map in m/d (Baker et al. 2003)	subsurface transport
16 locgw	local (within 500 m) mean of potential subsurface flux in m/d (Baker et al. 2003)	local water sources
17 wtdpth	local (within 500 m) mean depth to water table in m (Baker et al. 2001)	local storage capacity
18 cgrad	channel gradient using minimum cross-sectional DEM values 500 m from transect	local transport capacity
19 sinuos	stream length within 500 m of transect divided by 1000 (Schumm 1977)	stage related transport
20 vwidth	DEM-based estimate of valley bottom extent in m	local flood constraints
21 upwr	unit power for floods ($cgrad * qpeak / vwidth$) in watts/m	local flood constraints
22 ushear	unit shear for floods ($cgrad * carea^{0.40} / vwidth$) in N/m	effect of local constraints
23 fldelv	mean flood plain elevation along vwidth line (relative to minimum elevation) in m	flood vulnerability
24 trngrd	transect gradient from total change in elevation over the length of field transect	flood vulnerability
25 om	weighted average of organic matter depth from transect sampling plots in cm	site wetness, shears

Data Analyses

Identification and discrimination of forest assemblages were accomplished using agglomerative clustering by Ward's method (hierarchical grouping) of tree species basal area in PC-ORD (Sneath and Sokal 1973, McCune and Mefford 1999). The clusters were visually inspected in three-dimensional ordination space using Non-Metric Multi-Dimensional Scaling (NMDS; Clarke 1993) of relative abundance and Bray-Curtis dissimilarity. NMDS arranges samples so that ranked pairwise distances between samples (dissimilarity) match as closely as possible to Euclidean distance in ordination space. The distortion of the distance matrix by the ordination is measured using a stress coefficient, which is minimized during iterative ordination runs. We selected an appropriate number of

dimensions after 80 runs with real data from a random start, based on marginal reductions in stress for each additional axis and the stability of the solution. The significance of the solutions was assessed using a Monte-Carlo simulation of 100 random runs. A final solution for three dimensions was reached after 27 iterations. Based on comparisons of the cluster dendrogram and NMDS ordinations, we selected seven clusters for summarization and further analysis.

Cluster groups were summarized and described using tree species relative abundance, indicator species scores, species diversity indices, and field notes (Figure 2). Species basal area, richness, and soil characteristics from each forest sample were weighted by their linear extent along each valley transect to generate a compositional and geomorphic description of

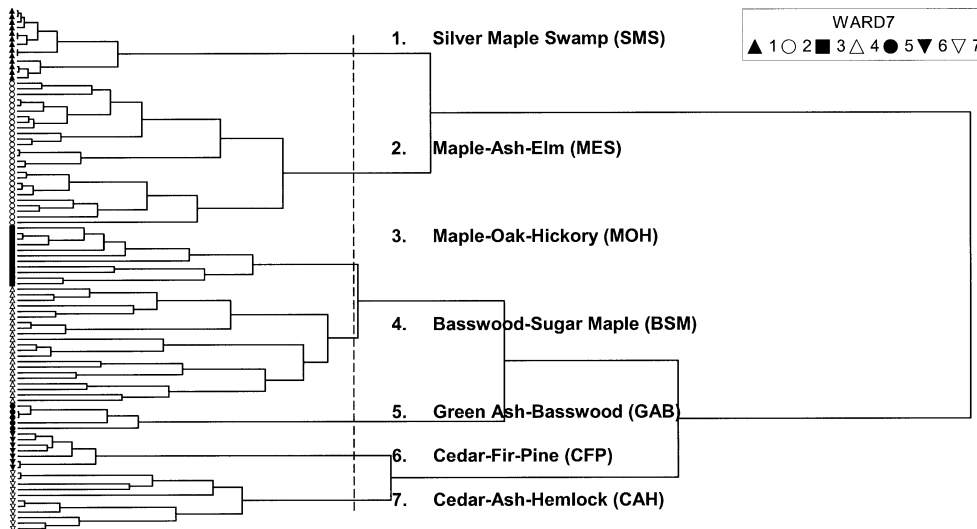


Figure 2. Cluster dendrogram of riparian forest samples using Ward's method. The dashed line, numbered labels, and identification symbols indicate the seven clusters chosen for further analysis.

every aquatic-terrestrial gradient. In addition, Shannon-Weiner Indices of Diversity (H'), Richness (S), and Evenness (E) were computed for each transect (Magurran 1988). Indicator species analysis was performed using the method of Dufrene and Legendre (1997) in PC-ORD to identify strong associations between certain species and a particular cluster group. Using this statistical approach, a species might receive a weak indicator score despite high relative abundance in a single forest sample within a group, or receive a strong indicator score without ever dominating a forest sample within a group. Using observed associations among various predominant species, their autecology, prominent indicator species scores, and NMDS axes, we then developed expectations about the physical site conditions that might give rise to the various riparian forest assemblages. We used forward step-wise regression to detect relationships between species data (represented by NMDS site scores) and map-based environmental indices.

