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EFFECTS OF FLOW PATTERN ON RIPARIAN SEEDLING RECRUITMENT ON SANDBARS IN THE WISCONSIN RIVER, WISCONSIN, USA

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Abstract: In riparian ecosystems, river flow is the dominant driver influencing ecological process and pattern, including the recruitment of riparian tree species. In a four-year field study (1997–2000) of seedling recruitment on sandbars in the Wisconsin River, I evaluated the hypothesis that the timing of seed dispersal and river flow interact to determine the annual composition of pioneer tree seedling cohorts. In the final three years of the study (1998–2000), growing season flow pulses strongly influenced the species composition and density of new seedling cohorts. Mortality rates of new seedlings exceeded 90% during the 1998 and 1999 flow pulses, and species composition shifted to dominance by *Acer saccharinum* following the 1999 flow pulse. Different species dominated the cohort of each year: in 1997, 83% of new seedlings were *Betula nigra*; in 1998, 63% were *Salix* spp. (*S. nigra* 39%, *S. exigua* ssp. *interior* 24%); in 1999, 89% were *Acer saccharinum*; and in 2000, 71% were *S. exigua* and 23% were *Betula nigra*. Cohorts retained their initial differences in species composition for at least one year after establishment. The three years (1998–2000) with summer flow pulses produced very low end-of-the-growing-season densities of new seedlings (<0.1 seedlings/m² on random plots), and subsequent mortality in the first year after establishment further reduced seedling numbers by 53–94% on monitored plots. Thus, although summer flow patterns during the first year of growth strongly influenced species composition of seedling cohorts, low seedling densities and high overwinter mortality likely reduce the long-term impacts of initial cohort differences on successional trajectories.

Key Words: disturbance, flooding, phenology, regeneration niche, riparian vegetation, seed dispersal, seedling demography

INTRODUCTION

Flow is a “master variable” that controls ecological dynamics in fluvial systems (Poff et al. 1997). Human management of rivers influences the timing, magnitude, and duration of flow events and, thus, has profound influence on biotic structure and process in rivers. Many tree species that colonize river sediments have a temporal dispersal and germination window that coincides with the recession of the annual spring peak flow, resulting in dispersal to moist, mineral substrates that are suitable for germination (Fenner et al. 1985, Walker et al. 1986, Johnson 1994, Karrenberg et al. 2002). The requirements of co-occurrence of suitable flows and open substrate for establishment, correct timing in relation to species dispersal windows (Fenner et al. 1985, Mahoney and Rood 1998, Rood et al. 1998), and subsequent flows that do not remove

the seedlings (Scott et al. 1996) may produce recruitment that is episodic in riparian systems (Bradley and Smith 1986, Baker 1990, Stromberg et al. 1991, 1993, Scott et al. 1997).

Flow regulation can result in increased (Johnson 1994) or decreased (Rood and Mahoney 1990) recruitment of pioneer tree seedlings, depending on the nature of flow alteration and the geomorphologic setting of the river (Scott et al. 1996, Friedman et al. 1998, Johnson 1998). On meandering rivers, recruitment occurs after moderate magnitude, medium to high frequency floods that promote lateral channel migration and formation of point bars (Johnson et al. 1976, Johnson 1992, Richter and Richter 2000). On rivers with stable channel locations, recruitment occurs on overbank flood deposits from low frequency, high magnitude floods (Baker and Walford 1995, Scott et al.

1997). On braided rivers, vegetation colonizes the channel bed during prolonged low flow periods (Johnson 1994, Friedman et al. 1996a,b). Following recruitment, the magnitude and timing of subsequent flows strongly influence seedling survival on all of these systems (Fenner et al. 1985, Johnson 1994, Scott et al. 1997, Rood et al. 1998, Shafroth et al. 1998, Johnson 2000).

Dispersal phenology is an important component of the regeneration niche for pioneer riparian tree species (Grubb 1977, Niiyama 1990). Because of different dispersal phenologies, species may respond individually to a given sequence and magnitude of hydrologic events (Noble 1979, Streng et al. 1989, Niiyama 1990, Craig and Malanson 1993). Theoretically, greater variation among years in the timing and frequency of disturbance should favor a greater range of regeneration strategies. Thus, annual or multi-year variation in timing and magnitude in flood events (and low flows) could promote the development and maintenance of high plant species diversity in floodplain communities (Grubb 1977, Streng et al. 1989, Niiyama 1990, Jones et al. 1994), and changes in hydrologic conditions could lead to long-term shifts in species composition and age-structure in riparian forests (Johnson 1992, Barnes 1997).

