Distribution and abundance of trees in floodplain forests of the Wisconsin River: Environmental influences at different scales

Turner, Monica G.[1*]; Gergel, Sarah E.[2]; Dixon, Mark D.[3] & Miller, James R.[4]

[1]*Department of Zoology, Birge Hall, University of Wisconsin, Madison, WI 53706, USA;* [2]*Department of Forest Sciences and Centre for Applied Conservation Research, University of British Columbia, Vancouver, B.C. Canada V6T 1Z4;* [3]*Department of Plant Biology, Arizona State University,Tempe, AZ 85287, USA;* [4]*Department of Natural Resource Ecology and Management and Department of Landscape Architecture, Iowa State University, Ames, IA 50011, USA;* *Corresponding author; Fax +16082656320; E-mail mgt@mhub.zoology.wisc.edu*

Abstract.
Questions: 1. How do physiography, flooding regime, landscape pattern, land-cover history, and local soil conditions influence the presence, community structure and abundance of overstorey trees? 2. Can broad-scale factors explain variation in the floodplain forest community, or are locally measured soil conditions necessary?

Location: Floodplain of the lower 370 km of the Wisconsin River, Wisconsin, USA.

Methods: Floodplain forest was sampled in 10 m × 20 m plots (*n* = 405) during summers of 1999 and 2000 in six 12- to 15-km reaches.

Results: Species observed most frequently were *Fraxinus pennsylvanica*, *Acer saccharinum* and *Ulmus americana*. Physiography (e.g. geographic province) and indicators of flooding regime (e.g. relative elevation and distance from main channel) were consistently important in predicting occurrence, community composition, and abundance of trees. Correspondence analysis revealed that flood-tolerant and intolerant species segregated along the primary axis, and late-successional species segregated from flood-tolerant species along the secondary axis. Current landscape configuration only influenced species presence or abundance in forests that developed during recent decades. Land-cover history was important for tree species presence and for the abundance of late-successional species. Comparison of statistical models developed with and without soils data suggested that broad-scale factors such as geographic province generally performed well.

Conclusions: Physiography and indicators of flood regime are particularly useful for explaining floodplain forest structure and composition in floodplains with a relatively high proportion of natural cover types.

Introduction

Understanding spatial relationships shaping riparian forest structure and dynamics is a key to understanding the function of river ecosystems (Bayley 1995; Meyer & Swank 1996; Naiman & Decamps 1997; Tabbachi et al. 1998). Many studies have related riparian vegetation to flow regulation (e.g. Williams & Wolman 1984; Rood & Mahoney 1990; Nilsson et al. 1991; Johnson 1992, 1994; Nilsson et al. 1997; Friedman et al. 1998; Nilsson & Berggren 2000) or an array of environmental conditions in floodplains (e.g. Johnson et al. 1976; Johnson 1994; Smith 1996); some have considered explanatory variables that vary with scale (e.g. Bendix 1994; Baker 1989; Baker & Barnes 1998; van Coller et al. 2000). However, few have simultaneously examined the relative influence of multiple types and scales of variables that may affect floodplain forests. We studied forests in the floodplain of the Wisconsin River (Wisconsin, USA) to address two questions: 1. How do physiography, flooding regime, landscape pattern, land-cover history, and local soil conditions influence the presence, community structure and abundance of overstorey trees? 2. Can broad-scale physiographic factors explain variation in the floodplain forest community, or are locally measured soil conditions necessary to predict/explain variation?

Floodplain vegetation may be influenced by both broad-scale physiographic patterns and fine-scale variation in soils. Large rivers often flow through several ecoregions that encompass a range of land forms, soils, and climate conditions, and this variation may provide a coarse-scale filter on species pools or relative dominance (Baker & Barnes 1998). Physiography may influence floodplain width, channel slope and morphology, sediment characteristics, and flood intensity (Hupp 1982; Hupp & Osterkamp 1996; Bendix 1994; Baker & Barnes 1998; Tabacchi et al. 1998; Corkum 1999) and hence affect riparian forest development. Soil properties such as texture, pH, and nutrient concentrations also may

vary over fine scales, and this heterogeneity can also influence riparian vegetation (Streng et al. 1989; Jones et al. 1994; Robertson & Augspurger 1999).