RESULTS

Riparian Forest Composition and Structure

Acer saccharinum (L.) and *Fraxinus pennsylvanica* (Marsh.) each occurred in all but one of the cluster types. Along with *Thuja occidentalis* (L.), they were the most common riparian tree species in Lower Michigan. Other relatively ubiquitous riparian trees species included *A. saccharum* (Marsh.), *Carpinus caroliniana* (Walter), *F. americana* (L.), *F. nigra* (Marsh.), *Salix* spp., *Tilia americana* (L.), and *Ulmus americana* (L.). Nevertheless, all of the seven clusters in Figure 2 were readily distinguishable based on both relative abun-

dance and indicator species (Table 2). The riparian forest cluster types were labeled Silver Maple Swamp (SMS), Maple-Elm-Sycamore (MES), Maple-Oak-Hickory (MOH), Basswood-Sugar Maple (BSM), Green Ash-Basswood (GAB), Cedar-Fir-Pine (CFP), and Cedar-Ash-Hemlock (CAH). Tree basal area ranged from 36.13 m²/ha in the MOH type to 47.16 m²/ha in the GAB type, whereas all indices of diversity were minimized in the GAB and CFP types and maximized in the MOH type (Table 3).

In the SMS riparian type (cluster 1; Figure 2), the mean relative abundance of *A. saccharinum* was greater than 50 percent (Table 2), and species richness and species evenness were relatively low (Table 3). *Acer saccharinum* and *F. pennsylvanica* were also the principal species in the MES riparian type (cluster 2; Figure 2), yet these transects had a more variable species composition. In the MOH riparian cluster (cluster 3; Figure 2), we identified nine indicator species, yet no single species was predominant (Table 2). Consequently, this type had the greatest index values for diversity, richness, and evenness (Table 3). The BSM type (cluster 4; Figure 2) was characterized by significant indicator scores for three tree species, as well as an abundance of *F. pennsylvanica* and *F. nigra* (Table 2), although field observations suggested that the occurrence of both *Fraxinus* species along these transects was concentrated in seeps or in low areas near the river channel. Relative to the BSM forests, the GAB type (cluster 5; Figure 2) had a much greater proportion of *F. pennsylvanica*, as well as the highest basal area and lowest diversity indices across all clusters (Tables 2 and 3). Both the CFP and CAH (clusters 6 and 7, respectively; Figure 2) riparian types were distin-

Table 2. Mean relative abundance (%) and indicator score significance (*) for selected tree species† across seven riparian forest types in Lower Michigan.

