Ecological Monographs, 72(4), 2002, pp. 465–485

RIPARIAN TREE SEEDLING DISTRIBUTION ON WISCONSIN RIVER SANDBARS: CONTROLS AT DIFFERENT SPATIAL SCALES

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Abstract. We investigated the influence of physical characteristics at the local (quadrat) and landscape (sandbar, channel, and river cross-section) scale on the distribution of pioneer tree seedlings (*Acer saccharinum*, *Betula nigra*, *Populus deltoides*, and *Salix* spp.) on 30 sandbars along a 16-km reach of the Wisconsin River in 1998. At the landscape scale, new seedlings were most frequent in side channels that were inactive (stagnant) at low river flow, older seedlings were most frequent in narrower side channels, and saplings were most frequent on higher sandbars and in narrower channels. At the local scale, seedling occurrence in individual 1×2 m quadrats ($n = 692$) was significantly related to the horizontal and topographic position and the vegetative cover on the quadrat. Landscape relationships for species that dispersed prior to a small midsummer flood (*Acer* and *Betula*) were stronger than models for later dispersers (*Populus* and *Salix*), and models for old seedlings and saplings were stronger than those for new seedlings. Both local and landscape variables were significant for explaining local seedling occurrence, and significant landscape $\times$ local scale interactions suggested that the influences of some local variables on seedling occurrence were conditional on landscape context. All in all, our results suggest that both local and landscape variables influence the distribution of riparian vegetation, that the influence of local variables may be constrained by landscape context, and that the influence of landscape variables may increase with seedling age.

Key words: Acer saccharinum; Betula nigra; *fluvial geomorphology; hierarchy; landscape ecology; multiple spatial scales; plant demography;* Populus deltoides; *riparian vegetation;* Salix exigua; Salix nigra; *succession.*

INTRODUCTION

Ecological processes and populations of organisms may be influenced by patterns and processes at multiple spatial and temporal scales (Delcourt and Delcourt 1988, Levin 1992, Pearson 1993, Reed et al. 1993, Andrén 1994, Robinson et al. 1995, Richards et al. 1996, Poff 1997, Harding et al. 1998, Gergel et al. 1999). According to hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986, 1989), the behavior of fine-scale mechanistic processes is influenced by constraints operating at broader spatial and temporal scales. Hierarchical levels are defined by the frequency of processes important to the phenomena of interest, with ''slower'' processes providing the context or trajectory within which the ''faster'' processes occur. Within this framework, spatial and temporal scales usually covary, with lower frequency processes occurring at broader spatial scales, and high-frequency processes occurring at finer spatial scales. O'Neill et al. (1989) extended hierarchical concepts to the structuring of landscapes, assuming that processes that occur at discrete spatiotemporal scales create a hierarchy of characteristic patch sizes within the landscape (see also Kotliar and Wiens 1990). We follow their approach by investigating the influence of controls at different spatial scales on the distribution and demography of riparian tree seedlings on Wisconsin River sandbars.

Geomorphological and biological research have suggested that many processes and patterns in rivers may be inherently linked in a functional hierarchy (Schumm and Lichty 1965, Frissell et al. 1986, Naiman et al. 1992, van Coller et al. 2000). The concept of the graded stream, for example, assumes that a hierarchy of linked physical processes interact to adjust channel characteristics (morphology and process) to a dynamic equilibrium (Knighton 1998). In stream ecology, the importance of valley conditions for understanding stream characteristics and local biota (Hynes 1975) suggests hierarchical linkage. More recently, recognition of the hierarchical nature of the physical habitat template (Poff 1997) has become foundational in studies of stream communities (Richards et al. 1996), stream classification schemes (Frissell et al. 1986, Naiman et al. 1992), and in ecological theory (Gregory et al. 1991, Poff 1997, Naiman et al. 2000).

Some authors (Baker 1989, Bendix 1994*a*) have pointed out that multiscale influences on riparian vegetation are not necessarily linked in a causal hierarchy. Relevant processes occurring at different spatiotem-

Manuscript received 15 March 2000; revised 13 June 2001; accepted 14 August 2001; final version received 31 October 2001.

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poral scales may be hierarchically linked or may exert direct, independent influences on the phenomena of interest. That is, broad-scale factors may influence local conditions indirectly through their effects on finer scale pattern and process (hierarchical), or may exert direct influence on the phenomena of interest (covariant, nonhierarchical). The controls on riparian vegetation structure may be a complex combination of hierarchical and nonhierarchical factors, making separation of the relative influences of fine- and broad-scale processes difficult (Bendix 1994*a*). Because of this, Bendix (1994*a*), in his study of the effects of broad-scale (longitudinal) and fine-scale (transverse) factors on riparian vegetation composition, excluded variables that were strongly functionally linked between levels, or included only the effects manifest at the lower (local) end of the hierarchy, where the effects of physical variables on vegetation were assumed to be direct. In contrast, Baker (1989) focused on watershed-scale characteristics and de-emphasized local geomorphic variables in his study of montane riparian vegetation. Conclusions regarding multiscale influences on riparian vegetation may be highly dependent on the assumptions, variables, and analyses used, as well as the spatial scales considered (Bendix 1994*a*, van Coller et al. 2000). However, if hierarchical controls are important, then explicit consideration of multiscale linkages in pattern and process may lead to a more complete understanding of the controls on riparian vegetation dynamics (Bendix and Hupp 2000).

We examined the influence of physical variables at fine (within sandbar) and broad (river cross-section, channel, sandbar level) spatial scales on the local occurrence (in 1×2 m quadrats) of seedlings of pioneer riparian trees within a 16-km segment of the Wisconsin River. Our research had several goals: (1) to determine the individual physical variables at different spatial scales that were related to seedling distribution; (2) to determine the importance of fine (within sandbar) and broad (among sandbars and higher) scale variables on the distribution of seedlings of different ages and species groups; and (3) to determine the extent to which these variables might be linked in a hierarchical causal framework.

Based on the linkage between broader spatial scales and longer time scales, we predicted that the distribution of older seedlings (seedling persistence) would be more strongly related to broad-scale factors than would the distribution of first-year seedlings (seedling establishment). Thus, initial seedling establishment should be a more fine-grained process and persistence a more coarse-grained process. We also predicted that the relative influence of broad-scale factors would differ for new seedlings having different dispersal times relative to a minor flood event, with early-dispersing (pre-flood) species constrained in their distribution by coarse-scale flood-induced heterogeneity in seedling mortality, and with later dispersing (post-flood) species exhibiting a finer-grained distribution and weaker relationships to broad-scale factors.

In this study, we considered ''local'' variables to be those that could be measured uniquely at the quadrat level, at the spatial resolution of centimeters to meters. These included elevation relative to river stage, local sediment characteristics, vegetative and litter cover, and topographic and horizontal position. Each of these variables may influence the interaction between fluvial geomorphic processes and the probability of seed deposition, germination, and survival at a given location (McBride and Strahan 1984, Hupp 1992, Friedman et al. 1996*a*, Shafroth et al. 1998, Cooper et al. 1999). ''Landscape'' variables were those that could be measured at the resolution of the entire sandbar, the individual channel, or the river cross-section. If hierarchical controls are important, these ''landscape'' characteristics may provide constraints or context for the influence of the ''local'' variables by affecting the routing and delivery of flow, sediment, and propagules, and also the intensity of disturbance occurring at the quadrat.

Seedling establishment is a key stage in the functional linkage between fluvial geomorphic processes and riparian vegetation structure and dynamics (Fenner et al. 1985, Baker 1990, Rood and Mahoney 1990, Stromberg et al. 1991, Johnson 1994, Scott et al. 1996, 1997, Cooper et al. 1999). However, few studies (Johnson 1994, Fetherston et al. 1995) have examined the effects of within-channel spatial heterogeneity on seedling establishment and survival. Most demographic studies of early-successional riparian trees have emphasized temporal factors, such as annual or seasonal variation in flow (Fenner et al. 1985, Scott et al. 1997, Shafroth et al. 1998), over spatial factors, or have used space-for-time substitution (Glenn-Lewin and van der Maarel 1992). However, spatial distribution of seed sources (Hanson et al. 1990, Fastie 1995) and spatial heterogeneity in geomorphic processes (erosion, deposition) may influence the spatial distribution of colonization (Nilsson et al. 1993, Auble and Scott 1998), as well as subsequent seedling persistence (Scott et al. 1996, Cooper et al. 1999, Friedman and Auble 1999). Consideration of the controls at multiple scales that influence woody seedling demography would be a valuable contribution to this body of literature and would yield greater understanding of riparian vegetation dynamics (Bendix and Hupp 2000).

Study Area

The study area is a 16-km reach of the Wisconsin River between the Wisconsin Dells and the town of Portage, in Sauk and Columbia Counties, Wisconsin, USA. (Fig. 1). Flow is modified by a power-generating dam (Kilbourn) 16 km upstream, which may cause diurnal fluctuations in river stage of 0–0.4 m, especially at lower flows. Another reservoir (Lake Wisconsin) begins ~20 km downstream of the study area. A series

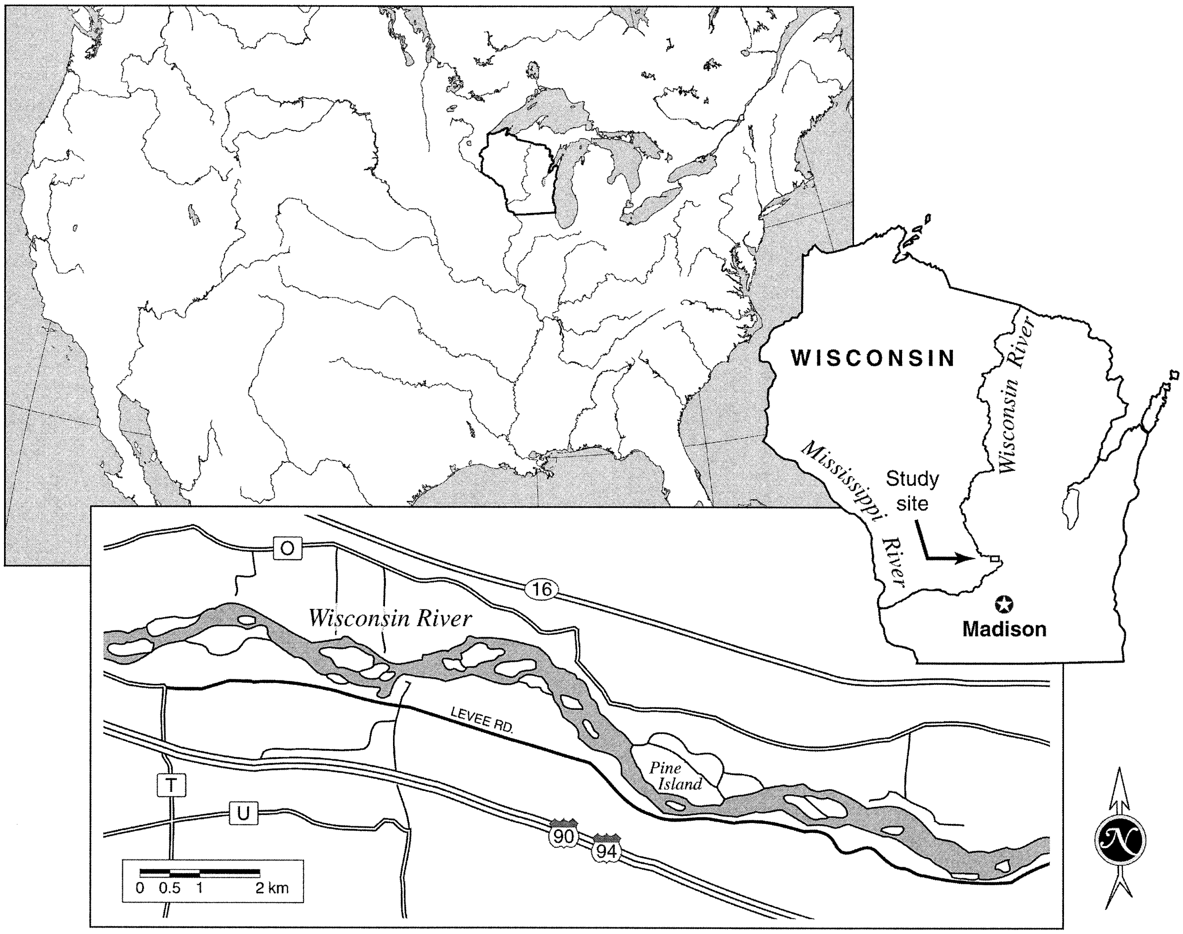

FIG. 1. Map of study area.

of dams and reservoirs farther upstream is estimated to have reduced annual peak flows on the order of 10–20% (Krug and House 1980). Although extensive alteration of flows occurred before 1900, much of this reduction in peak flows was due to the construction of the three largest reservoirs (Dubay, Petenwell, and Castle Rock) between 1940 and 1950 (Krug and House 1980, Durbin 1997). No new dams or other major flow alterations have occurred in the last 50 yr.