Floodplain forests are strongly influenced by flood regime (Decamps et al. 1988), as flood frequency, duration, timing, and intensity interact with species life-history requirements to determine tree species distributions (Streng et al. 1989; Jones et al. 1994; Hupp & Osterkamp 1985, 1996). Large river-floodplain systems such as the Wisconsin River typically have predictable seasonal floods of sufficient duration that the flood is an expected event to which organisms have adapted (Junk et al. 1989; Sparks 1992; Poff et al. 1997). Variability in flow can enhance diversity in floodplain systems (Poff et al. 1997; Tockner et al. 2000). Topographic heterogeneity can ensure that some portion of the floodplain will meet the requirements for a species during the flood and low-flow periods, if not the same locations every year (Sparks 1992). Elevation affects hydroperiod (flood frequency and duration) and thus influences species distributions and abundances (Menges & Waller 1983; Auble et al. 1994; Hughes 1997). Distance from the main river channel, elevation, and local topography may all be reasonable indicators of flooding regime that affect floodplain forests (Johnson et al. 1976; Streng et al. 1989; Hupp & Osterkamp 1996; Gergel et al. 2002a).

Current landscape pattern and past land cover may be important for explaining patterns in floodplain forests. Patch size or position within a patch may influence vegetation structure of floodplain forests through dispersal limitation or variation in abiotic conditions (Ranney & Johnson 1977; Ranney et al. 1981; Hanson et al. 1990; Chen et al. 1999). Historical land use can explain significant variation in contemporary plant communities (e.g., Foster 1992; Motzkin et al. 1996; Pearson et al. 1998), but its importance for contemporary riparian vegetation is poorly understood. Historical agriculture has been shown to influence secondary bottomland forests (Hosner & Minckler 1963; Knutson & Klaas 1998).

Methods

Study area

The Wisconsin River flows ca. 700 km from its source in northern Wisconsin to its confluence with the Mississippi River (Fig. 1), dropping 328 m in elevation and draining 31 800 km^2. Our study region included the spatial extent of 100-yr floods (based U.S. Federal Emergency Management Agency maps) on the lower 370 km of the river. The floodplain varies from wide and flat, where small elevational differences foster a fine-grained

mosaic of distinct suites of species (e.g. Noble 1979; Robertson & Augspurger 1999; Gergel et al. 2002a), to narrow and steep. Dams on the Wisconsin River have reduced flow variability; summer and fall low flows (summer-fall) are augmented, and floods (winter-spring) are reduced (Krug & House 1980; Dixon 2001). Setback levees (earthen levees built on the floodplain but away from the river) were constructed in the early 1900s in the Wisconsin Dells reach.

The lower Wisconsin River traverses three geographic provinces: the Northern Highland, Central Plain, and Western Upland (Martin 1965; Fig. 1). Geologically, the Northern Highland province is characterized by multiple glacial moraines from the most recent Pleistocene glaciation (12 000 - 16 000 yr B.P.), and soils are dominated by glacial tills. The Central Plain province is composed of Cambrian (500 million years BP) sandstone lowlands and includes the lake bed of Glacial Lake Wisconsin. Dominant soils include sandy outwash plains and lacustrine flats. The final 150 km to the Mississippi River are dam-free, include large amounts of protected lands, and traverse the unglaciated Western Upland province characterized by soft sandstones and limestone (Durbin 1997) and more coarse-textured soils.

Fig. 1. Map of the study region showing the Wisconsin River and the major geographic provinces (after Martin 1965) through which it flows. Locations of the six reaches are indicated numerically; descriptive information about each study reach can be found in Table 2.

Study design and data collection

We sampled vegetation in six 12 to 20 km long study reaches (Fig. 1). Reaches were chosen to be well distributed geographically; to avoid reservoirs, dams, and extensive areas of urban river bank development; and to contain abundant, regularly flooded forest. In larger forest patches (at least 1.2 km wide), five sampling points were located at 125-m intervals along randomly established transects perpendicular to the main channel. Sampling points (usually one to three) were located at random in smaller forest patches and always separated by at least 125 m. We attempted to sample across the range of conditions (elevation, distance from river, patch size, past land use) that occurred throughout the floodplain, but we only sampled areas that were currently in forest cover. During summers of 1999 and 2000, we placed 10 m × 20 m sample plots in a consistent position at each sampling point ($n = 405$). Each plot was located using a global positioning system, and we recorded whether the site was leveed or unleveed, and the location of the plot relative to the levee. All trees ≥ 2.5 cm diameter at breast height (DBH) were identified to species and the DBH recorded. We calculated basal area and stem density by species and plot, then summed relative density and relative basal area to produce a single importance value (range, 0 to 2).