Tree Species and Code	Ward's Method Cluster							Total
	SMS	MES	MOH	BSM	GAB	CFP	CAH	
<i>Abies balsamea</i> (Abba)	0.0	0.0	0.3	3.6	0.4	6.7**	4.1	1.6
<i>Acer negundo</i> (Acne)	1.0	4.1**	1.3	0.4	0.0	0.0	0.3	1.2
<i>Acer nigrum</i> (Acni)	0.7	1.6	7.5*	0.2	0.0	0.0	0.0	1.5
<i>Acer rubrum</i> (Acru)	0.0	0.0	0.0	0.2	0.4	2.6**	2.3	0.5
<i>Acer saccharinum</i> (Acsn)	53.3**	22.7	16.6	1.9	2.7	0.0	0.4	21.2
<i>Acer saccharum</i> (Acsa)	1.0	0.5	4.6	11.7**	0.6	0.0	2.0	3.1
<i>Alnus rugosa</i> (Alru)	0.0	0.0	0.0	0.7	2.0	3.3**	2.8	0.8
<i>Betula papyrifera</i> (Bepa)	0.0	0.0	0.2	0.4	0.3	4.4	3.5**	0.8
<i>Carpinus caroliniana</i> (Cpca)	0.4	0.6	1.8	3.5	0.8	0.0	0.1	1.1
<i>Carya cordiformis</i> (Caco)	2.3	1.5	9.2**	0.6	0.0	0.0	0.6	2.3
<i>Carya ovata</i> (Caov)	0.7	1.4	1.6	0.1	0.0	0.0	0.0	0.6
<i>Celtis occidentalis</i> (Ceoc)	1.0	1.1	1.5	1.4	0.0	0.0	0.2	0.9
<i>Crataegus spp.</i> (Crsp)	0.1	0.4	1.6*	0.3	0.0	0.0	0.0	0.3
<i>Fagus grandifolia</i> (Fagr)	0.7	0.4	3.7**	1.4	0.0	0.0	0.0	1.0
<i>Fraxinus americana</i> (Fram)	0.3	0.7	2.8*	2.7	0.2	0.0	0.1	1.0
<i>Fraxinus nigra</i> (Frni)	2.3	1.6	3.3	11.4	8.7	3.3	10.6*	5.3
<i>Fraxinus pennsylvanica</i> (Frpe)	18.7	28.0	7.5	15.3	60.6**	0.0	9.0	18.7
<i>Juglans cinerea</i> (Juci)	0.0—	0.0	0.4**	0.0	0.0	0.0	0.0	<0.1
<i>Juglans nigra</i> (Juni)	0.3	1.9	3.0**	0.1	0.0	0.0	0.0	0.8
<i>Larix laricina</i> (Lala)	0.0	0.0	0.0	0.0	0.0	0.6**	0.0	<0.1
<i>Ostrya virginiana</i> (Osvi)	0.0	0.2	0.1	0.7**	0.0	0.0	0.3	0.3
<i>Physocarpus opulifolius</i> (Phop)	0.0	0.0	0.0	0.0	0.0	0.0	0.2**	<0.1
<i>Picea glauca</i> (Pigl)	0.0	0.0	0.4	0.2	0.2	1.2	5.1**	0.8
<i>Pinus resinosa</i> (Pire)	0.0	0.0	0.0	0.0	0.0	0.0	0.3**	<0.1
<i>Pinus strobus</i> (Pist)	0.0	0.0	0.4	1.7	0.0	4.2**	2.9	1.0
<i>Platanus occidentalis</i> (Ploc)	0.9	5.5**	1.2	0.3	0.0	0.0	0.0	1.3
<i>Populus balsamifera</i> (Poba)	0.0	0.0	0.0	1.2	1.7	0.9	4.7*	0.9
<i>Populus deltoides</i> (Pode)	1.0	3.8**	1.9	0.1	0.0	0.0	0.1	1.2
<i>Populus tremuloides</i> (Potr)	0.1	0.2	0.4	3.4*	0.0	0.0	0.7	0.7
<i>Quercus bicolor</i> (Qubi)	1.0*	0.4	0.0	0.0	0.0	0.0	0.0	0.3
<i>Quercus macrocarpa</i> (Quma)	2.3	4.3	8.9**	1.9	0.0	0.0	0.4	2.9
<i>Quercus rubra</i> (Quru)	1.2	0.7	3.0**	1.5	0.0	0.0	0.3	1.1
<i>Salix spp.</i> (Sasp)	1.2	2.8**	0.3	0.5	0.3	0.0	0.1	0.9
<i>Thuja occidentalis</i> (Thoc)	0.4	0.6	1.5	5.0	8.2	67.0**	34.0	10.8
<i>Tilia americana</i> (Tiam)	3.0	2.2	7.9	23.7**	10.4	1.7	6.5	7.7
<i>Tsuga canadensis</i> (Tsca)	0.1	0.0	0.1	0.2	0.0	0.0	5.0**	0.7
<i>Ulmus americana</i> (Ulam)	4.4	8.1**	5.0	2.1	1.9	0.5	0.7	3.8
<i>Ulmus rubra</i> (Ulru)	0.0	0.0	1.6*	0.3	0.0	0.0	0.0	0.3
<i>Zanthoxylum americanum</i> (Zaam)	0.0	0.0	0.0	0.0	0.2	0.0	0.5*	0.6

† Includes 98% of total basal area sampled. Remaining species had mean relative abundance < 0.1% and included *B. alleghaniensis* (Beal), *Gleditsia triacanthos* (Gitr), *Gymnocladus dioicus* (Gydi), *Liriodendron tulipifera* (Litu), *Morus rubra* (Moru), *Picea mariana* (Pima), and *Q. alba* (Qual).

* $p < 0.1$, ** $p < 0.05$ in Monte-Carlo significance tests of species indicator scores (not shown, Dufrene and Legendre 1997).

guished by the predominance of *Thuja occidentalis* and the conspicuous absence or reduced abundance of *A. saccharinum* and *F. pennsylvanica* (Table 2). Despite the mono-specific dominance of the CFP type, indicator species analysis revealed six significant associates. *Alnus rugosa* ((Du Roi) Sprengel) received a significant indicator score for the CFP type despite the fact that it showed a strong affinity for stream banks in both the CFP and CAH types (Table 2). Relative to the CFP type, transects in the CAH cluster were char-

acterized by greater richness, diversity, and evenness, as well as significant indicator scores for seven tree species (Tables 2 and 3).