Much of the length of the study reach is bounded by the levees on the north and south sides of the river, generally offset from the riverbank into the floodplain by 50–500 m. The channel morphology is island braided (Schumm 1985, Knighton 1998), with a high width-to-depth ratio, numerous mid-channel islands, and large sandbars. The gradient of the channel and valley is low (~0.3 m/km), flowing through the lake plain of former glacial Lake Wisconsin (Clayton and Attig 1989). A USGS gaging station below Kilbourn Dam (U.S. Geological Survey gaging station, 05404000 at Wisconsin Dells) has provided a continuous record of flow since October 1934 (Fig. 2). The average daily flow over the period of record is 195 m^3/s, with the maximum and minimum daily flows on record at 2044 m^3/s (14 September 1938) and 30 m^3/s (19 August 1936), respectively. The average annual peak flow is ~1020 m^3/s. The largest recent peak, at 1674 m^3/s on 24 June 1993, was the sixth largest in the 63 yr of record and the largest since 1973. Annual peak flows

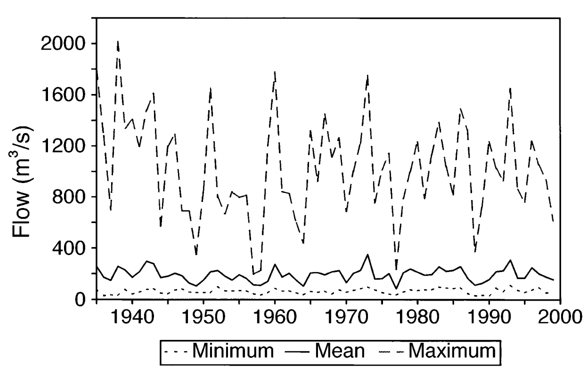

FIG. 2. Annual (water year) maximum, mean, and minimum mean daily river flows (m^3/s) at the Wisconsin Dells gaging station, Wisconsin, USA.

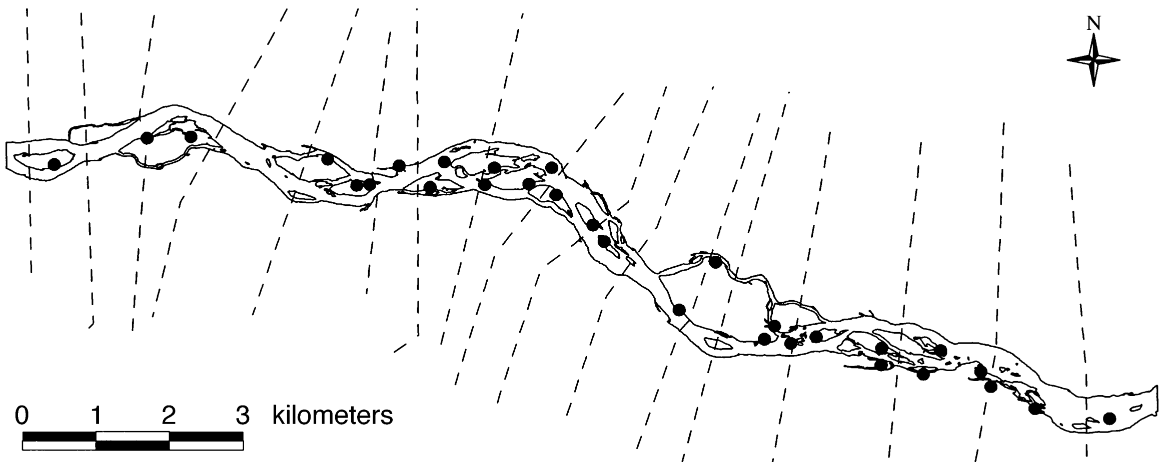

FIG. 3. Map of sampling locations (solid dots) and river cross-sections (dashed lines) within the study area.

are primarily related to spring snowmelt, with over half (56%) of the historic annual peak flows in March or April, but with occasional rainfall-related floods in the summer or fall.

A time series of historic aerial photographs suggests that portions of the floodplain converted from open braided channels in the 1930s to floodplain forest in the early 1950s and later, with tree colonization occurring along and between islands and in former secondary channels. Relative to the 1937 channel, unvegetated channel area declined 11.5% from 1937 to 1968 and 5% from 1968 to 1995 (M. D. Dixon, *unpublished data*). The topography of the floodplain suggests a fluvial geomorphic origin from island reattachment and channel abandonment processes (Osterkamp and Costa 1987, Friedman et al. 1996*b*, Osterkamp 1998), with moist swale areas and drier alluvial ridges. Floodplain vegetation includes areas of oak savanna, sedge meadows, and low and mixed floodplain forest (Ware 1955, Curtis 1959, Liegel 1988). Silver maple (*Acer saccharinum*) and river birch (*Betula nigra*), and to a lesser degree cottonwood (*Populus deltoides*) and black willow (*Salix nigra*), dominate the swales and other areas of low floodplain forest, and the areas that have converted from river channel to woodland since the 1930s. These species, along with sandbar willow (*Salix exigua*) and Missouri River willow (*Salix eriocephala*), appear to be the dominant species colonizing young sandbars and thus were the focal species in this study.

METHODS

New seedlings (germinated in 1998), older seedlings (<0.5 m tall and germinated before 1998), and saplings (>0.5 m tall, with dbh <2.5 cm) were sampled on 30 sandbars within the active channel of the Wisconsin River between late August and mid-November 1998. A lower intensity sampling effort was also conducted in 1999 on 32 sandbars. Data from 1999 were used only to assess the degree of variation in seedling distributions between years and were not included in other analyses. New seedlings were identified based on their small size, lack of a woody stem, and their occurrence on sites without permanent vegetation. For *Salix exigua*, the main species that spread extensively by suckering, sprouts were distinguished from new seedlings by leaf shape (Argus and Goff 1964). Sprouts were classified as old seedlings or saplings, depending on their size.

Candidate sandbars were located on 1995 aerial photographs and were marked and numbered on USGS topographic maps. These were classified according to the position of the sandbar relative to islands and the mainland (upstream end of island, downstream end, island side, mainland side, and isolated sandbar). Of these, 30 were selected systematically as sampling sites in order to achieve representative coverage of different sandbar positions and geographic coverage of the study area (Fig. 3).

Transect sampling

In 1998, three 2 m wide belt transects were established within each sandbar to characterize patterns of topography and seedling occurrence (Fig. 4). During the 1999 sampling, only one transect per sandbar was established. Each sandbar was divided longitudinally into thirds, with a transect being placed at a stratified random distance within each third. Each transect was begun at water's edge, oriented perpendicular to the direction of river flow, and continued across the sandbar until the opposite sandbar–channel margin or a permanently vegetated bank was encountered. All tree seedlings within 1 m of each side of the transect were noted by species, size/age class (new seedlings, old seedlings, or saplings), and position along the transect. Using a rod and level, we measured elevation (to the nearest 0.01 m) at the center of each 1-m transect segment in which seedlings occurred and at other locations

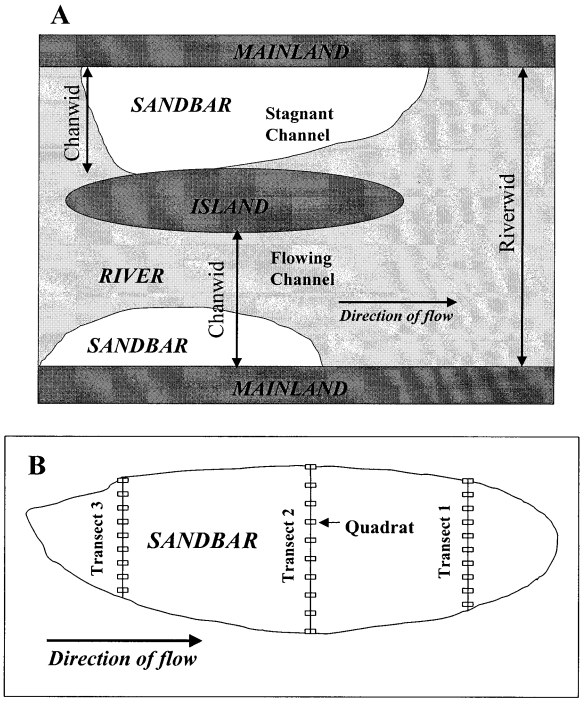

FIG. 4. Diagrams of river and sampling protocol: (A) schematic of channel variables; (B) transect and quadrat placement on sampled sandbars.

sufficient to characterize transect topography. Elevations were expressed relative to the water surface.

Within each transect, ~10 evenly spaced 1-m segments were selected as quadrats (1 × 2 m) for more intensive sampling (Fig. 4). In addition to elevation, the number of tree seedlings or saplings present by species and size/age class; the percentage cover of forbs, grass, bare ground, seedlings, shrubs, and litter; and the sediment type (sand, silt, gravel, or a combination) were recorded for each quadrat.

Hydrologic modeling

We used HEC-RAS software (Hydrologic Engineering Center 1998) to model longitudinal variation in hydrologic variables and stage–discharge relationships within the study reach. HEC-RAS models water surface profiles for steady, one-dimensional, gradually varied river flow by solving for energy losses due to friction and channel expansion/contraction between river cross-sections. We parameterized the model using estimates of hydraulic roughness (Manning's *n*) and measurements of river cross-sections at ~0.8-km intervals throughout the study reach (Fig. 3), obtained from the Wisconsin Department of Natural Resources (A. Lulloff, *personal communication*). These inputs had been used earlier by the Department of Natural Resources to model the potential impacts of the levees on flooding in the nearby town of Portage. We ran the model for lower flows, using estimated stage–discharge relationships for a National Weather Service gage near the downstream end of the study area and discharge estimates at the Wisconsin Dells gage, upstream of the study area, to provide boundary conditions. Model performance, however, is probably less accurate at low flows than at flood flows (Hydrologic Engineering Center 1998) because of the enhanced importance of spatial heterogeneity in channel bed topography and hydraulic roughness at lower river levels. Because our model results were not verified against more detailed local measurements of stage and discharge in the field, our estimates of river stage and quadrat elevation should be considered approximate (K. W. Potter, *personal communication*).

Calibration of elevations

Because quadrat elevations were measured relative to the water surface at the time of sampling, these elevations needed to be corrected for differences in river stage within and among dates. We estimated discharge at the time of sampling for each site based on provisional 15-min gage readings at Wisconsin Dells and empirically estimated flow travel times from the gage to the sampling site. Using stage–discharge relationships obtained from HEC-RAS model results for the nearest cross-section(s), we then calculated the difference in water surface elevation between the flow at the time of sampling and a reference flow of 99 m^3/s. We used this difference in stage to adjust our field surveys, in order to express all plot elevations relative to the reference flow of 99 m^3/s.

Quadrats occurring below the stage of the reference flow (99 m^3/s) are inundated, on average, >85% of the days of the year (>309 d/yr) on an annual basis (1970–1999 water years), and were inundated on ~65% of the days during the growing season (15 May–30 September) in 1998. Because these quadrats were inundated most of the time and were nearly devoid of seedlings, we excluded all quadrats below the reference stage from further analyses. Of the remaining quadrats, all are inundated by the mean annual peak flow (1020 m^3/s) and the median quadrat elevation (in terms of inundating flow) is inundated on ~30% of the days (113 d/yr), on an annual basis.