The central question of this research is whether temporal variation in river flow interacts with the timing of seed dispersal and germination to influence regeneration and foster coexistence of different pioneer riparian tree species on sandbars in the Wisconsin River. Specifically, (1) do years that differ strongly in growing season flow patterns differ in the species composition and density of new seedlings, (2) can these differences be explained as a function of the timing of flows, seedbed availability, and seed dispersal, (3) do cohorts with different initial species compositions retain those differences at least one year after establishment, and (4) is variability in initial species composition among seedling cohorts likely to have a long-term impact on successional trajectories and community composition?

METHODS

Study Area

The study area is a 16-km reach of the Wisconsin River, between Wisconsin Dells and Portage, Wisconsin (Columbia and Sauk Counties), USA (Figure 1). The Wisconsin has a long history of flow alteration, with 24 reservoirs on the mainstem or tributaries upstream, primarily for power generation (Durbin 1997). Most existing dams were constructed in the late 1800s or early 1900s. The nearest upstream dam is the Kil-

bourn Dam (completed 1909), approximately 16 km from the upper end of the reach (Durbin 1997). The operation of Kilbourn Dam for power generation can cause diurnal stage fluctuations of 0–0.4m in the study area, with fluctuations most pronounced during low flow periods. The Prairie du Sac dam occurs approximately 40 km downstream from the study area, with slackwater effects of its reservoir, Lake Wisconsin, extending to within 10–15 km of the study area. Three of the largest storage reservoirs on the system (Petenwell, Castle Rock, and Dubay) were completed between 1940 and 1950, greatly increasing the capacity for capture and storage of flood waters (Krug and House 1980, Durbin 1997). These, in combination with smaller pre-existing dams, are estimated to have reduced the magnitude of the annual peak flow by around 20% and the 100-year flood by 10% at Wisconsin Dells (Krug and House 1980). No new dams or other major flow alterations have occurred in the last 50 years. Levees occur along much of the study reach but are set back 50–500m from the river in most places, minimizing their effect on river hydrology under all but the largest flows (Gergel et al. 2002).

The planform of the river is island braided (Schumm 1985), with a wide and shallow channel, vegetated mid-channel islands, large sandbars, and channel bedforms (dunelets, etc.) typical of sandy, bedload-dominated rivers (Knighton 1998). River energy gradient is low (approximately 0.3 m/km), and bed substrates are sand or gravel, with the river flowing through the outwash plain of former glacial Lake Wisconsin (Clayton and Attig 1989). The general mode of floodplain formation appears to be through island formation and channel narrowing and abandonment, as evidenced by ongoing and past patterns of forest establishment within narrower side channels and between groups of islands (Dixon et al. 2002).

Historic daily flows (1935–2000) were determined from a USGS gaging station (#05404000 at Wisconsin Dells) located just below Kilbourn Dam. Average daily flows were approximately 195 m³/s, with mean annual low flows at 65 m³/s and peak flows at 1020 m³/s. Most annual peak flows were related to snowmelt, with the majority (56%) occurring in March or April. Large floods have also occurred at other seasons, with the largest flood on record in September 1938 (2044 m³/s) and the largest recent flood in June 1993 (1674 m³/s).

Vegetation in the floodplain is diverse, with areas of wet floodplain forest, *Quercus-Carya* woodland, wet meadow, sand prairie, and savanna (Liegel 1988, Gergel et al. 2002). Wet floodplain forests along the river are dominated by silver maple (*Acer saccharinum* L.), river birch (*Betula nigra* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and American elm (*Ulmus americana* L.), with eastern cottonwood (*Populus del-*