Species-Environment Relations

Indirect ordination of species data from the sample transects using NMDS resulted in a separation of the seven clusters across three dimensions (final stress = 12.8), and two of these ordination axes accounted for

Table 3. Mean values and 95% confidence intervals of basal area and selected diversity indices across seven riparian types in Lower Michigan. Both basal area and plot richness represent averages of three prism-plots weighted by the linear extent of the sampled assemblage along each transect.

Index	Ward's Method Cluster							Mean
	SMS	MES	MOH	BSM	GAB	CFP	CAH	
Basal Area (m ² /ha)	42.2 (3.8)	38.5 (3.9)	36.1 (4.14)	37.5 (3.0)	47.2 (10.2)	39.0 (3.1)	37.8 (4.0)	39.65
Plot Species Richness	3.9 (0.4)	4.4 (0.6)	5.4 (0.6)	5.0 (0.4)	3.5 (0.9)	3.7 (0.4)	5.3 (0.9)	4.49
Transect Species Richness	9.9 (1.6)	11.8 (2.9)	14.8 (2.3)	10.9 (2.2)	7.6 (3.1)	7.6 (2.8)	13.0 (2.9)	11.06
Shannon Diversity (H')	1.4 (0.2)	1.8 (0.3)	2.2 (0.2)	1.8 (0.1)	1.2 (0.4)	1.1 (0.2)	1.9 (0.2)	1.67
Evenness (E)	0.6 (0.04)	0.8 (0.04)	0.8 (0.04)	0.8 (0.04)	0.6 (0.09)	0.6 (0.05)	0.7 (0.04)	0.71
Number of indicators	2	6	9	4	1	7	7	—

69% of the variation in species data (Figure 3). NMDS Axis 1 ($R^2 = 0.531$) was positively correlated with the mean relative abundance of *Thuja occidentalis* (0.791), *Abies balsamea* ((L.) Miller; 0.556), and *Fraxinus nigra* (0.526) and negatively correlated with the abundance of *Acer saccharinum* (-0.673) and *U. americana* (-0.529). This axis clearly distinguished the SMS, MES, and MOH riparian types on the left from the BSM and GAB types in the center and the CAH and CFP types on the right. In contrast, NMDS Axis 2 ($R^2 = 0.159$) showed strong positive correlations with *A. saccharum* (0.505) and *Tilia americana* (0.637) and negative correlations with *A. saccharinum* (-0.592). This axis distinguished among the SMS,

MES, and MOH riparian types, as well as among the BSM, GAB, and CFP types.

Stepwise regression of the NMDS sample scores indicated that each axis was related to a combination of mapped variables:

$$\begin{aligned}
 \text{NMDS1} = & 3.15 - 0.25(\text{avtmp}) + 0.04(\text{locgw}) \\
 & - 0.28(\text{vwidth}) + 0.43(\text{shdslp}) \\
 & + 0.22(\text{p/pet})
 \end{aligned}$$

This model accounted for 83% of the variation in the first NMDS Axis ($p < 0.001$). Each of these explanatory variables was significantly correlated with the NMDS Axis 1 ($p < 0.001$), suggesting that positioning