Mid-season flow peak and species groups

On 29 June 1998, a flow of 606 m^3/s occurred on the study area (Fig. 5), inundating ~97% of the eventual quadrat locations, 93% of them by >0.5 m, and 100% of the quadrats containing new seedlings. This was not a large ''flood,'' on an annual basis, and was smaller than the spring peak in 1998 (937 m^3/s) and the mean annual peak (1020 m^3/s). Flows of this magnitude or greater have occurred during the growing season (15 May–30 September) in 14 of the last 30 yr and on 3% of the days (12 d/yr) in an average year.

Based on high post-flood seedling mortality on a set of permanent plots (Dixon 2001), we hypothesized that this midsummer flow pulse had a strong influence on

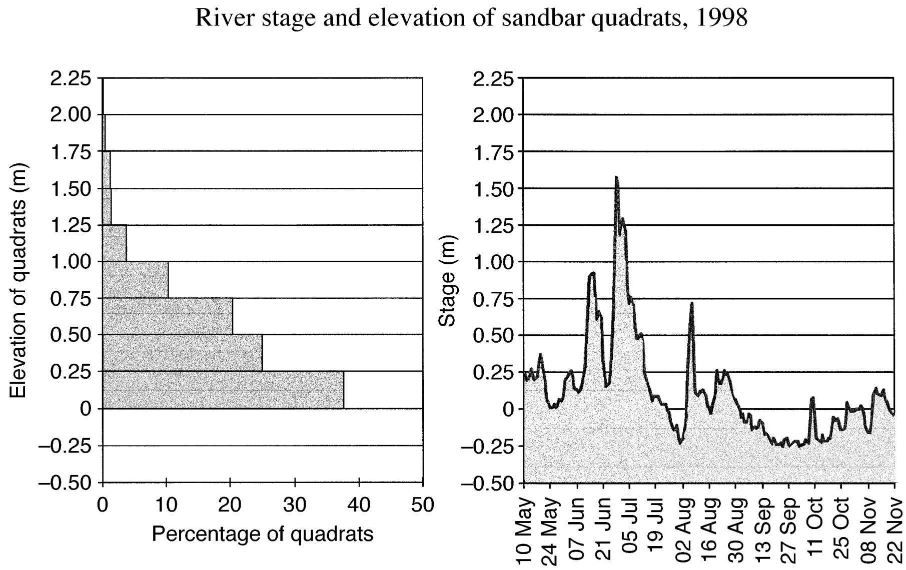

FIG. 5. Elevation distribution of quadrats, relative to river stage, and estimated river stage (m) for spring and summer 1998.

the distribution and abundance of seedlings that had germinated earlier in the season. We therefore divided new and older seedlings into early-dispersing and late-dispersing species groups relative to the 29 June flow. Dates of dispersal for each species (Table 1) were determined from the literature (Leopold and Jones 1947, Schopmeyer 1974, Burns and Honkala 1990), from field observations of seeding trees, and from sticky seed traps at several locations within the study area in 1999 and 2000. Species that had probably dispersed >90% of their seeds prior to 29 June were included in the ''early-disperser'' group, and the rest were included in the ''late-disperser'' group. The early-disperser group consisted of *Acer saccharinum* and *Betula nigra*. The late-disperser group consisted of the *Salix* species (*S. exigua* and *S. nigra*) and *Populus deltoides*, all of which are in the family Salicaceae. Some of the late-disperser group may have included *Salix eriocephala* seedlings, which dispersed earlier in the season, but were difficult to distinguish from first-year *Salix nigra* seedlings.

TABLE 1. Seed dispersal dates from the literature and from the study area in 1999 or 2000, for focal tree species.

	Seed dispersal dates	
Species	Literature†	Field data
Early dispersers		
Acer saccharinum	April–June 15 May–8 June‡	22–31 May§ (15 May–16 June)‖
Betula nigra	May–June	5–16 June§ (5 June–19 July)‖
Late dispersers		
Populus deltoids	May–mid-July	29 May–1 July§ (29 May–6 August)‖
Salix sp.	May–July	22 May–10 July§ (14 May–19 July)‖
S. exigua	May–July	22 May–10 July¶
S. eriocephala	June	13 May–10 June#
S. nigra	June–July	9 June–1 July¶

† Seed dispersal dates are derived from Schopmeyer (1974) unless otherwise noted.
‡ Dates are from Leopold and Jones (1947).
§ Dates by which cumulative seed numbers in sticky traps were between 10% and 90% of the total number of seeds collected during 1999.
‖ Earliest and latest dates of observed seed dispersal during 1999.
¶ Earliest and latest dates on which seeds were observed being dispersed from individual trees during 1999.
# Earliest and latest dates on which seeds were observed being dispersed from individual trees during 2000.

Definition of explanatory variables

Local.—Within-sandbar (hereafter, local) variables were calculated from the topographic surveys and from sediment and cover observations at each quadrat. Variables included elevation, slope and concavity/convexity of quadrat location (relative to adjacent quadrats), occurrence within concave areas of the sandbar that might pond water (''basin'' variable), lateral distances to land or active river channels (expressed as ordinal indices), vegetative and litter cover, and an ordinal index of silt content in the surface sediment (Fig. 6, Tables 2 and 3).

From our original list of local variables, we retained only those that differed significantly (t test or χ^2, $P < 0.05$) between quadrats with seedlings and those without seedlings. Of these, we excluded variables that were strongly intercorrelated ($R > 0.7$) or that were strongly functionally related. This reduced our original list to 10 quadrat-level variables: quadrat elevation above the reference water surface, index of distance to land, index of distance to river, index of silt content, occurrence

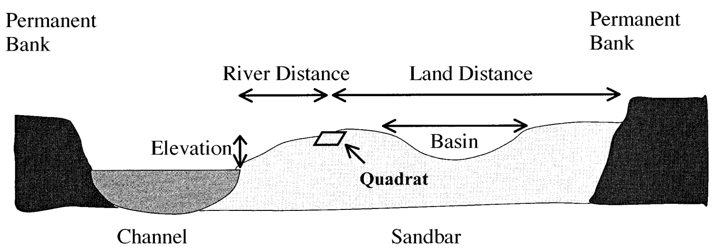

FIG. 6. Schematic of sandbar profile and definition of quadrat-level physical variables.

of the quadrat in a basin, percent forb cover, percent grass cover, percent litter cover, percent shrub cover, and mean slope (Table 3).

Based on the findings of other researchers and our own field observations, we hypothesized that these variables might influence the delivery of seeds to the quadrat via hydrochory or anemochory and might affect subsequent seedling growth and survival. In particular, several studies have found that elevation above water surface datum may be a good surrogate for many factors influencing plant distribution (Auble et al. 1994), including the deposition of waterborne seeds (Nilsson et al. 1993, Auble and Scott 1998), the duration and frequency of inundation (Auble et al. 1994), the probability of removal of seedlings by ice or erosive flows (Johnson 1994, 2000, Mahoney and Rood 1998), and the probability of drought mortality (Johnson 1994, 2000, Mahoney and Rood 1998, Cooper et al. 1999). Sediment texture may also influence seedling distribution and survival through its influence on storage of

TABLE 2. Definitions of physical habitat variable names.

Habitat variable	Definition
a) Landscape variables	
River cross-section	
Energy slope	River energy gradient slope at cross-section (m/m)
WDratio	Total width of wetted river width divided by maximum channel depth on cross-section
Channel	
Chanwid	Width of individual channel containing focal sandbar (m)
Flow status	Categorical variable for flow status of individual channel during sampling (−1, stagnant; 1, flowing)
Sandbar	
Length	Estimated sandbar length (1.5 × distance between most upstream and most downstream transect) (m)
LWratio	Ratio of estimated sandbar length to mean sandbar width
Median elevation	Median elevation of quadrats in the sandbar (m)
b) Local variables	
Topographic position	
Elevation	Elevation of quadrat above reference water level (for flow of 99 m^3/s) (m)
Basin	Categorical variable for whether quadrat is in an area that would pond water (0, no; 1, yes)
Basin elev	Elevation of quadrats that occur in basins (basin × elevation). Weighted as 0 in non-basins (m)
Mean slope	Average of absolute values of slope between focal quadrat and adjacent quadrats
Horizontal position	
Land dist	Ordinal index of lateral distance to a permanently vegetated bank (1, 0–5 m; 2, 5.1–10 m; 3, 10.1–20 m; 4, >20 m or land separated by active channel)
River dist	Ordinal index of lateral distance to flowing river channel (1, 0–5 m; 2, 5.1–10 m; 3, 10.1–20 m; 4, >20 m or separated from flowing channel by a permanently vegetated bank)
Sediment and cover	
Grass	Percent cover of grass
Forb	Percent cover of forbs
Litter	Percent cover of litter and coarse woody debris
Shrub	Percent cover of shrubs
Silt	Ordinal index of sediment texture (1, gravel; 2, sand/gravel or sand/cobble; 3, sand; 4, sand/silt; 5, silt or silt/sand).

TABLE 3. Summary statistics for local sandbar variables, by quadrat (n = 692), for 1998.

Level and variable name†	Mean	1 SD	Median	Minimum	Maximum
Topographic position					
Elevation (m)	0.457	0.350	0.381	0	2.065
Basin‡	0.240	0.427	0	0	1
Basin elev (m)	0.095	0.222	0	0	1.621
Mean slope (m/m)	0.018	0.033	0.008	0	0.440
Horizontal position					
Land dist§	3.15	1.12	4	1	4
River dist§	3.14	1.08	4	1	4
Sediment and cover					
Grass (%)	5.44	15.39	0	0	95
Forb (%)	2.09	6.70	0	0	80
Shrub (%)	0.44	2.80	0	0	35
Litter (%)	3.12	10.13	0	0	85
Silt§	3.04	0.47	3	1	5

† Variable abbreviations are as in Table 2.
‡ Categorical variable (0, 1).
§ Ordinal indices (1–4 or 1–5).

moisture (McBride and Strahan 1984, Cooper et al. 1999) and resistance to erosion (Friedman and Auble 1999). Cover by herbaceous plants or shrubs may compete with seedlings for light, nutrients, and moisture. However, cover by both vegetation and litter may also increase substrate stability and deposition of silt, and may even reduce substrate temperatures via shading, thereby reducing drought stress (Cooper et al. 1999). We hypothesized that quadrats closer to a permanent bank might experience higher delivery of windblown seeds and lower flow velocities because of the roughness effects of bank vegetation and obstructions by bank orientation and fallen logs, whereas quadrats closer to the active river channel might be more likely to suffer mortality due to erosion or burial. Finally, based on field observations, we hypothesized that concavity of the quadrat location might influence the probability of deposition of seeds and fine sediments during recession of higher flows, and might also provide environments sheltered from minor flow increases.

Only the 10–13 quadrats per transect with data on vegetation cover and sediments were included in the analyses of local seedling distributions. This helped to ensure relatively even sampling among sandbars, maximized the use of measured elevations rather than those estimated from interpolation, and reduced the influence of within-transect spatial autocorrelation on model residuals. Quadrats that occurred on permanently vegetated banks were eliminated from all analyses.

Landscape.—Physical characteristics that were measured at the sandbar level or higher were considered landscape variables. These included indices of sandbar size, shape, and elevation (Birkeland 1996); width and flow status (stagnant or flowing at low river discharges) of the channel in which the focal sandbar occurred (Johnson 1994); and hydrologic characteristics of the river cross-section (Baker 1989, Malanson and Butler 1990, Bendix 1994*a*, *b*, Birkeland 1996). As such, these could be considered three different scales or sub–levels within the class of landscape variables. Other studies have found these or similar variables to influence the distribution, demography, and mortality of riparian or riverine vegetation (Hupp 1982, Baker 1989, Malanson and Butler 1990, 1991, Bendix 1994*a*, *b*, Johnson 1994, Birkeland 1996, van Coller et al. 2000).

The width of the individual channel (''Chanwid'') within which the sandbar occurred was estimated from 1:10 000 scale aerial orthophotographs taken in 1995. Because of the island-braided morphology of the river, channel width often referred to individual side channels (anabranches) rather than to the entire wetted width of the river. To avoid confusion, we used ''Chanwid'' to refer to the width of the individual channel within which a focal sandbar occurred, and ''River width'' to represent the sum of channel widths at a given river cross-section (Fig. 4). Within this paper, use of the words ''channel'' and ''river'' should also be understood in this sense.