Soils were sampled in each plot from the top 20 cm using a 3-cm diameter unslotted alloy soil probe at three random locations. The three samples were composited, air dried, then analysed at the Wisconsin Soil and Plant Analysis Laboratory, Madison, Wisconsin, to obtain estimates of pH, percent organic matter, phosphorus, magnesium, calcium, potassium, percent silt, percent clay and percent sand. Soil samples or some laboratory analyses were missing from 42 plots; therefore, the sample size for analyses that included locally measured soil variables was 363.

For each plot, we used a geographic information system (GIS, Arc/Info) to extract variables representing the effects of physiography, flooding regime, and land cover (summarized in Table 1). For physiography, we used geographic province, river distance to the Mississippi River confluence, and northing (latitudinal position based on GPS data). We described flood regime in terms of distance to the main channel of the Wisconsin River, elevation relative to the 100-yr flood elevation (using a 0.6 m digital terrain model or by extrapolating from topographic maps), and position relative to levees. More negative values of relative elevation indicate wetter sites with higher likelihood of flooding. For current landscape pattern, we used distance to forest edge and size of the forest patch containing the plot. Land-cover history was represented by obtaining the land cover that was present in the 1930s, 1960s and 1990s (Freeman et al. 2003) and assigning an ordinal score reflecting how long that plot had been in forest cover.

Data analysis

For soil variables, multivariate data reduction was done using factor analysis with varimax rotation, and rotated factor scores were used to evaluate loadings of individual variables on factor scores (Anon. 1996).

Table 1. Environmental variables and abbreviations used in this study and grouped by categories used in interpretation of results.

Variable (abbreviation)	Description	Source
Physiography		
Geographic province (Prov)	1 = Western Upland; 2 = Central Plain; 3 = Northern Highland.	Martin (1965)
Distance upriver from the Mississippi River (Distmiss)	River distance to the confluence with the Mississippi (km)	This study
Northing	Northern coordinate in Universal Transverse Mercator (UTM)	This study
Flooding regime		
Distance to river (Distriv)	Lateral distance (m) of plot from the channel of the Wisconsin River	This study
Relative elevation (m) (RelElev)	Plot elevation relative to the 100-yr flood elevation; positive values dry, negative wet	Digitized from FEMA maps
Levee	1 = upland of levee; 0 = unleveed or between the river and the levee	This study
Current landscape configuration		
Distance to forest edge (DistFor)	Closest distance (m) to edge of the forest patch	This study
Patch area (Pcharea)	Area (ha) of forest patch	This study
Land-cover history		
Land-cover history (Hist)	Ordinal variable with 1 = forested in the 1930s, 1960s and 1990s; 2 = non-forest in the 1930s, forest in 1960s and 1990s; 3 = non-forest in the 1930s and 1960s, forest in the 1990s	Freeman et al. (2003)
Locally measured soils		
Soil factor 1 (Fert)	Soil fertility (nutrients and pH; see Table 3)	This study
Soil factor 2 (Text)	Soil texture (see Table 3)	This study
Percent organic matter (OM)	Percent organic matter of soil	This study

Pearson correlation coefficients were also computed among all environmental variables.

Variation in species presence as a function of the environmental variables (Table 1) was examined using stepwise forward logistic regression (Anon. 1996) for tree species that occurred on ≥ 15 % of the sampling plots and for which we observed at least 150 individuals. *Quercus velutina* and *Q. ellipsoidalis* were combined for analysis because of difficulty in distinguishing between them in the field. We used the logit model (Trexler & Travis 1993) and fit the logit by using a maximum likelihood method. Adequacy of all logistic regression models was assessed by the significance of the parameters in explaining variation (likelihood ratio χ^2-test and Wald's test) and the fit of the predictions to data (goodness-of-fit, with percent concordance reported). Models were developed separately with and without soils data and results compared to determine the predictive power gained by including the fine-scale soils data. All variables retained in the model were significant at $P \leq 0.05$.