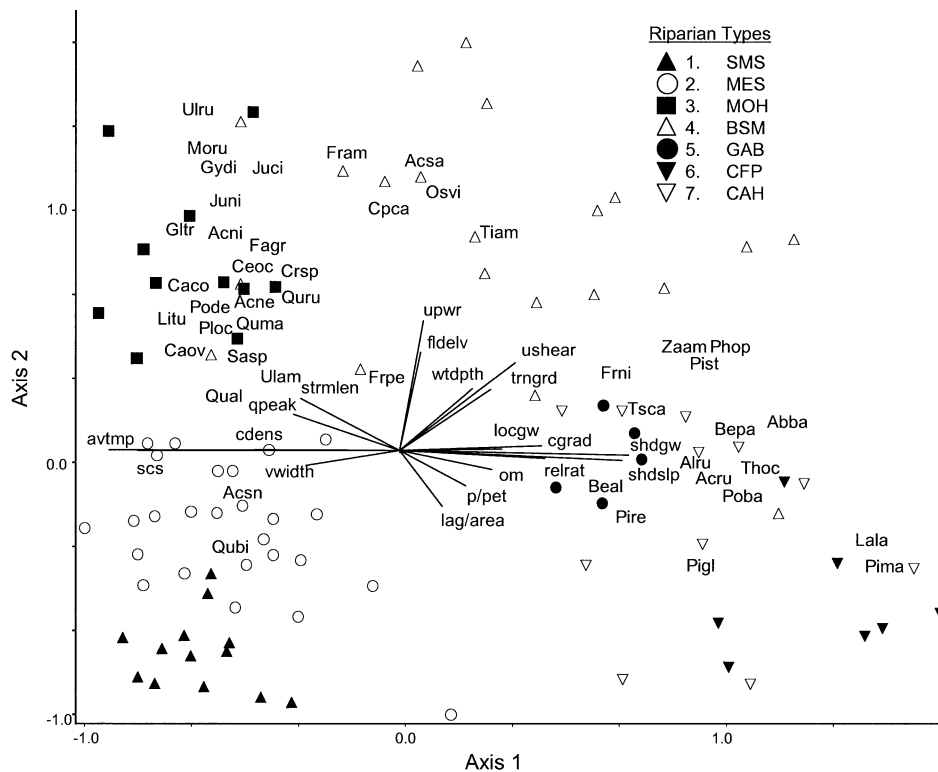


Figure 3. Scatterplot of Non-Metric Multi-Dimensional Scaling ordination of forest samples showing discrimination of forest types, tree species centroids computed by weighted averaging, and correlation with selected environmental variables.

on the first axis was a response to these factors or their close correlates.

$$\text{NMDS2} = -4.02 + 0.15(\text{upwr}) - 0.05(\text{p/pet}) \\ + 0.01(\text{fldelv})$$

This model accounted for 42% of the variation in the second NMDS Axis and was also highly significant ($p < 0.001$). Although both species and sample scores were entirely orthogonal, a number of the environmental variables from Table 1 were highly correlated either with one another or both NMDS axes (Figure 3). For example, SCS curve number and catchment ground-water delivery were not selected in the Axis 1 regression, despite a strong correlation with both the first Axis and each other.

DISCUSSION

This study represents the first broad-scale description of riparian forest patterns under various hydrologic and geomorphic settings in the upper Midwest. In contrast to many descriptions of riparian forests, our sampling design reflected a conscious effort to encompass both lateral and longitudinal patterns of variation in riparian vegetation. As a result, many tree species occurred across a wide variety of riparian types. This overlap reflects the fact that, for many species, suitable habitat conditions or similar disturbance events may occur at micro-sites along riparian gradients more broadly characterized by distinct hydrogeomorphic conditions. Conversely, marked variation among valley morphology, river hydrology, and regional climate resulted in sharp distinctions among the weighted relative abundance of tree species, and these differences were evident in both the cluster analysis and NMDS ordination (Figures 2 and 3). Such differences would likely be further emphasized by herbaceous vegetation, but we did not sample non-woody species.

The character of riparian types in Figure 3 may be interpreted on the basis of either NMDS axes or the site-indicator values of riparian tree species. Axis 1 clearly separated the southern bottomland species of the MOH and MES types from the northern hardwood and conifer species of the CFP and CAH types, and we observed a similar north-south climatic gradient in the pattern of mean annual temperature. The strong thermal gradient between northern and southern Lower Michigan was complemented by a sharp change in geology (Figure 4; Farrand and Bell 1982, Albert et al. 1986). The high sand hills in north-central Lower Michigan lead to higher valley slopes, greater ground-water potential, and exceptionally stable streams (Baker and Barnes 1998, Baker et al. 2003). In contrast, greater proportions of till and lake plain in the south-

ern Lower Peninsula appear to encourage more extensive agriculture, contribute to higher SCS curve numbers and greater drainage density, as well as the potential for hydrologic disturbance and surface-water flooding on the left side of NMDS Axis 1. Accordingly, the SMS, MES, and MOH riparian types contained a proportionately large abundance of floodplain species such as *A. saccharinum*, *Populus deltoides* (Bartr. ex Marsh.), and *U. americana*.