Four of the sampled sandbars were in narrow side channels that were inactive (stagnant) during the low-flow conditions at the time of sampling. Presumably, these channels were stagnant because of a higher bed elevation than adjacent channels, or because of upstream obstruction. Flow status (Table 2) was scored as a dichotomous variable, with ''−1'' representing the four stagnant channels and ''1'' representing the 26 flowing channels.

Sandbar length, size, and shape were not measured systematically in the field. However, several metrics of sandbar size and shape were computed from the GPS coordinates for individual transects and from transect lengths (Table 2). An index of length (''Length'') was obtained by calculating the distance between the marker pins of transects 1 (most downstream) and 3 (most upstream), and then multiplying by 1.5. Sandbar width (''Width'') was estimated from the mean length of the three transects within each sandbar. An index of sandbar area (''Area'') was computed by multiplying estimated sandbar length and mean width. An index of sandbar shape (''LWratio'') was computed by dividing sandbar length by mean sandbar width (Table 2). Sandbar elevation was quantified by the maximum, median, and the standard deviation of all quadrat elevations on the transect-level topographic surveys.

Several hydrologic variables (Table 2) were computed for river sub-reaches using the HEC-RAS model. Calculations were made for a flow of 142 m^3/s, approximately the mean discharge during the summer of 1998. These included the river energy slope (''Energy slope''), stream power, velocity, total width of wetted channel perimeter (''River width''), maximum and average (hydraulic radius) depth, and average channel bed shear stress, at each cross-section. These variables express longitudinal variation in hydrologic conditions

TABLE 4. Summary statistics for landscape variables, by sandbar ($n = 30$), for 1998.

Level and variable name†	Mean	1 SD	Median	Minimum	Maximum
River cross-section					
Energy slope (m/km)	0.337	0.282	0.226	0.056	1.083
WDratio‡	206.2	94.2	170.4	93.0	389.0
Channel					
Chanwid (m)	260.7	149.8	235	20	490
Flow status§	0.73	0.69	1	−1	1
Sandbar					
Length (m)	343.6	190.4	320.4	66.0	860.5
LWratio‡	7.33	4.23	6.28	1.53	18.20
Median elevation (m)	0.401	0.183	0.372	0.110	0.537

† Variable abbreviations are as in Table 2.
‡ Ratio.
§ Categorical variable (−1, 1).

among the cross-sections in the study area. Hydrologic variables were assigned to a given sandbar site according to the nearest cross-section, or were averaged between adjacent cross-sections when both were approximately equidistant from the sandbar. We calculated two separate indices of width-to-depth ratio, based on dividing river width by either maximum (''WDratio'') or mean (''WHratio'') cross-section depth. The index based on maximum depth was used in subsequent analyses, because exploratory analyses found it to be more strongly correlated with sandbar-level seedling densities.

From our original list of landscape variables, we initially excluded variables that were strongly correlated with each other ($R > 0.7$); of those remaining, we retained for further analyses only those that were significantly ($P < 0.05$) correlated with sandbar-level seedling or sapling densities. This reduced our original list to seven variables: energy slope and width–depth ratio at the cross-section (sub-reach) level, channel width and flow status at the channel level, and sandbar length, length–width ratio, and median elevation (Table 4).

Statistical analysis

Sandbar-level seedling densities.—Seedling densities (number per square meter) were estimated for each sandbar by summing the total seedling counts of the three transects, dividing by the sum of the transect lengths, and dividing by the belt transect width (2 m). All transect segments that were at or above the reference water surface (≥0 m relative elevation) and that were not on permanently vegetated banks were used in the computations.

The relationships between sandbar-level seedling densities and the seven landscape-level physical variables were determined using univariate Pearson correlation analyses and multiple linear regression (SAS Institute 1990). Prior to the regressions, seedling densities were log-transformed [$\log_{10}$(density + 0.002)] to achieve normality. Explanatory power was assessed using the coefficient of determination, R^2. Residuals were examined for normality and equality of variance via scatter plots. Residuals did not significantly deviate from a normal distribution and showed little evidence of heteroscedasticity. Inspection of empirical semivariograms suggested that the influence of spatial autocorrelation among sandbars on the model residuals was minimal.

Because our landscape variables were measured at three different levels or spatial scales (sandbar, channel, sub-reach), we also performed an exploratory path analysis (Li 1975, Munro and Page 1993) using a series of multiple linear regressions, to determine if sandbar-level seedling densities were influenced by significant hierarchical relationships among the variables measured at the river sub-reach (cross-section), individual channel, and sandbar levels. For instance, characteristics of the river cross-section (e.g., energy gradient or width–depth ratio) might influence the characteristics of individual channels (e.g., channel width), which might influence the size and shape of sandbars that occurred within them, which might then influence the environment for seedling colonization and survival. We assumed that any causal relationships would occur from higher hierarchical levels (e.g., variables measured at the river sub-reach scale) to lower levels (variables measured at the channel or sandbar scale). The results of path analyses revealed no significant interlevel relationships among the landscape variables. Because of this, landscape variables were treated as one hierarchical level for further analyses.

Local-level seedling occurrence.—Because of the non-normal distribution of seedling abundances among quadrats, and particularly because of the large number of zeroes in the data set, logistic regression (SAS Institute 1990, Trexler and Travis 1993, Menard 1995) was used to model the relationship between local- or landscape-level explanatory physical variables and the presence or absence of seedlings in each quadrat.

Logistic regression analyses were performed using the GLIMMIX macro of SAS, version 6.12 (Littell et

TABLE 5. Seedling and sapling density and frequency at the sandbar and quadrat level in 1998, by age class and dispersal timing.

	New seedlings			Old seedlings		
Species	Density per sandbar (no./m^2) Mean (1 SE)	No. sandbars present (n = 30)	No. quadrats present (n = 692)	Mean (1 SE) density per sandbar (no./m^2)	No. sandbars present (n = 30)	No. quadrats present (n = 692)
Early dispersers						
Acer saccharinum	0.0152 (0.0065)	15	18	0.0089 (0.0061)	7	11
Betula nigra	0.0195 (0.0177)	10	9	0.0637 (0.0377)	9	14
Total	0.0347 (0.0199)	17	24	0.0726 (0.0393)	9	19
Late dispersers						
Populus deltoides	0.0057 (0.0017)	15	10	0.0145 (0.0072)	12	11
Salix exigua	0.0137 (0.0053)	17	11	0.0382 (0.0107)	20	29
Other *Salix* spp.	0.0174 (0.0057)	14	16	0.0152 (0.0065)	11	17
Total	0.0363 (0.0115)	21	29	0.0678 (0.0185)	23	46
Total seedlings	0.0717 (0.0242)	24	47	0.1416 (0.0442)	23	59

al. 1996). GLIMMIX is a macro for fitting generalized linear mixed models using the MIXED procedure in SAS. Use of PROC MIXED enabled us to include the sandbar × transect interaction as a random effect, thereby accounting for the hierarchical structure of our sampling design and producing the appropriate error terms for testing the effects of landscape and local variables in a single model. We tested several different models of within-transect spatial autocorrelation of seedling numbers on quadrats using a repeated-measures analysis, but failed to find interpretable, significant trends. Thus, individual quadrats within a transect were treated as independent samples.

Prior to the combined analyses, variables that were not significant in individual local and landscape models were eliminated. The remaining variables were combined into one analysis, including first-order interactions between each local and landscape variable. Nonsignificant interactions were removed through a manual, backward elimination procedure, based on log-likelihood ratio tests, with a threshold of $P \leq 0.05$ for retention of variables in the model.

In order to clarify the direct effects of local and landscape variables, multiple linear or logistic regressions were used to model each of the 10 local variables as a function of the seven landscape variables. The residuals of these analyses were then used in place of the original local variable values in a second combined logistic regression analysis. This approach enabled us to test the direct influence of the local variables on quadrat-level seedling occurrence, after the indirect influence of the landscape variables had been removed.

RESULTS

Overall densities

Mean sandbar-level densities of riparian tree seedlings were low on the sandbars sampled in 1998, with old seedlings having higher densities than new seedlings or saplings (Table 5). Relative abundance of individual species was fairly even for new seedlings. Densities of old seedlings were dominated by *Betula nigra* and *Salix exigua*. Saplings were dominated by *S. exigua*. Seedling densities were also low in 1999 (not shown), but nearly 90% of the new seedlings were *Acer saccharinum*. Midsummer flow pulses occurred in both years: in late June of 1998 and late July of 1999 (Fig. 7). Data from permanent demography plots suggested that the flow pulses in both years were associated with relatively high mortality of both new and second-year seedlings (Dixon 2001).

Sandbar-level seedling abundance and landscape variables

Multiple linear regressions using landscape variables captured 35–52% of the variation in 1998 sandbar seedling densities, by age class, using the best-three-variable models (Table 6). For new seedlings (Table 6), seedling densities were highest on sandbars within channels that were stagnant at the time of sampling. However, only four of the 30 sampled sandbars occurred in stagnant channels, so the high seedling densities on these few sites strongly influenced the overall regression. Removal of this variable (channel flow status) resulted in much weaker models for new seedling density.

Old seedling and sapling abundances were strongly related to sandbar characteristics and channel width (Table 6). Densities of old seedlings were higher in narrower individual channels, particularly those that were stagnant, and on sandbars with higher median elevation. Sapling densities were higher on longer sandbars with a higher length-to-width ratio and with higher median elevation, as well as in narrower channels.

Relationships between landscape variables and seedling densities differed between the pre-flood (early-dispersing) and post-flood (late-dispersing) species groups (Table 7). Among the new seedlings, densities of both early- and late-dispersing species were highest in side channels that were stagnant at low flow. How-

TABLE 5. Extended.

Saplings		
Mean (1 SE) density per sandbar (no./m^2)	No. sandbars present (n = 30)	No. quadrats present (n = 692)
0.0003 (0.0003)	1	0
0.0011 (0.0005)	5	0
0.0013 (0.0006)	5	0
0.0029 (0.0018)	5	3
0.0651 (0.0210)	16	34
0.0080 (0.0025)	12	8
0.0760 (0.0220)	20	41
0.0775 (0.0221)	20	42

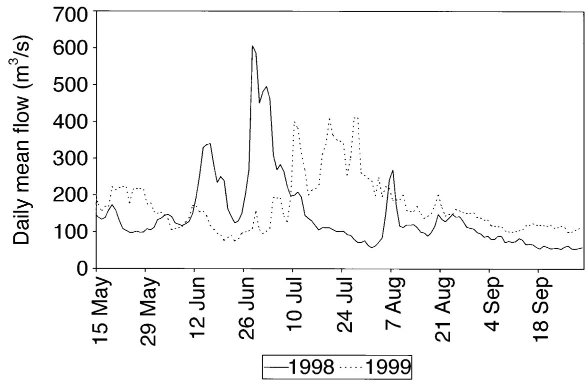

FIG. 7. Growing season (15 May–30 September) daily river flows (m^3/s) in 1998 and 1999 at the Wisconsin Dells gaging station.

ever, the correlation was weak for late dispersers, with the relationship nearly three times stronger for early dispersers than for late dispersers (R^2 = 0.38 and 0.11, respectively, for the single-variable model). Best-three-variable models were twice as strong for early dispersers (R^2 = 0.42) as for late dispersers (R^2 = 0.20). Regression models for older seedlings did not show strong differences in explanatory power between the early- and late-disperser species groups (R^2 = 0.45 and 0.44, respectively). No comparisons were made between species groups for saplings, because nearly all (>90%) were of late-dispersing species (primarily *Salix exigua*).