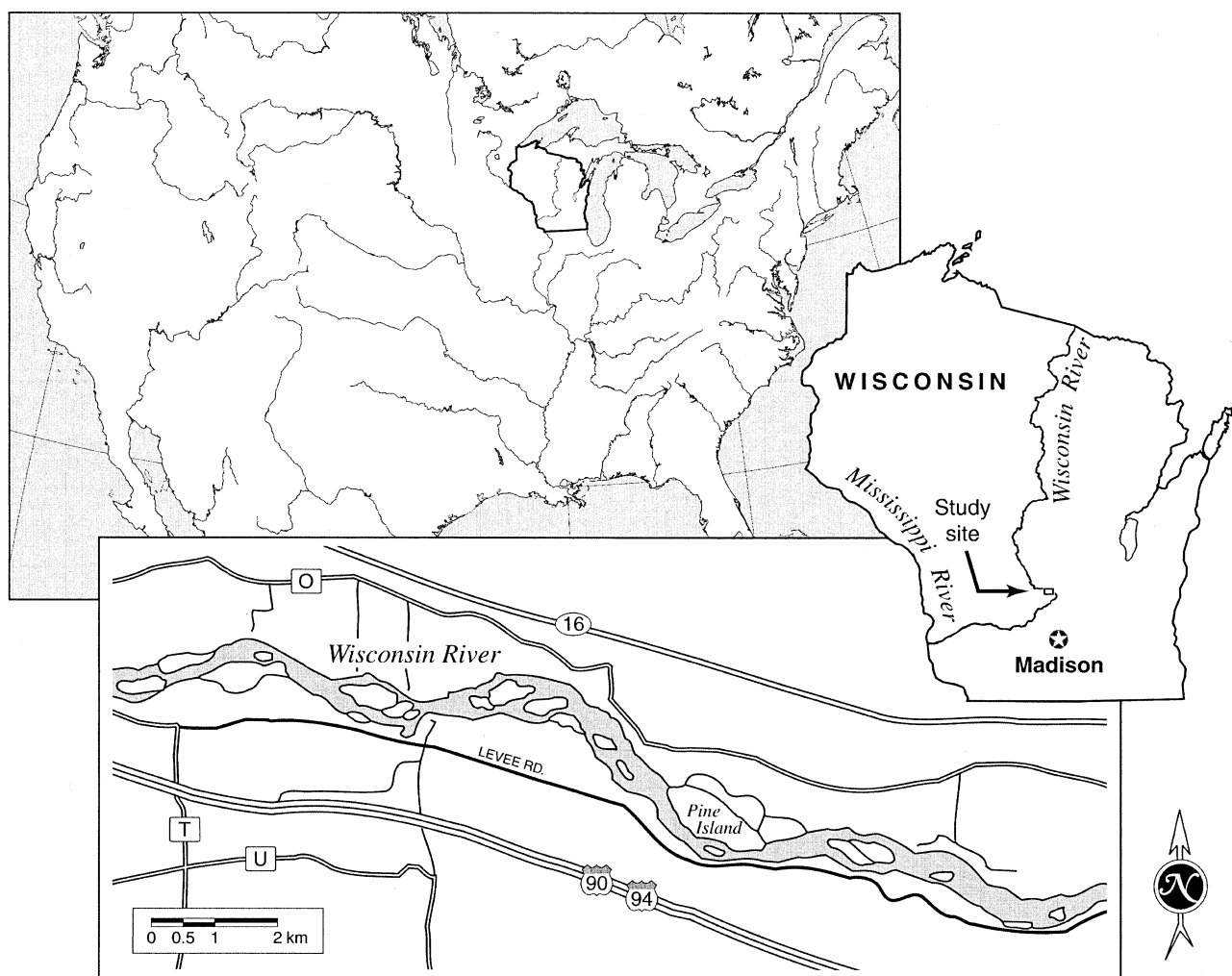


Figure 1. The study area is a 16-km reach of the Wisconsin River between the towns of Wisconsin Dells and Portage (Columbia and Sauk Counties), Wisconsin, USA.

toides Bartr.) and black willow (*Salix nigra* Marsh.) prominent in some areas. Early successional sites on river sandbars are dominated by seedlings or saplings of sandbar willow (*S. exigua* Nutt. ssp. *interior* (Rowlee) Cronq.), black willow, Missouri River willow (*S. eriocephala* Michx.), river birch, silver maple, cottonwood, and green ash.

Focal Species

River birch, silver maple, eastern cottonwood, black willow, sandbar willow, and Missouri River willow were the principal species colonizing open sandbar habitats and were the focal species of this study. All have seeds dispersed by wind and water, with dispersal occurring during the spring or summer. Good seed crops occur in most years, germination occurs soon after dispersal in all species, and seed longevity is

short (Schopmeyer 1974, Burns and Honkala 1990). All are relatively shade-intolerant, flood-tolerant, fast-growing, and capable of colonizing moist, bare mineral substrates. Species differ in seed size, dispersal adaptations of the seed, and the peak and breadth of the dispersal interval. Silver maple has significantly larger seeds than the other species, has greater shade tolerance, and is less dependent on mineral substrates for germination (Hosner and Minckler 1963, Burns and Honkala 1990, Barnes 1997). Sandbar willow and Missouri River willow attain only shrub stature and do not occur in established floodplain forests within the study area. After colonization of a site by seed or vegetative means, both spread clonally by root sprouting (Krasny et al. 1988, Burns and Honkala 1990, Craig and Malanson 1993). The other species are also capable of stem or root sprouting in response to injury or burial (Barnes 1985, Burns and Honkala 1990,

Craig and Malanson 1993) but do not appear to spread clonally.