We used correspondence analysis (CA; ter Braak & Šmilauer 1998) on tree species presence/absence data to examine variation in forest community structure, and canonical correspondence analysis (CCA) to include the environmental variables (Økland 1996). A forward-selection procedure was used to identify the subset of variables that best explained the variation in the species data; a given variable is retained in the CCA if its addition significantly ($P \leq 0.05$) improves model fit (ter Braak & Šmilauer 1998). In the resulting diagram, selected environmental variables are depicted as vectors. To de-emphasize the effect of rare species, only species that occurred on ≥ 5% of the plots were included in the ordinations.

Species were aggregated into functional groups (flood-tolerant, flood-intolerant, and late-successional) based on their limits of tolerance to flooding and shade (Barnes & Wagner 1981; Burns & Honkala 1990; Iverson & Prasad 1998) and consistent co-occurrence in ordination space. Density, basal area, and importance values were then determined for each functional group on each plot. Multiple regression was used to predict the importance value of each functional group based on the set of environmental variables. Models were again developed separately with and without the soils data. Finally, to determine whether the importance of current landscape configuration varied with land-cover history, we estimated multiple regression models separately for plots that had been in forest continuously since the 1930s and those that had reforested since the 1960s.

Results

Environmental variables

A range of environmental conditions was represented in each study reach (App. 1). Factor analysis revealed strong positive relationships among soil pH and nutrients (Factor 1, Table 3). Soil texture was represented by Factor 2, with increasing values indicating soils with higher silt and clay content and lower sand content (App. 2). Scores for factors 1 and 2 (hereafter referred to as soil fertility and soil texture, respectively) were used in subsequent analyses. Percent soil organic matter was retained as a separate variable. Among the remaining environmental variables, there were strong correlations among the physiographic indicators. In the regression models used to evaluate importance value by functional group, we used geographic province and distance from the Mississippi, which more finely separates the geographic position of the plots. There was a significant positive correlation ($r = 0.32$; $P = 0.001$) between distance to the Wisconsin River and patch area, indicating that larger forest patches could contain plots located farther from the river, as expected. Finally, patch area was negatively related to northing ($r = -0.33$, $P = 0.0001$), indicating the presence of larger forest patches in the less modified southern portions of the floodplain.

Species presence and frequency of occurrence

We encountered 43 tree species (App. 3) among a total of 6910 trees ≥ 2.5 cm DBH in the 405 sampling plots. Fourteen tree species were present on ≥ 5% of the plots, and eight species occurred on ≥ 15% of the plots (Fig. 2). *Fraxinus pennsylvanica* was observed most frequently, occurring in 61% of all plots. *Acer saccharinum* and *Ulmus americana* were also widespread, each occurring in ca. 50% of the plots sampled.

Logistic regression models based on broad-scale predictors were generally effective in predicting occurrence of the eight most common species (Table 2). When local soil variables were not included in the models, geographic province was significant for five species (Table 2a). Most species were more frequent in the Western Upland, but *Quercus velutina* and *Betula nigra* were more frequent in the Central Plain (Fig. 2a). Variables related to flooding regime were significant for seven species, with *Quercus velutina* + *Q. ellipsoidalis* being more frequent at drier sites and the other species more frequent at wetter sites. Land-cover history was also important, with *Quercus bicolor*, *Fraxinus pennsylvanica*, *Celtis occidentalis*, and *Carya cordiformis* more likely to occur in the older forests
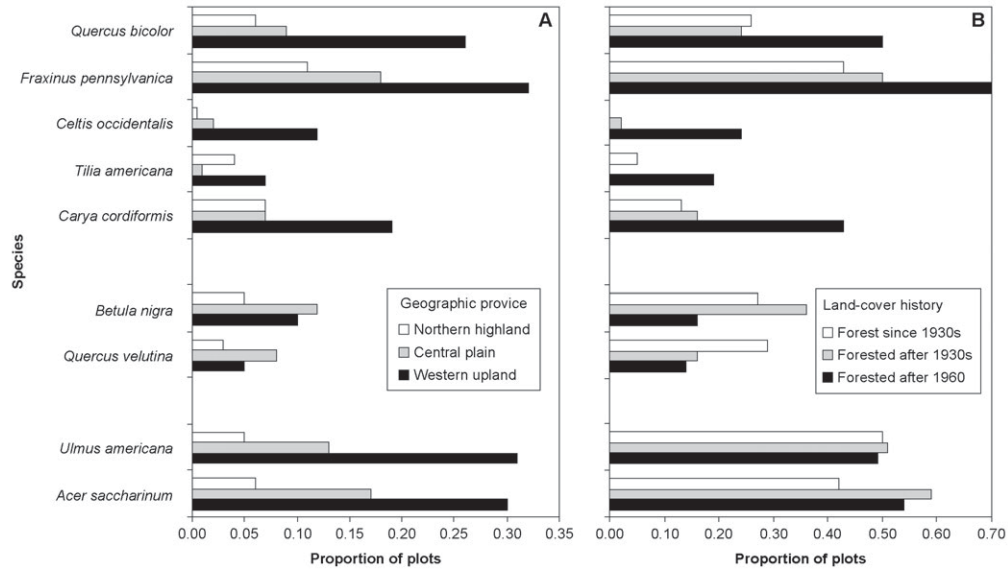
Fig. 2. Proportion of sampled plots within six reaches of the 100-yr floodplain of the lower Wisconsin River in which tree species were present (**a**) among the three geographic provinces, and (**b**) based on historic land cover.