NMDS Axis 2 further distinguished among the SMS, MES, and MOH riparian types. SMS transects, low on Axis 2, showed a correlation with low valley unit power, low shears, and low cross-sectional elevations. Thus, not only would such riparian types be more susceptible to extensive over-the-bank flooding and excessive siltation, the duration of inundation was likely to be prolonged due to the low transport capacity of the surrounding valley bottom. The geographic distribution of our SMS transects suggested an association with small, low-gradient rivers in the interlobrate areas of southeastern and north-central Lower Michigan (Figure 4), as well as along larger rivers below dams (Baker and Barnes 1998). Studies by Barnes (1997) and Nelson and Sparks (1998) compared historical surveys with modern inventories under managed flood regimes in the Midwest. Both found that the relative abundance of *A. saccharinum* increased dramatically over other historically dominant floodplain trees as damming and flood-control measures have reduced seasonal flood peaks, prolonged flood events, or stabilized channels. Such measures may have given *A. saccharinum* a competitive advantage over other trees by reducing a once varied spectrum of hydrologic events to a specific, predictable, and prolonged seasonal inundation. Baker and Barnes (1998) described the strong predominance of *A. saccharinum* in floodplain forests along exceptionally stable rivers of northwestern Lower Michigan with prolonged, low energy floods, and similar assemblages have been observed throughout New England (Kearsley 1999).

The scatter of MES transects along the NMDS Axis 2 was correlated with higher floodplain elevations and increased flood unit power when compared to the SMS type. Accordingly, forest samples reflected an increased abundance of *F. pennsylvanica* relative to *A. saccharinum* and association with *Platanus occidentalis* (L.), *A. negundo* (L.), *Populus deltoides*, and *Salix* spp. *Fraxinus pennsylvanica* is also flood-tolerant in Lower Michigan and considered hardy when subjected to a variety of disturbance regimes (Taylor 1972). *Acer negundo*, *Salix* spp., and *P. deltoides* often occur in places where more intense flood flows create canopy gaps or new alluvial surfaces for seedling germination and establishment (Kearsley 1999, Johnson 2000). In addition, *Platanus occidentalis* was frequent-