Quadrat-level seedling occurrence

Local and landscape influence on quadrat seedling occurrence.—In our logistic regression models, channel flow status was the only landscape variable that significantly influenced the probability of occurrence of new seedlings at the quadrat level (Table 8). Overall, probability of occurrence of new seedlings was nearly six times higher on quadrats in stagnant channels than in flowing channels. The influence of flow status may have been at least partly mediated through its interaction with quadrat elevation, grass cover, and forb cover (Table 8, Fig. 8). The slope of the negative relationship between seedling occurrence and quadrat elevation was similar in flowing and stagnant channels, but the intercept was much higher for quadrats in the stagnant channels. Thus, the probability of seedling presence was higher across all quadrat elevations in stagnant channels. Average quadrat elevation was higher for both seedling and nonseedling plots in stagnant channels. Grass cover was significantly associated with new seedling presence only in flowing channels. Forb cover was significantly associated with new seedling presence only in stagnant channels (Fig. 8).

For older seedlings, channel width was the only landscape variable that significantly influenced the probability of occurrence at the quadrat level (Table 8). There were no significant interactions between channel width and the local variables, suggesting that their effects were additive. That is, channel width did not influence the slope of the relationship between the local variables and the probability of seedling occurrence on the quadrat.

Channel width and sandbar median elevation were both important landscape variables influencing quadrat-level sapling occurrence, and both had significant interactions with local variables (Table 8, Figs. 9 and 10). Saplings were ~2.6 times more likely to occur on quadrats in narrower (<100-m) channels than in wider (>100-m) channels, and were 1.6 times more likely to occur on sandbars with a median elevation >0.37 m than on those with a lower median elevation. The pos-

TABLE 6. Univariate Pearson correlation coefficients (R) and multiple regression analyses of the relationship between landscape physical variables and log-transformed sandbar-level seedling density, by age class.

Variables† and measurement scale	Seedling age classes		
	New	Old	Sapling
River cross section			
Energy slope	0.400*	0.306	0.094
WDratio	0.394*	0.289	0.146
Channel			
Chanwid	−0.229	−0.623*	−0.413*
Flow status	−0.507*	−0.529*	−0.308
Sandbar			
Length	−0.157	0.143	0.441*
LWratio	0.110	0.295	0.420*
Median elevation	0.022	0.379*	0.529*
Regression models			
R^2, best three variables	0.350	0.493	0.520
R^2, all variables	0.374	0.528	0.541
Seedling density on sandbar			
New		0.278	0.006
Old	0.278		0.740*
Sapling	0.006	0.740*	

* Satistically significant correlation ($P \leq 0.05$).
† Variable abbreviations are as in Table 2.

TABLE 7. Univariate Pearson correlation coefficients (R) and multiple regression analyses of the relationship between landscape physical variables and log-transformed sandbar-level seedling densities, by age and dispersal timing.

Variables† by measurement scale	Seedling age classes			
	New, early	New, late	Old, early	Old, late
River cross section				
Energy slope	0.395*	0.224	0.432*	0.120
WDratio	0.303	0.308	0.395*	0.152
Channel				
Chanwid	−0.405*	0.088	−0.563*	−0.535*
Flow status	−0.613*	−0.333	−0.573*	−0.413*
Sandbar				
Length	−0.174	−0.032	−0.204	0.254
LWratio	0.123	−0.013	0.220	0.242
Median elevation	0.161	−0.088	0.179	0.398*
Regression models				
R^2, best three variables	0.416	0.205	0.453	0.445
R^2, all variables	0.427	0.276	0.485	0.465
Seedling density on sandbar				
New, early		0.283	0.604*	0.310
New, late	0.283		0.220	0.148
Old, early	0.604*	0.220		0.356
Old, late	0.310	0.148	0.356	
Sapling	0.131	−0.048	0.215	0.808*

* Statistically significant correlation ($P \leq 0.05$).
† Variables are as defined in Table 2.

itive relationship between sapling occurrence and quadrat elevation was significant only in channels >100 m wide (Fig. 10). Mean elevation of sapling quadrats did not differ significantly in narrow and wide channels, but the elevation of non-sapling quadrats was substantially lower on sandbars in wide channels.

Sandbar median elevation interacted with quadrat elevation, grass cover, and the presence of a concave basin to influence the presence of saplings (Table 8, Fig. 10). On lower sandbars (median elevation < 0.37 m), quadrat elevation was much more strongly related to sapling presence than on high (median elevation > 0.37 m) sandbars. Sapling presence was only positively associated with basins on higher sandbars.

After factoring out the influence of landscape variables on local variables, most local variables still had significant direct effects on seedling presence (Table 8). New seedling presence was negatively associated with quadrat elevation, distance to land, and elevation within a basin, and was positively associated with grass cover, forb cover, and occurrence of the quadrat within a basin. The basin effects, in fact, became significant only after landscape influences had been factored out. For old seedlings, presence was positively associated with the silt index, grass cover, shrub cover, distance from river, and elevation within a basin, and was negatively associated with quadrat elevation, occurrence within a basin, and distance to land. The elevation and basin effects became significant only after removal of landscape influences on the local variables. Finally, sapling presence was positively associated with elevation, occurrence within a basin, and grass cover. The direction of the basin effect actually changed following removal of the landscape influence, being negative prior to factoring out landscape effects, and positive after factoring out landscape effects on the local variables (Table 8).

Landscape variables appeared to exert important influences on quadrat-level occurrence of new seedlings in both the early- and late-dispersing groups (Table 9). As in the multiple regression analyses, channel flow status had a significant influence on the presence of both species groups, at least in part through interactions with local variables (Table 9, Figs. 11 and 12). In addition, river width–depth ratio had a significant influence on the distribution of early dispersers, through its interaction with quadrat elevation and grass cover (Fig. 11). For the early-disperser group, six interactions between the landscape and local variables were significant, whereas for the late-disperser group, only two interactions were significant (Table 9). For the early dispersers, the negative influence of quadrat elevation on seedling presence was only significant in river cross-sections with a lower width–depth ratio (less than the median of 170), apparently due to occurrence of seedlings at higher elevations in river sub-reaches with a higher width–depth ratio (Fig. 11).

Frequency of early dispersers was nearly 10 times higher in stagnant channels than in flowing channels, whereas late-disperser frequency was 4.6 times higher in stagnant channels. Also, frequency of occurrence of new seedlings of early dispersers was 3.4 times higher

TABLE 8. Statistically significant ($P \leq 0.05$) terms in logistic regression models of the relationship between local and landscape variables and seedling/sapling presence at the quadrat level, by age class.

Variables†	Seedling age classes: New	Old	Sap.
Local			
Elevation	−*	(−)	+*
Basin	(+)	(−)	−(+)
Basin elev	(−)	(+)	
Mean slope			
Land dist	−*	−*	
River dist	+	+*	
Grass	+*	+*	+*
Forb	+*		
Litter			
Shrub		+*	
Silt		+*	
Landscape			
Energy slope			
WDratio			
Chanwid		−	(−)
Flow status	(−)		
Sandbar length			
Sandbar LWratio			
Sandbar median elevation			+
Landscape × local interactions			
Flow status × elevation	−		
Flow status × grass	+		
Flow status × forb	−		
Sandbar median elevation × elevation			−
Sandbar median elevation × grass			−
Sandbar median elevation × basin			+
Chanwid × elevation			−

Notes: Signs of the slope coefficients are indicated by + or −. Parentheses indicate relationships that are significant only after the removal of landscape effects on local variables. Symbols without asterisks or parentheses represent terms that were significant only prior to the removal of landscape effects on local variables. Sap. = sapling.

* Significant both before and after the removal of landscape effects on local variables at $P \leq 0.05$.

† Variable abbreviations and definitions are in Table 2.

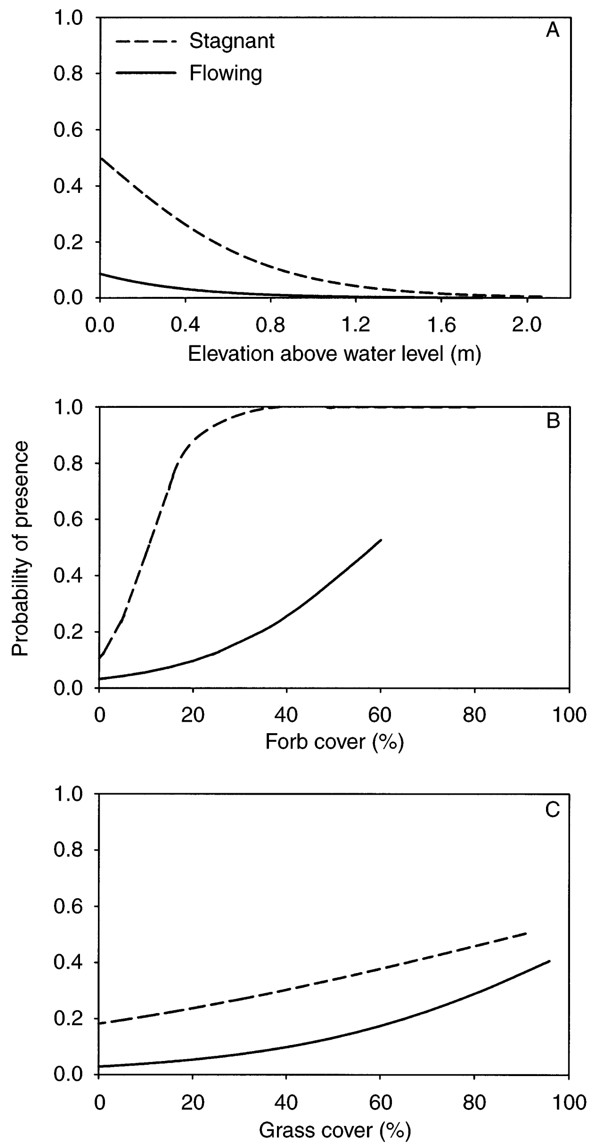

FIG. 8. Modeled probability of quadrat-level new seedling presence for significant landscape × local interaction terms in logistic regression models: (A) flow status × elevation, (B) flow status × forb, and (C) flow status × grass.

in cross-sections with a higher width–depth ratio. Similar models could be obtained by replacing width–depth ratio with river energy slope, which was significantly correlated with width–depth ratio ($R = 0.63$). Thus, new seedlings of early dispersers were more frequent in river sub-reaches with higher width–depth ratio, which also tended to have steeper gradients, and both early and late dispersers were more frequent on quadrats in stagnant channels (Table 9).

Comparison of 1998 and 1999 data

General patterns of new seedling distribution, with respect to local variables, were similar in 1998 and 1999. The main difference is that 1999 seedlings occurred at slightly higher elevations above water level (Fig. 13) or at higher inundating discharges. In 1998, new seedling quadrats averaged significantly lower elevation than non-seedling quadrats, whereas in 1999, seedling quadrats had significantly higher mean elevation than non-seedling quadrats. These general differences also persisted when only new maple seedlings were compared across the two years.

In contrast, the relationship of seedling density to landscape variables was markedly different between 1998 and 1999, particularly for new seedlings. In 1999, the only significant landscape variables for predicting new seedling density were sandbar median height and channel flow status, whereas 1998 densities were correlated with channel flow status and the cross-section level hydrologic variables: river energy slope and width–depth ratio. Relationships for old seedlings and saplings were relatively similar between 1998 and 1999, although channel width did not have a significant

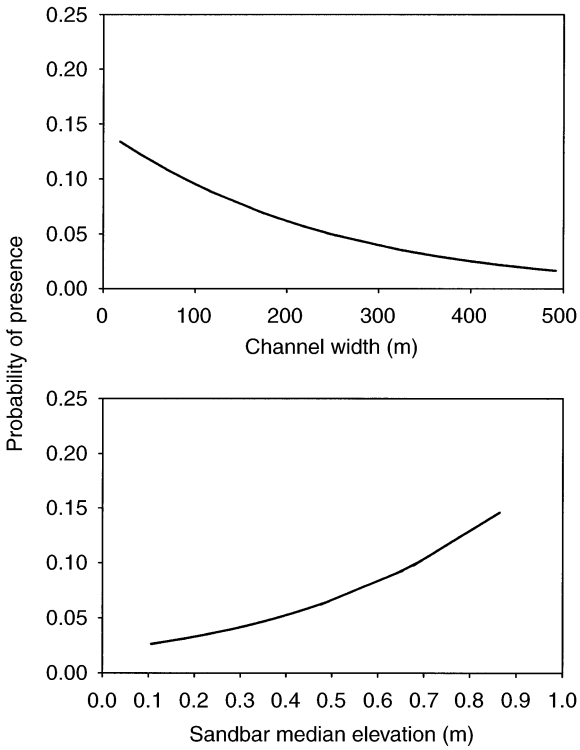

FIG. 9. Modeled probability of quadrat-level sapling presence for significant landscape terms in logistic regression models.

influence on old seedling density in 1999. Aside from sandbar median elevation, indices of sandbar size and shape could not be computed for the 1999 sample. Additionally, the 1999 relationships may be weaker than those in 1998 if the lower sampling effort per sandbar (one transect instead of three) was less adequate for characterization of sandbar-level seedling densities.