(Fig. 2b). In contrast, *Betula nigra*, which is shade intolerant and relatively short lived, and *Quercus velutina* were more frequent on plots that became forested since the 1930s. The occurrence of *Acer saccharinum* and *Ulmus americana* did not differ by land-cover history (Fig. 2b). Current landscape pattern influenced only two species, with occurrence of *Quercus bicolor* and *Q. velutina* increasing with distance from forest edge.

When locally measured soil variables were included in the logistic regression models, the percent concordances increased modestly or remained similar (Table 2b).

Table 2. Results of logistic regression models that predict the occurrence of eight tree species in the 100-yr floodplain of the Wisconsin River. Models (**a**) excluding and (**b**) including locally obtained soil data. All significant variables have $p < 0.05$, and sign for each significant variable is shown; NS indicates that no indicators within that category were significant. Numbers in parentheses under each species indicate the frequency of plots in which the species was observed. DistFor = Distance from forest edge; DistMist = distance to the Mississippi River; DistRiv = Distance to river; Fert = soil fertility; Hist = history; OM = Percentage organic matter; Prov = province; RelElev = relative elevation; Text = soil texture.

Species (Number of plots)	Physiography	Flooding regime	Land cover history	Current landscape		Concordance
(a) Models 'excluding' (405 plots)						
Acer saccharinum (215)	DistMiss (–)	RelElev (–) Levee (–)	NS	NS		64.0%
Betula nigra (89)	NS	Relelev (–)	Hist (+)	NS		62.3%
Carya cordiformis (132)	NS	DistRiv (–)	Hist (–)	NS		66.1%
Celtis occidentalis (63)	Prov (–)	DistRiv (–)	Hist (–)	NS		83.3%
Fraxinus pennsylvanica (249)	NS	DistRiv (–) Levee (–)	Hist (–)	NS		63.9%
Quercus bicolor (165)	Prov (–)	–Levee	Hist (–)	DistFor (+)		68.4%
Quercus velutina (68)	Prov (–)	+Levee	Hist (+)	DistFor (+)		71.4%
Ulmus americana (201)	Prov (–)	NS	NS	NS		64.8%
(b) Models 'including' (363 plots)						
Species (Number of plots)	Physiography	Flooding regime	Land-cover history	Current landscape	Soils	Concordance
Acer saccharinum (188)	NS	NS	NS	NS	Fert (+)	70.3 %
Betula nigra (70)	NS	1.1376 Levee	NS	NS	Text (–)	64.6 %
Carya cordiformis (124)	NS	NS	Hist (–)	NS	Fert (–)	68.5 %
Celtis occidentalis (59)	Prov (–)	–DistRiv	Hist (–)	NS	NS	83.1%
Fraxinus pennsylvanica (222)	NS	DistRiv (–) Levee (–)	NS	+DistFor	NS	63.9%
Quercus bicolor (152)	Prov (–)	DistRiv (–) RelElev (–)	Hist (–)	NS	Fert (–)	72.2 %
Quercus velutina + ellipsoidalis (63)	NS	Levee (+)	Hist (+)	NS	OM (–) Fert (–) Text (–)	85.2%
Ulmus americana (181)	Prov (–)	Levee (–)	Hist (+)	NS	Text (+)	68.7%

The soil factors were significant in six models. Flooding indicators and geographic province remained significant for many models. For *Acer saccharinum*, the soil fertility factor was the only significant predictor, with presence more likely in soils with higher pH and cation concentrations. Models predict higher *Betula nigra* occurrence on sandy soils and on less frequently flooded positions upland of levees. Land cover history was important in models even when soils variables were also significant.