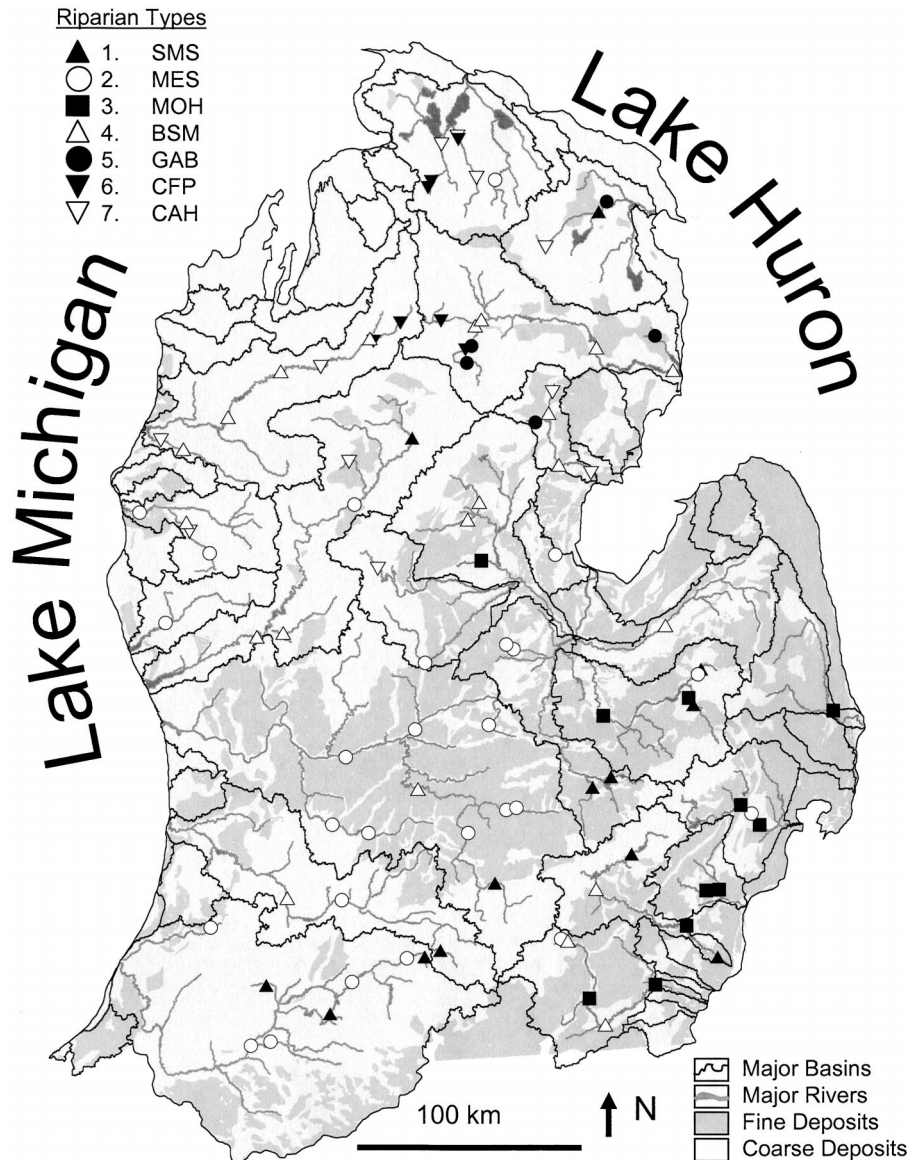


Figure 4. Map of sampling locations classified into seven riparian types across major river basins and surficial geology (after Farrand and Bell 1982) showing coarse deposits (moraines, ice-contact terrain, glacial outwash, dunes) and fine deposits (moraines, till plains, lacustrine plains).

ly observed on sandy accumulations in Lower Michigan, such as levees or splays, which were common in high-power floodplains. In a discussion of floodplain plant assemblages in Massachusetts, Kearsley (1999) noted that many floodplain forest descriptions throughout the Eastern U.S. have found *A. saccharinum* mixed with *F. pennsylvanica* and *U. americana* in proportions similar to the MES type (Buell and Wistendahl 1955, Brown and Peterson 1983, Dunn and Stearns 1987, Hardin et al. 1989, Dollar et al. 1992). In our sample, the MES type was distributed widely throughout southern Lower Michigan across a range of stream sizes and local geomorphic contexts (Figure 4).

In addition to elevated valley bottoms and flood

power, the MOH riparian type was positively related to upstream channel length, peak flows, and channel density, yet negatively related to lag time per unit catchment area. Therefore, extreme yet brief hydrographic storm responses in these larger systems were only marginally likely to be attenuated and experienced most intensely by trees at the channel margin. The MOH type had nine significant indicator species, as well as the highest richness and diversity scores, emphasizing the unique riparian habitat it provides within the lake-moderated climate of the Saginaw-Erie lake plain. Although *Q. macrocarpa* (Michaux), *U. rubra* (Muhl.), and *Carya cordiformis* (Wangenheim) K. Koch) are all known to occur in floodplains, they

are typically associated with periodic rather than prolonged flooding, as well as seasonally moist conditions (Hosner and Minckler 1963, Barnes and Wagner 1981, Barnes 1985). Many of the floodplain indicator species of the MOH type are also nutrient-rich or mesic site indicators in Michigan (e.g., *A. nigrum* (Michaux), *F. americana* (L.), *Juglans nigra* (L.), *J. cinerea* (L.), *C. cordiformis*, *U. rubra*; Barnes and Wagner 1981) and markedly less tolerant of inundation during the growing season than *A. saccharinum* or *F. pennsylvanica* (Hosner and Mickler 1963, Barnes 1985). Thus, the MOH type was characterized either by infrequent floods or by a topographic diversity that prevents frequent inundation in a large proportion of its bottomlands.

Transects in the BSM cluster were distributed widely across NMDS Axis 1, indicating a certain compositional dissimilarity within the cluster that reflects its occurrence over a broad range of climatic and hydrologic contexts. The relatively flood-intolerant indicator species of the BSM riparian type (*A. saccharum*, *T. americana*), as well as the distribution of sites along Axis 1 and Axis 2, attested that these riparian areas were characterized by a lack of wetness due to stable river flows or bottomlands elevated well above the river channel and the local water table. Previous descriptions have noted that this riparian assemblage often occurred where rivers drop from high elevation outwash deposits and pass close to mapped end moraines (Baker and Barnes 1998). Head cutting through relatively resistant glacial till resulted in narrow, steeply sloping valleys along many large river systems, as well as seeps along valley margins. Small proportions of both *F. nigra* and *Thuja occidentalis*, both typically found on mucky or peaty soils, occurred as valleys intersect the water-table surface, although they occupied relatively small proportions of the valley bottom. Floods in the BSM riparian type, if they occurred, would therefore be very likely to show the great tractive power and high floodplain elevation implied by its position along NMDS Axis 2.