DISCUSSION

Vegetation distribution and channel conditions

Both fine- and broad-scale factors were important for explaining the distribution of seedlings and saplings. Seedling distribution in 1998, especially for new seedlings, was strongly linked to local physical characteristics of the quadrat location, such as elevation above the water surface, horizontal position relative to the floodplain edge and sandbar edge, and vegetative cover. At broader scales, differences in seedling density among sandbars were significantly correlated with variables that expressed whole sandbar and channel characteristics, particularly for older seedlings and saplings.

Channel width, flow status, and sandbar median elevation were all correlated with the distribution of older seedlings and saplings among sandbars. The negative relationship of channel width with old seedling and sapling density suggests that either seedling colonization or annual survival has been higher in narrower channels, at least over the last several years. The lack of a strong relationship between channel width and new seedling densities suggests that enhanced annual survival may be the more important process. The width and depth of an individual channel within a multi-channeled river reach may influence the routing, depth, and erosive energy of high flows (Osterkamp 1998, Tooth and Nanson 2000), as well as the potential for formation and conveyance of erosive ice flows at spring ice breakup (Smith 1980). In a survey of rivers in Alberta, Smith (1980) observed a threshold river width (~50 m) below which erosive ice flows were uncommon and above which frequent ice drives maintained an enlarged channel. On the Platte River in Nebraska, Johnson (1994) suggested that reduced conveyance of ice may be the mechanism responsible for higher annual survival of *Populus* and *Salix* seedlings within narrower channel braids. Ice scour has also been suggested as an important influence on spatiotemporal variation of seedling establishment and survival in other north temperate rivers (Auble and Scott 1998, Rood et al. 1998, Johnson 2000, Smith and Pearce 2000). The importance of ice scour for limiting vegetation encroachment in northern rivers and the possibility that ice scour is reduced in narrower channels may explain why densities of older seedlings and saplings were enhanced in narrower channels on the Wisconsin River.

The higher densities of new seedlings in stagnant channels also may have been related to channel width, despite the lack of a significant correlation between new seedling density and channel width. Channel flow status was correlated with channel width; the four stagnant channels were all <80 m wide. The higher sandbar median elevations in these channels and the absence of flow at low river discharges also suggest an elevated bed level, relative to adjacent flowing channels. Although the 1998 summer flood inundated all of the sandbar sites, the four in stagnant channels may have experienced lower shear stresses and, hence, lower mortality of new seedlings because of elevated bed levels or upstream obstructions that rerouted flows.

Multiple regression models suggested that the suite of landscape variables was more effective for explaining sandbar-level densities of older seedlings and saplings than for new seedlings overall, and for new seedlings of early dispersers than for those of late dispersers. We attribute the difference in model strength for early and late dispersers, at least in part, to the effects of the midsummer 1998 flow pulse. Among the new seedlings, the distribution of those establishing before 29 June (pre-flood) may have been structured by the spatially uneven effects of the small flood through higher mortality in larger, deeper channels and lower mortality in the more sheltered, shallow channels that were stagnant at lower flows. Seedlings that established after the flood (late dispersers) would not have passed through such a spatially explicit mortality filter, and thus would be more weakly associated with coarse-

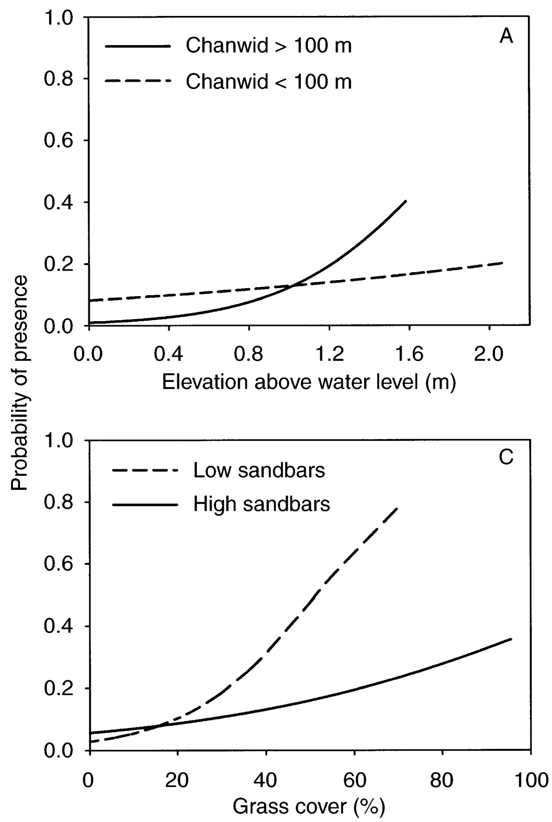

FIG. 10. Modeled probability of quadrat-level sapling presence for significant landscape × local interaction terms in logistic regression models: (A) channel width × elevation, (B) sandbar median elevation × elevation, (C) sandbar median elevation × grass, and (D) sandbar median elevation × basin. High sandbars are those with median elevations >0.37 m (the median value); low sandbars are those with median elevations <0.37 m.

scale spatial heterogeneity in channel conditions that influence disturbance intensity. The distribution of older seedlings and saplings presumably also has been structured by the influence of both landscape and local heterogeneity on the local expression of fluvial disturbance (such as ice scour and spring floods); hence, the greater similarity in model strength and significant landscape variables between the new seedlings of early dispersers and older seedlings and saplings. These results support our contention that initial seedling colonization should be less strongly linked to landscape variables than is longer term survival.

In this project, we treated the channel and sandbar characteristics measured in the field as a quasi-stable environment to which the colonization and survival of new and older seedlings and saplings responded, either directly as a function of static physical characteristics (e.g., sandbar median elevation) or indirectly as a function of the disturbance regimes associated with these landforms. This assumption is probably reasonable for the relationship between broad-scale factors (channel width, sandbar median elevation) and seedling distribution over the time scales (probably 1–5 yr) relevant to the new and older seedlings sampled in our study. However, the local conditions associated with older seedlings and saplings (e.g., plot elevation, sediment, herbaceous vegetation) may have been strongly influenced by the effects of seedling presence on geomorphic and biological processes, so that the direction of causality is ambiguous. Over longer time scales, broad-scale channel and sandbar conditions are also highly dynamic and may evolve partly as a function of the influence of vegetation on fluvial geomorphic processes (Osterkamp and Costa 1987, Hupp 1992, Church 1995, Friedman et al. 1996*b*, Tooth and Nanson 2000).

The relationships among channel width, flow status, sandbar elevation, and seedling and sapling abundance in our study suggest that some of our sites occurred in channels that were progressively narrowing, perhaps due to the linked effects of vegetation colonization and geomorphic change. Vegetation colonization and floodplain formation in braided, bedload-dominated river channels are associated with the channel-narrowing process (Osterkamp and Costa 1987, Church 1995, Friedman et al. 1996*a*, *b*, Scott et al. 1996, Osterkamp 1998). Vegetation colonizes the channel bed during low flows. The presence of vegetation increases hydraulic roughness in the channel, reducing the velocity of flood flows. Reduced velocities decrease the capacity of the flow to carry sediment, thus enhancing sedimentation,

TABLE 9. Statistically significant ($P \leq 0.05$) terms in logistic regression models of the relationship between local and landscape variables and new seedling presence at the quadrat level, by dispersal timing.

Variables†	Seedling age classes	
	New, early	New, late
Local		
Elevation	−	−*
Basin	+*	+*
Basin elev	−*	
Mean slope	+	−
Land dist	−*	
River dist	+*	
Grass	+*	+
Forb	(+)	+*
Litter		
Shrub	(−)	
Silt		+*
Landscape		
Energy slope		
WDratio	(+)	
Chanwid		
Flow status	(−)	−*
Sandbar length		
Sandbar LWratio		
Sandbar median elevation		
Landscape × local interactions		
Flow status × basin	−	+
Flow status × mean slope	−	
Flow status × land dist	+	
Flow status × forb	−	−
WDratio × elevation	+	
WDratio × grass	−	

Notes: Signs of the slope coefficients are indicated by + or −. Parentheses indicate relationships that are significant only after the removal of landscape effects on local variables. Symbols without asterisks or parentheses represent terms that were significant only prior to the removal of landscape effects on local variables.

* Significant both before and after the removal of landscape effects on local variables at $P < 0.05$.

† Variable abbreviations and definitions are in Table 2.

aggradation of the channel bed, and possibly channel narrowing. Bed aggradation and channel narrowing may then favor further colonization and spread by vegetation. Thus, there may be critical thresholds in channel width and depth, above which channel integrity is maintained, and below which a cascade of biophysical feedbacks may eventually result in channel abandonment and development of riparian thickets and forests.

Inherent in the channel-narrowing process is a linkage across spatial and temporal scales. Short-term processes and fine-scale conditions influence vegetation colonization, with the vegetation potentially altering local conditions through feedbacks on sedimentation and fluvial processes (Hupp 1992). Broader scale variation in fluvial geomorphic processes, such as the effects of channel width on ice scour (Smith 1980), may influence the probability of vegetation persistence. Long-term persistence of vegetation leads to cumulative changes in geomorphic processes that may affect whole sandbar and channel conditions, which, in turn, influence the probability of vegetation persistence and spread. The establishment and persistence of sandbar willow (*Salix exigua*), which comprised nearly 90% of the saplings in our study and is capable of vigorous clonal spread, may be particularly important to successional and geomorphic processes in the Wisconsin River.

Although some individual channels appear to be narrowing, we have assumed that river channel conditions overall are in quasi-equilibrium with the flow regime, or at least that the reach as a whole is not on a strong narrowing trajectory. Although local channel conditions may be in flux, the landforms and total channel area within a reach in a large river may be in dynamic equilibrium if the flow regime does not change substantially (Johnson 1994, 1997). In our study area, river channel area has declined by 17% since the 1930s (~5% since 1968; M. D. Dixon, *unpublished data*), perhaps in response to the impacts of three large dams constructed upstream (50–160 km) between 1940 and 1950 (Krug and House 1980, Durbin 1997). However, no new dams or other large flow alterations have occurred over the last 50 yr, and there is little evidence of system-wide channel narrowing occurring today. Thus, the association of seedlings with narrow channels is not merely an artifact of a widespread narrowing trajectory across all channels in the river.