Forest community structure

The first two axes in the Correspondence Analysis accounted for 29.6% of the variation in the tree species occurrence data. Species tended to segregate along the primary axis on the basis of flood tolerance, with flood-intolerant species clustering to the right of the origin (Fig. 3a). Late-successional species tended to segregate from flood-tolerant species along the secondary axis, although *Betula nigra* was noticeably separated from the other flood-tolerant species, and there was some overlap between the groups.

The first two axes in the Canonical Correspondence Analysis accounted for 11.4% of the variation in the tree species occurrence data. The variable describing land-cover history was especially important, as were variables associated with physiography (Fig. 3b). *Carya cordiformis, Celtis occidentalis, Tilia americana,* and *Fraxinus nigra* tended to occur on plots that were forested in the 1930s and 1960s, and the latter two species showed a strong association with plots further from forest edges. Flood intolerant species were associated with plots that were further up-river, higher in relative elevation, and further from the Wisconsin River channel. Flood-tolerant and late-successional species tended to have more southerly distributions. The positions of the individual species scores in the CCA and CA configurations were generally similar (Fig. 3).

Abundance of functional groups

Species that consistently occurred together (Fig. 3) and shared similar limits of tolerance were grouped as: flood-tolerant species: *Betula nigra, Acer saccharinum, Fraxinus nigra, F. pennsylvanica, Populus deltoides, Quercus bicolor, Salix nigra*, and *Ulmus americana*; flood-intolerant species: *Quercus ellipsoidalis, Q. rubra, Q. velutina, Prunus serotina,* and *Populus tremuloides*); and late-successional group: *Carpinus caroliniana, Carya cordiformis, Celtis occidentalis*, and *Tilia americana*. Across all sample plots, flood-tolerant species were most abundant in terms of stem density, basal area, and importance value. Basal area of flood-tolerant species
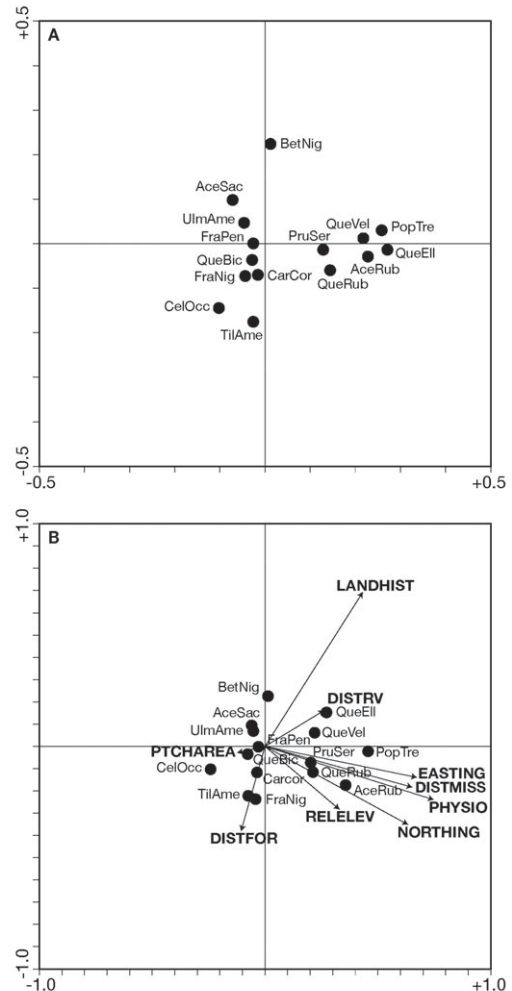
Fig. 3. a. Position of species in the space defined by the first two axes of the Correspondence Analysis of tree-community composition. **b.** Position of species and environmental variables defined by the first two axes of the Canonical Correspondence Analysis of environmental variables and tree-community composition. In both cases only species that occurred on ≥ 5% of the study plots (*n* = 405) were included in the analysis.

was high, averaging 19.6 m²/ha compared to about 5.4 m²/ha for flood-intolerant species and 1.9 m²/ha for late-successional species. Differences in density and basal area among functional groups were reflected in the importance values, with the flood-tolerant group averaging 1.3 per plot, the dry species 0.32 and the late-successional group 0.22.