The remaining three riparian types (GAB, CFP, CAH) were clustered on the right side of Axis 1, indicating a species composition associated with colder temperatures of northern Lower Michigan and smaller catchments dominated by subsurface water transport, higher slopes, and stable streams. These riparian types were also characterized by greater organic matter accumulation and an abundance of *T. occidentalis*. Closest to the ordination centroid, the species composition of GAB transects correlated with less extreme temperatures, a mix of surface and subsurface hydrologic sources, and the resulting predominance of *F. pennsylvanica* over *T. occidentalis*. In Lower Michigan, *T. occidentalis* is not particularly well-suited to sites that

experience extensive surface-water flooding, instead favoring rich soils and ground-water-fed wetlands (Barnes and Wagner 1981, Crow et al. 2000). Low scores for plot richness and transect diversity suggest that *F. pennsylvanica* dominance resulted from a competitive release in what was otherwise a highly productive environment.

The overwhelming predominance of *T. occidentalis*, along with significant indicators such as *Larix laricina* ((Du Roi) K. Koch) and *Abies balsamea*, indicated that the CFP riparian type was characterized by the cold, ground-water-fed wetlands common to north-central Lower Michigan (Figure 4; Voss 1972, Albert et al. 1986, Crow et al. 2000). This was corroborated by the distribution of the CFP type at the extreme right of NMDS Axis 1 and the bottom of Axis 2, where such crenal, headwater wetlands were also correlated with the smallest watersheds and the least upstream channels. The consistently extreme nature of such environments yielded low richness, diversity, and evenness scores (Table 3). Among species in these ground-water-sourced swamps, *T. occidentalis* is markedly more tolerant of shade than *L. laricina*, more tolerant of wetness than *Picea glauca* ((Moench) A. Voss) or *A. balsamea*, and has a greater affinity for basic soils than *P. mariana* ((Miller) BSP.) (Barnes and Wagner 1981).

Although the CAH riparian type had a species composition similar to the CFP type, it was more widely distributed across a broader range of NMDS, as well as geographic space (Figures 3 and 4). In general, the CAH transects were located in warmer climatic regions (Albert et al. 1986) and in local physiographic contexts that were less conducive to high rates of ground-water delivery to the entire river valley bottom than CFP transects (Baker et al. 2003). This lack of extensively wet conditions was reflected in the CAH species composition and indices of diversity, which increased because CAH transects, like those of the MOH type, encompassed a steep moisture gradient. While *Tsuga canadensis* ((L.) Carriere) and *P. glauca* are known to occur under moist conditions, *Pinus resinosa* (Aiton) is much better suited to well-drained soils (Voss 1972, Barnes and Wagner 1981). Therefore, the CAH type was characterized as having a greater proportion of well-drained, seasonally wet, and infrequently flooded conditions than either the GAB or CFP riparian types.

In contrast to many gradient analyses, our environmental variables were derived almost entirely from mapped information. Our underlying hypothesis was that spatial variation in riparian forest composition, in the absence of anthropogenic perturbation, was driven primarily by the proximal cues of both climate and the dynamics of the local hydroperiod. This hypothesis

was supported by the strong correlation of environmental variables with the gradients in community composition represented by NMDS ordination axes. We used mapped variables as surrogates for physical gradients associated with spatial patterns of regional climate, river hydrology, and valley physiography, yet they did not describe important factors influencing riparian tree species distributions, such as anthropogenic disturbance, fire, intra-specific differences across regions, and micro-site variation. The static, map-based predictions did not provide any information about dynamic influences on community composition such as the timing of disturbance events relative to seed germination or spring leaf flushing. Nevertheless, map-based models proved useful for interpreting and further characterizing the spatial patterning of riparian types and the hydrogeomorphic context of tree species occurrence. Not only did map-based characterizations correspond to species-based interpretations, they provided a broader perspective of riparian areas in the context of whole river systems and ecoregional variation. Recent research by Townsend (2001) suggests that further insight might be gained from resolving seasonal patterns of river flooding and valley wetness, as well as their spatial expression across the riparian landscape.

Because our samples described the land-water interface, they represented unique places where a complex hierarchy of regional climate, watershed processes, and/or local constraints could join to produce distinct hydrogeomorphic settings. Although the site-indicator capability of tree species proved useful for assessment of map-based indices, we found that similar biotic patterns occasionally arose from different physical contexts. As humans continue to modify rivers and riparian areas, the ability to retrace the patterns of natural physical variation in riparian areas and their relationship to watersheds and local landscapes is lost. Without such an understanding, management and restoration efforts are far less likely to meet desired targets. If similar local environmental conditions can result from very different landscape and watershed mechanisms, there is no guarantee that riparian systems appearing similar during site visits will respond similarly to perturbation. In fact, our findings suggest that extrapolating assumptions about riparian ecosystems from local studies alone is presumptive and that researchers need better and more explicit linkages between broad-scale variables and proximal physical cues in order to understand fully the drivers of riparian variation throughout the landscape.

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