Comparison of 1998 and 1999 seedling data

Patterns of distribution for new seedlings differed somewhat between 1998 and 1999, particularly in regard to quadrat elevation at the local level and sandbar elevation at the landscape level. Most local variables associated with new seedlings, however, did not differ significantly between years, and general patterns for old seedlings and saplings also remained similar. It is unlikely that the statistical models generated from either year (or from any one year) can adequately characterize ''typical'' conditions for seedling colonization, given that dispersal, germination, and short-term survival of seedlings are strongly influenced by the specific patterns of flow timing and magnitude in a given year. In our study, the occurrence and timing of midsummer flow pulses in both years may have had particularly strong impacts on seedling densities, species composition, and distribution patterns (Dixon 2001). Many other studies have also emphasized the temporal stochasticity and flow dependence of seedling establishment in riparian pioneers (Baker 1990, Johnson 1994, 2000, Scott et al. 1997, Shafroth et al. 1998). However, if seedling distributions are considered in the context of the flow conditions of a given year, then inferences about functional links between distribution and physical variables should be possible. Thus, the relationships of physical variables (particularly landscape) with new seedling distribution in 1998 (or 1999) should be understood within the hydrologic context of

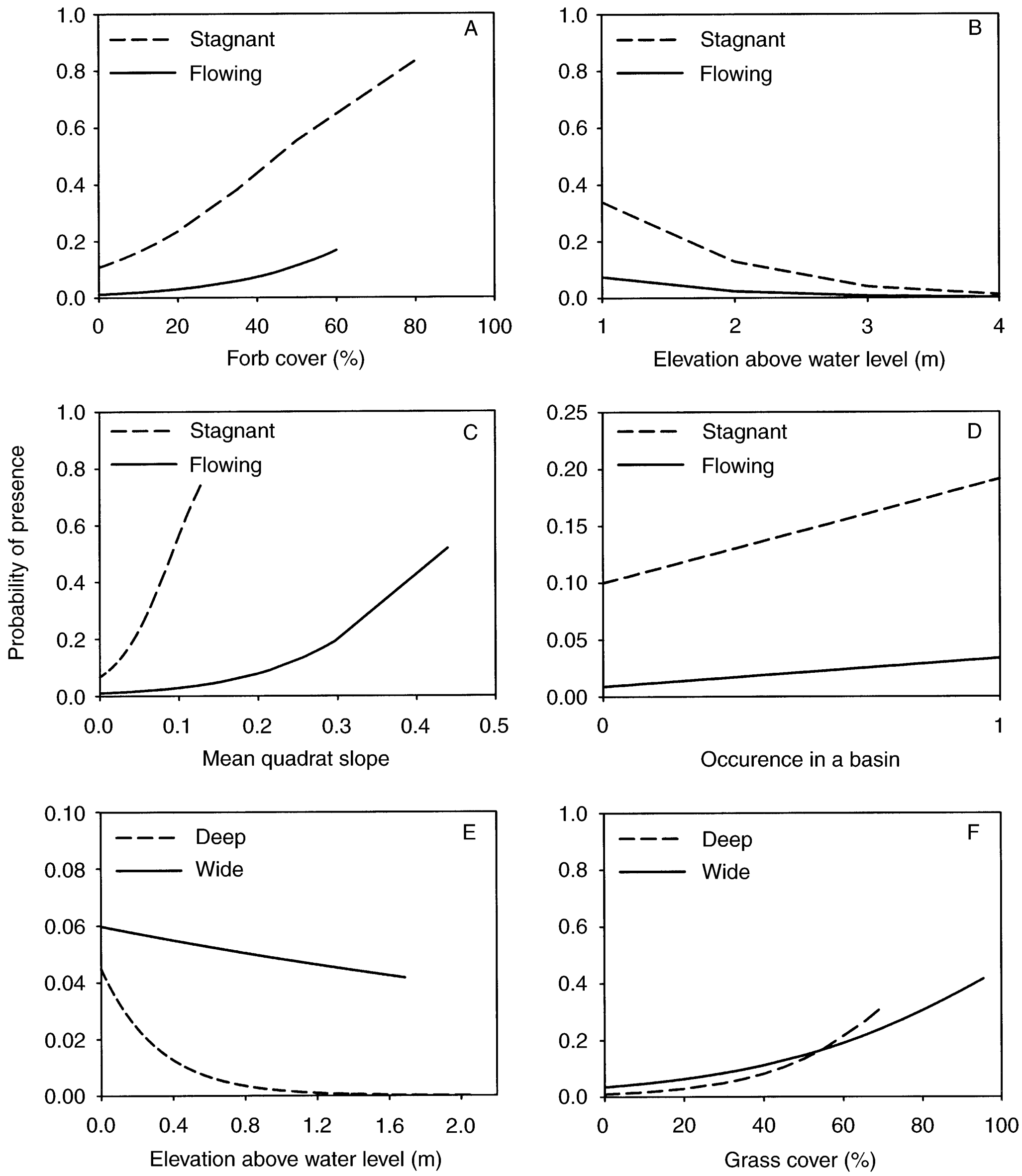

FIG. 11. Modeled probability of quadrat-level new seedling presence of early-dispersing species for significant landscape × local interaction terms in logistic regression models: (A) flow status × forb, (B) flow status × land distance index, (C) flow status × mean slope, (D) flow status × basin, (E) width–depth ratio × elevation, and (F) width–depth ratio × grass. ''Wide'' represents river cross-sections with a width–depth ratio of >170 (the median value), ''Deep'' represents cross-sections with a width–depth ratio of <170.

that year and should not be taken to represent all years. In contrast, the relationships between older seedlings or saplings and landscape variables integrate the effects of several years, and thus should be less sensitive to the specific flow conditions within the year of sampling.

Hierarchical controls on seedling distribution

Landscape factors may influence local seedling occurrence through a combination of hierarchical and nonhierarchical processes. First, landscape characteristics could exert a direct (nonhierarchical) influence on the probability of seedling occurrence at the quadrat level (Bendix 1994*a*). In other words, the influence of broad-scale variables would be relatively uniform across a set of local conditions. Second, landscape characteristics could indirectly influence seedling occurrence by shaping the local conditions to which seedling distribution responds. An example of this would be if variations in channel characteristics strongly controlled the local sediment texture and elevation of sediment bars in ways that influenced seedling coloniza-

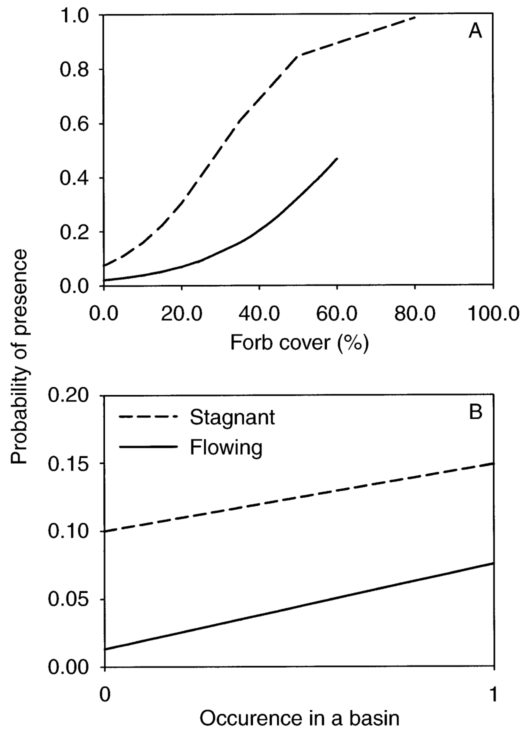

FIG. 12. Modeled probability of quadrat-level new seedling presence of late-dispersing species for significant landscape × local interaction terms in logistic regression models: (A) flow status × forb and (B) flow status × basin.

tion and persistence. In such a case, local variables would be strongly correlated with landscape context and might show a poor relationship with seedling occurrence after the influence of the landscape was factored out. Finally, the influence of local variables on seedling occurrence may be conditional on the landscape context even if the local conditions themselves are not controlled at the landscape level; in a statistical sense, landscape context would influence the slope and intercept of the function relating local conditions to seedling occurrence. We refer to these three possibilities as direct (nonhierarchical), indirect (hierarchical), and conditional hierarchical controls.

Our results suggest that landscape variables influenced local seedling occurrence through a combination of hierarchical and nonhierarchical controls. In particular, the occurrence of significant interactions between landscape and local variables suggests that the influence of local variables was conditional on landscape context. For some local variables, both the slope and the intercept of the relationship with seedling occurrence were constrained by the landscape context (channel width, flow status, sandbar elevation, etc.) within which the quadrat occurred. For example, in the significant interaction between channel flow status and forb cover, quadrat-level new seedling occurrence was higher in stagnant channels across all levels of forb cover (suggesting a direct effect of flow status), and the influence of forb cover on seedling occurrence was also much stronger in stagnant channels (suggesting a conditional, hierarchical effect of flow status). For older seedlings, the influences of local and landscape variables were apparently additive, in that the direct effects of channel width and the local variables were significant individually, with no significant landscape × local interactions.

Finally, there are likely to have been indirect effects of landscape characteristics on seedling occurrence, through landscape controls on local conditions. This is suggested by the significant (albeit weak) correlations of landscape variables with local variables (Table 10). However, the weakness of these correlations, along with the fact that strong local effects on seedling occurrence remained after landscape influences were factored out, suggest that these indirect effects were weak. Thus, although local and landscape characteristics are not strictly independent, the strength of direct local effects suggests that local conditions were not mere surrogates for the influence of the landscape.

Conclusions regarding the relative effects of broad- and fine-scale processes are highly dependent on the extent of the study area, the grain of the sampling units, the variables chosen, and the phenomena of interest (Bendix 1994*a*, van Coller et al. 2000). Our scales of analysis excluded consideration of broader watershed-scale (Baker 1989) and physiographic-system (Baker and Barnes 1998) effects, but permitted consideration of finer scale influences (Bendix 1994*a*) on riparian tree seedling establishment and persistence within our system. Because the specific processes that influence

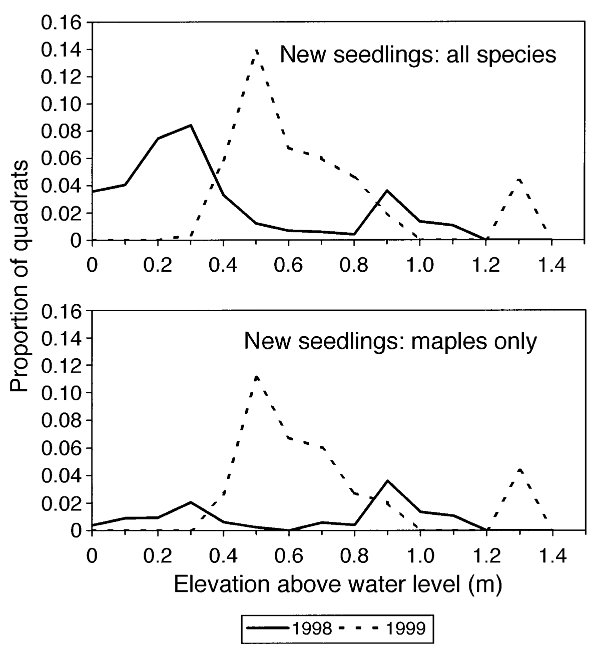

FIG. 13. Comparison of elevation distribution of transect segments (1 × 2 m) with new seedlings in 1998 and 1999, using continuous belt transect data.

TABLE 10. Pearson correlations (R) between landscape and local variables at the quadrat level ($n = 692$). Correlation coefficients that are significant at $P \leq 0.05$ are in boldface.

Local variables	Landscape variables: River cross-section		Channel		Sandbar		
	Energy Slope	WDratio	Chanwid	Flow Status	Length	LWratio	Median Elevation
Elevation	−0.028	0.014	**−0.124**	**−0.195**	**0.131**	0.055	**0.478**
Basin	0.067	−0.061	**−0.142**	**−0.171**	**0.121**	0.010	**0.150**
Basin elev	0.017	**−0.094**	**−0.146**	**−0.187**	**0.114**	−0.010	**0.255**
Mean slope	0.068	0.073	**−0.132**	−0.052	−0.067	**0.156**	−0.004
Land dist	**−0.249**	**−0.272**	**0.366**	**0.283**	**0.257**	**−0.349**	**−0.082**
River dist	**0.174**	−0.045	**−0.136**	**−0.303**	**0.186**	**−0.204**	**0.186**
Grass	**0.128**	**0.239**	**−0.178**	**−0.136**	**−0.168**	**0.183**	0.030
Forb	**0.197**	**0.139**	**−0.182**	**−0.135**	−0.073	**0.101**	**−0.091**
Shrub	−0.042	−0.034	**−0.095**	−0.067	**0.115**	**0.092**	0.067
Litter	**0.333**	**0.253**	**−0.251**	**−0.334**	**−0.127**	**0.138**	0.024
Silt	**0.167**	**0.141**	**−0.211**	**−0.200**	−0.073	**0.125**	0.027

Note: Variable abbreviations and definitions are in Table 2.

vegetation distribution may be difficult to discern unambiguously or difficult to measure at a single point in time, we used static physical variables or simulated hydrodynamic conditions as surrogates for process.