Soils (where included) or province (when soils not included) explained the most variance in abundance of flood-tolerant species, followed by indicators of flooding regime (Table 3). When soils data were not included in the models, land-cover history and current landscape configuration were significant but explained little variation. Flood-tolerant species were more abundant on

finer, more basic soils with higher nutrient concentrations and percentage organic matter, or in the more southern province. Flood-tolerant species also were more abundant in wetter sites (lower relative elevations and in unleveed locations or streamside of levees); distance from the Wisconsin River was not significant in any of the models. Overall, the model with the locally measured soils increased r^2 from 0.26 to 0.32.

Flood regime and geographic province explained most variance in the importance value of flood-intolerant species, with soil variables adding little explanatory power (Table 3). Land-cover history was also significant, but it explained little variance. Flood-intolerant species were found at drier sites (higher relative elevations, upland of levees, and farther from the river) and in forests that had established more recently. The explained variation in the model that used geographic province was similar to that which included locally measured soils.

Variation in late-successional species was not well explained by the multiple regression models (Table 3). Of the variance that was explained, two-thirds was accounted for by land-use history, with flooding regime next in importance. Late-successional species were more abundant in the forests that had been in forest cover since the 1930s and also in locations that would have higher likelihood of flooding. Soil variables contributed little explanatory power.

Table 3. Multiple regression results for models with and without locally measured soils variable for predicting relative importance value for functional groupings of tree species in the Wisconsin River floodplain. Area = Percentage area; for other abbreviations, see Table 2.

Group	Models without soils data		Models with soils data	
	Model r^2 ($n = 404$)	Significant variables (partial r^2)	Model r^2 ($n = 362$)	Significant variables (partial r^2)
Flood -intolerant	0.43	+Levee (0.24) +Prov (0.14) +RelElev (0.02) +DistRiv (0.01) +DistFor (0.01) +Hist (0.01)	0.46	+Levee (0.25) +Prov (0.15) +Fert (0.02) +RelElev (0.01) +DistRiv (0.01) +Hist (0.01) −OM (0.01)
Flood -tolerant	0.26	−Province (0.14) −Levee (0.07) −RelElev (0.03) −DistFor (0.01) −Hist (0.01)	0.32	+Factor1 (0.20) −Levee (0.05) −DistMiss (0.04) −RelElev (0.01) +OM (0.01) −Distfor (0.01)
Late-successional	0.14	−Hist (0.10) −DistRiv (0.02) +Area (0.01) −Levee (0.01)	0.16	−Hist (0.09) −DistRiv (0.03) +Area (0.01) −Levee (0.01) −Factor1 (0.01) −Prov (0.01)

Multiple regression models for the importance values of functional groups estimated separately by land-cover history classes demonstrated a changing influence of current landscape pattern. For sites forested since the 1930s, geographic province and flooding regime were key predictors for both flood-tolerant (model $r^2 = 0.28$; $P = 0.0001$) and flood-intolerant species (model $r^2 = 0.31$; $P = 0.0001$). For plots with more recently established forest, the current landscape configuration was also significant. Importance of flood-intolerant species increased with distance to forest edge, whereas flood-tolerant species showed the reverse pattern. In both cases, the partial r^2 (0.16 and 0.14 for flood-intolerant and flood-tolerant, respectively) was about half of the explained variance.

Discussion

Environmental influences on floodplain forests

In the Wisconsin River floodplain, indicators of physiography and flood regime were particularly important in predicting occurrence, community composition, and abundance of trees. This is consistent with the known influence on riparian forests of major physical factors of river catchments, including bedrock geology, geomorphic features, soil character, climate, and hydrological regimes (Tabacchi et al. 1998). It is difficult to disentangle the relative contributions of geologic substrate, climate and river regulation along the Wisconsin River from the overall influence of physiography because these all vary with geographic province. For example, the Western Upland province contained the highest frequency of flood-tolerant species and also had the largest patches of continuous floodplain forest. The Central Plain province contained the highest frequency of flood-intolerant species; levees were also found only within this province, but soils are characteristically sandy. Thus, physiographic region was a significant but synthetic variable reflecting the strong influence of the abiotic template on the forest community (Curtis 1959).

Soil characteristics explained little additional variation beyond that explained by province. This suggests that the effects of soil variation on the mature floodplain forest may be most pronounced at broad spatial scales, or that soils are of only modest importance. Other studies (e.g. Robertson & Augspurger 1999; Streng et al. 1989; Jones et al. 1994) have observed significant effects of soil texture and microtopography on riparian forests. Local variation in soil properties may be of greater importance for tree seedling establishment than for mature forest stands, which may now have conditions that differ substantially from those present during tree recruitment.

Relative elevation contributed to heterogeneity in tree occurrence and abundance, as observed elsewhere (Robertson & Augspurger 1999). Distance from the main channel of the river was important in some models but generally contributed less explanatory power. The secondary importance of distance from the river may reflect the complex patterns of backwaters and sloughs that produce very wet local conditions that may be relatively far from the main channel. Effects of levees were consistent with results reported by Yin et al. (1997) and Gergel et al. (2002a). The mature floodplain forests of the Wisconsin River seldom experience stand-replacing floods, and our data are consistent with a frequent low-intensity flood regime (Auble et al. 1994; Tabacchi et al. 1998; Richards et al. 2002; Dixon et al. 2002; Gergel et al. 2002a). The relationships reported here would likely not apply following a large infrequent flood that would alter patterns of forest development (Sparks et al. 1990; Turner et al. 1998; Yin 1998).

Current configuration of forest cover was not usually important for species presence or abundance, except in forests that developed during recent decades. However, we only sampled well-developed forests, and spatial configuration could be important when non-forest patches are succeeding to forest and seed dispersal is important. Forest habitat was also relatively abundant and well connected (Freeman et al. 2003), conditions for which theory suggests a lesser influence of spatial configuration (e.g. Gardner et al. 1987; With & King 1997). Current landscape configuration could be important in other floodplain systems, particularly if natural riparian habitats were sparse and fragmented (Gergel et al. 2002b).

Land-cover history, which has not often been considered in studies of floodplain vegetation, was important for species presence and for the abundance of late-successional species in the Wisconsin River floodplain forest. The pattern of historical land use that characterizes the Wisconsin River floodplain is spatially complex (Burgi & Turner 2002; Freeman et al. 2003) introducing additional heterogeneity in riparian vegetation that is not directly related to predictable zones of elevation or distance from the river.

Local vs. broad-scale explanatory power

Comparisons of the statistical models for species presence and the abundance of functional groups suggested that the broad-scale variables, especially geographic province, generally performed as well as models including locally measured soil conditions. Other studies have also observed effects of broad-scale geographic variables (Baker & Barnes 1998). For example, Baker (1989) found geographic variables to be significantly but weakly correlated with overall variation in vegetation along a 300-km length of river in the Rocky Mountains. However, the geographic variables contributed to spatial variation in the processes that controlled vegetation structure, suggesting a linkage between macro- and micro-variables.

Indicators of flooding regime were also very important; these varied locally and were estimated separately for each plot using readily available data. Another study (Gergel et al. 2002a) conducted in the Wisconsin Dells reach employed detailed hydrologic modeling using HEC-RAS software (Hydrologic Engineering Center-River Analysis System, US Army Corps of Engineers, Anon. 1998) combined with 2-ft contour digital elevation data to reconstruct the past flood regime of 100 plots from 1938 to 1997. This more detailed and expensive estimate of flood regime explained about 45% of the variation in functional groupings similar to those used in this study (Gergel et al. 2002a). This is clearly an improvement, yet the simple indicators of flood regime that we used were informative and reasonably cost-effective.

Other predictors were sometimes statistically significant, but usually did not contribute much explanatory power in the models. For example, although patch attributes and edges have been suggested as important in riparian systems (e.g. Pringle et al. 1988; Naiman et al. 1988; Wigley & Roberts 1997), metrics of current landscape configuration were not strong predictors of floodplain forest vegetation along the Wisconsin River. This suggests that quantifying landscape pattern in floodplains with well-connected natural vegetation may not be necessary for explaining forest community composition. However, the importance of land-cover history in explaining current vegetation in the floodplain forests of the Wisconsin River suggests a new predictor variable that might be helpful to measure in other studies. Overall, our results suggest that physiography and indicators of flood regime are particularly useful for explaining floodplain forest structure and composition in floodplains with a relatively high proportion of natural cover types.

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