Overall, our results suggest that both broad- and fine-scale factors influence seedling establishment and persistence, with landscape context constraining the influence of local factors. Consideration of both broad- and fine-scale factors, and the type and strength of linkage that occurs between scales (the means by which landscape factors influence local processes), may be important for understanding the response of riparian vegetation to hydrologic disturbances or to human alteration of the flow regime. In this paper, we have considered relatively short-term influences by local and landscape variables on vegetation distribution. However, the potential for vegetation colonization to influence geomorphic processes and landform development (Osterkamp and Costa 1987, Malanson and Butler 1990, Hupp 1992, McKenney et al. 1995) suggests that local factors may cumulatively influence landscape-level change over longer time scales. Multiscale influences on riparian vegetation and geomorphic landform dynamics should be studied over a range of temporal scales to gain a more complete understanding (Schumm and Lichty 1965, Bendix and Hupp 2000).

ACKNOWLEDGMENTS

Funding was provided by a University of Wisconsin Alumni Research Foundation graduate fellowship, an EPA STAR graduate fellowship, the Sand County Foundation, and by the Wisconsin River Floodplain Project (EPA STAR program, Ecological Indicators, Agreement Number R826600-01-0). Willis Brown, James Crants, James O'Brien, Owen Boyle, Chris Lenhart, Sarah Gergel, Sun-Young Jeong, and many others supplied valuable assistance in the field. Jim Miller, Tania Schoennagel, Paul Zedler, Steve Carpenter, David Mladenoff, James Knox, Ken Potter, Cliff Hupp, and two anonymous reviewers provided constructive suggestions on the manuscript. Al Lulloff of the Wisconsin Department of Natural Resources provided river cross-section data for the hydrologic modeling. Special thanks go to Kevin McAleese and Brent Haglund of the Sand County Foundation for use of GPS equipment and the boat. Thanks also to the Aldo Leopold Foundation, Sand County Foundation, Pat Kaiser of the Wisconsin DNR, and Phil Pines for access to field sites.

LITERATURE CITED

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**:355–366.

Argus, G. W., and F. G. Goff. 1964. Preliminary reports on the flora of Wisconsin. Number 51. Salicaceae. The genus *Salix*—the willows. Transactions of the Wisconsin Academy of Sciences, Arts and Letters **53**:217–272.

Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. Ecological Applications **4**:544–554.

Auble, G. T., and M. L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. Wetlands **18**(4):546–556.

Baker, M. E., and B. V. Barnes. 1998. Landscape ecosystem diversity of river floodplains in northwestern Lower Michigan, U.S.A. Canadian Journal of Forest Research **28**:1405–1418.

Baker, W. L. 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. Annals of the Association of American Geographers **79**(1):65–78.

Baker, W. L. 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. Journal of Biogeography **17**:59–73.

Bendix, J. 1994*a*. Scale, direction, and pattern in riparian vegetation–environment relationships. Annals of the Association of American Geographers **84**(4):652–665.

Bendix, J. 1994*b*. Among-site variation in riparian vegetation of the southern California transverse ranges. American Midland Naturalist **132**:136–151.

Bendix, J., and C. R. Hupp. 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes **14**:2977–2990.

Birkeland, G. H. 1996. Riparian vegetation and sandbar morphology along the lower Little Colorado River, Arizona. Physical Geography **17**(6):534–553.

Burns, R. M., and B. H. Honkala, technical coordinators. 1990. Silvics of North America. Volume 2, Hardwoods. USDA Forest Service, Agriculture Handbook 654. USDA, Washington, D.C., USA.

Church, M. 1995. Geomorphic response to river flow regulation: case studies and time-scales. Regulated Rivers: Research and Management **11**:3–22.
Clayton, L., and J. W. Attig. 1989. Glacial Lake Wisconsin. Geological Society of America Memoir 173, Boulder, Colorado, USA.
Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. Regulated Rivers: Research and Management **15**: 419–440.
Curtis, J. H. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.
Delcourt, H. R., and P. A. Delcourt. 1988. Quaternary landscape ecology: relevant scales in space and time. Landscape Ecology **2**:23–44.
Dixon, M. D. 2001. Woody vegetation dynamics on Wisconsin River sandbars: spatial and temporal controls on seedling recruitment. Dissertation. Ph.D. University of Wisconsin, Madison, Wisconsin, USA.
Durbin, R. D. 1997. The Wisconsin River: an odyssey through time and space. Spring Freshet Press, Cross Plains, Wisconsin, USA.
Fastie, C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology **76**(6):1899–1916.
Fenner, P., W. W. Brady, and D. R. Patton. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. Journal of Range Management **38**:135–138.
Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology **13**:133–144.
Friedman, J. M., and G. T. Auble. 1999. Mortality of riparian box elder from sediment mobilization and extended inundation. Regulated Rivers: Research and Management **15**: 463–476.
Friedman, J. M., W. R. Osterkamp, and W. M. Lewis, Jr. 1996*a*. Channel narrowing and vegetation development following a Great Plains flood. Ecology **77**:2167–2181.
Friedman, J. M., W. R. Osterkamp, and W. M Lewis, Jr. 1996*b*. The role of vegetation and bed-level fluctuations in the process of channel narrowing. Geomorphology **14**:341–351.
Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management **10**(2):199–214.
Gergel, S. E., M. G. Turner, and T. K. Kratz. 1999. Scale-dependent landscape effects on north temperate lakes and rivers. Ecological Applications **9**:1377–1390.
Glenn-Lewin, D. C., and E. van der Maarel. 1992. Patterns and processes of vegetation dynamics. Pages 11–59 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession. Chapman and Hall, New York, New York, USA.
Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540–551.
Hanson, J. S., G. P. Malanson, and M. P. Armstrong. 1990. Landscape fragmentation and dispersal in a model of riparian forest dynamics. Ecological Modelling **49**:277–296.
Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Sciences (USA) **95**:14843–14847.
Hupp, C. R. 1982. Stream-grade variation and riparian-forest ecology along Passage Creek, Virginia. Bulletin of the Torrey Botanical Club **109**:488–499.
Hupp, C. R. 1992. Riparian vegetation recovery patterns following stream channelization: a geomorphic perspective. Ecology **73**:1209–1226.
Hydrologic Engineering Center. 1998. HEC-RAS river analysis system, user's manual. Version 2.2. U.S. Army Corps of Engineers, Davis, California, USA.
Hynes, H. B. N. 1975. The stream and its valley. Verhandlungen. Internationale Vereinigung für theoretische und angewandte Limnologie **19**:1–15.
Johnson, W. C. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. Ecological Monographs **64**: 45–84.
Johnson, W. C. 1997. Equilibrium response of riparian vegetation to flow regulation in the Platte River, Nebraska. Regulated Rivers: Research and Management **13**:403–415.
Johnson, W. C. 2000. Tree recruitment and survival in rivers: influence of hydrological processes. Hydrological Processes **14**:3051–3074.
Knighton, D. 1998. Fluvial forms and processes, a new perspective. John Wiley, New York, New York, USA.
Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**:253–260.
Krug, W. R., and L. B. House. 1980. Streamflow model of Wisconsin River for estimating flow frequency and volume. U.S. Geological Survey Water-Resources Investigations Open-File Report **80–1103**.
Leopold, A., and S. E. Jones. 1947. A phenological record for Sauk and Dane Counties, Wisconsin, 1935–1945. Ecological Monographs **17**:81–122.
Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1983.
Li, C. C. 1975. Path analysis. Boxwood Press, Pacific Grove, California, USA.
Liegel, K. 1988. Land use and vegetational change on the Aldo Leopold Memorial Reserve. Transactions of the Wisconsin Academy of Sciences, Arts and Letters **76**:47–68.
Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.
Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands **18**(4):634–645.
Malanson, G. P., and D. R. Butler. 1990. Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, U.S.A. Arctic and Alpine Research **22**:183–194.
Malanson, G. P., and D. R. Butler. 1991. Floristic variation among gravel bars in a subalpine river. Arctic and Alpine Research **23**:273–278.
McBride, J. R., and J. Strahan. 1984. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. American Midland Naturalist **112**:235–245.
McKenney, R., R. B. Jacobson, and R. C. Wertheimer. 1995. Woody vegetation and channel morphogenesis in low-gradient, gravel-bed streams in the Ozark Plateaus, Missouri and Arkansas. Geomorphology **13**:175–198.
Menard, S. 1995. Applied logistic regression analysis. Sage University Paper series on Quantitative Applications in the Social Sciences, 07-106. Sage, Thousand Oaks, California, USA.
Munro, B. H., and E. B. Page. 1993. Statistical methods for health care research. Second edition. J. B. Lippincott, Philadelphia, Pennsylvania, USA.
Naiman, R. J., S. R. Elliott, J. M. Helfield, and T. C. O'Keefe. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. Hydrobiologia **410**:79–86.
Naiman, R. J., D. G. Lonzarich, T. J. Beechie, and S. C. Ralph. 1992. General principles of classification and the assessment of conservation potential in rivers. Pages 92–123 *in*

P. J. Boon, P. Calow, and G. E. Petts, editors. River conservation and management. John Wiley, New York, New York, USA.

Nilsson, C., E. Nilsson, M. E. Johansson, M. Dynesius, G. Grelsson, S. Xiong, R. Jansson, and M. Danvind. 1993. Processes structuring riparian vegetation. Current Topics in Botanical Research **1**:419–431.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.

O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology **3**:193–205.

Osterkamp, W. R. 1998. Processes of fluvial island formation, with examples from Plum Creek, Colorado and Snake River, Idaho. Wetlands **18**:530–545.

Osterkamp, W. R., and J. E. Costa. 1987. Changes accompanying an extraordinary flood on a sand-bed stream. Pages 201–224 *in* L. Mayer and D. Nash, editors. Catastrophic flooding. Binghampton Symposium in Geomorphology. Volume 18. Allen and Unwin, Boston, Massachusetts, USA.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology **8**:3–18.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society **16**:391–409.

Reed, R. A., R. K. Peet, M. W. Palmer, and P. S. White. 1993. Scale dependence of vegetation–environment correlations: a case study of a North Carolina piedmont woodland. Journal of Vegetation Science **4**:329–340.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences **53**(Supplement 1):295–311.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987–1990.

Rood, S. B., A. R. Kalischuk, and J. M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. Wetlands **18**:557–570.

Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environmental Management **14**:451–464.

SAS Institute. 1990. SAS/STAT user's guide. Version 6, fourth edition. Volumes 1 and 2. SAS Institute, Cary, North Carolina, USA.

Schopmeyer, C. S., technical coordinator. 1974. Seeds of woody plants in the United States. USDA Forest Service, Agricultural Handbook Number 450. USDA, Washington, D.C., USA.

Schumm, S. A. 1985. Patterns of alluvial rivers. Annual Review of Earth and Planetary Sciences **13**:5–27.

Schumm, S. A., and R. W. Lichty. 1965. Time, space, and causality in geomorphology. American Journal of Science **263**:110–119.

Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications **7**:677–690.

Scott, M. L., J. M. Friedman, and G. T. Auble. 1996. Fluvial process and the establishment of bottomland trees. Geomorphology **14**:327–339.

Shafroth, P. B., G. T. Auble, J. C. Stromberg, and D. T. Patten. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. Wetlands **18**:577–590.

Smith, D. G. 1980. River ice processes: thresholds and geomorphologic effects in northern and mountain rivers. Pages 323–343 *in* D. R. Coates and J. D. Vitek, editors. Thresholds in geomorphology. Allen and Unwin, London, UK.

Smith, D. G., and C. M. Pearce. 2000. River ice and its role in limiting woodland development on a sandy braid-plain, Milk River, Montana. Wetlands **20**:232–250.

Stromberg, J. C., D. T. Patten, and B. D. Richter. 1991. Flood flows and dynamics of Sonoran riparian forests. Rivers **2**:221–235.

Tooth, S., and G. C. Nanson. 2000. The role of vegetation in the formation of anabranching channels in an ephemeral river, Northern plains, arid central Australia. Hydrological Processes **14**:3099–3117.

Trexler, J. C., and J. Travis. 1993. Nontraditional regression analyses. Ecology **74**:1629–1637.

van Coller, A. L., K. H. Rogers, and G. L. Heritage. 2000. Riparian vegetation–environment relationships: complementarity of gradients versus patch hierarchy approaches. Journal of Vegetation Science **11**:337–350.

Ware, G. H. 1955. A phytosociological study of lowland hardwood forests in southern Wisconsin. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.