New (1st year) seedlings of all species were distinguished from those from previous year cohorts based on their size, appearance, lack of a woody stem, and occurrence on otherwise uncolonized substrates. Among the willows, first-year seedlings of *Salix nigra* were difficult to distinguish from the less common *S. eriocephala*. For the purposes of this study, all first-year seedlings of this type were recorded as *S. nigra*. Seedlings of *S. exigua* were easily distinguished from the other *Salix* species. Seedlings and root sprouts of *S. exigua* were distinguished from each other on the basis of leaf morphology (Argus and Goff 1964).

Seed Dispersal Sampling

Temporal patterns of seed dispersal were monitored in 1999 and 2000. Sticky traps (Kollmann and Goetze 1998) were established at two sandbar sites in 1999 and three in 2000, and placed close to the channel-forest edge, near trees or shrubs of the focal species. Traps were composed of a 0.6×0.6 m wooden platform, coated with an adhesive (Tree Tanglefoot Pest Barrier, The Tanglefoot Company, Grand Rapids, Michigan), and mounted on top of a 1-m pole. Four traps were established per site in 1999 and 5 in 2000. Traps were visited on 1–2 week intervals from mid-May to early August. At each visit, the traps were inspected and tallied for numbers of maple, birch, cottonwood, and willow seeds; scraped clean; and re-coated with the adhesive.

Seed numbers per visit were totaled across all traps and sites. Totals were used to determine the timing of peak dispersal and the dispersal period for each species but not to estimate areal density of seed rain. The peak dispersal period for each species was defined by the dates between which 10–90% of the cumulative seed fall occurred. For *Acer* in 1999, the start of the peak dispersal period was designated as the day that seed traps were installed (May 15) rather than the date by which at least 10% of the seeds had been sampled (May 22) because seed fall had already begun.

Because willow seeds on the traps could not be identified to species, seed release was monitored on individuals (ramets) of *Salix nigra*, *S. exigua*, and *S. eriocephala* adjacent to the seed trap sites in 1999 (one site) and 2000 (both sites). In 1999, I counted 10–25 unmarked saplings or trees per species and noted whether or not each individual was dispersing seeds (capsules open, with plumed seeds being released) on the date of the visit. Because of the difficulty in distinguishing post-dispersal female trees from male trees and concern that my 1999 counts may have been biased toward individuals that were releasing seeds (par-

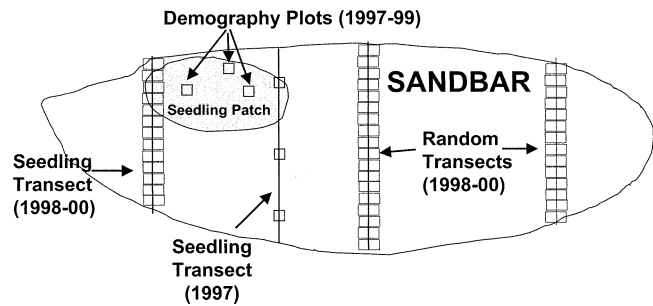


Figure 2. Schematic of demography plot and transect sampling protocol for 1997–2000.

ticularly with *S. eriocephala*), I limited my counts in 2000 to a set of marked individual trees and saplings. An individual tree was considered to be actively dispersing seeds if greater than approximately 10% of the capsules had opened and if greater than 10% of the seeds remained on the tree. The earliest and latest days of active dispersal, as defined above, were used to characterize the dispersal interval for each willow species.

No dispersal data were collected for 1997 and 1998. In order to evaluate how flow and dispersal timing influenced seedling recruitment in those years, I assumed that dispersal periods in 1997 and 1998 were identical and were a composite of those observed in 1999 and 2000. Potential dispersal periods for 1997 and 1998 were constructed from the earliest and latest dates of peak (10–90%) and total dispersal in 1999 and 2000 for each species.

Seedling Sampling

Sampling to determine the composition of first-year seedling cohorts was conducted in late August–November of each year (1997–2000). Twelve sandbars were sampled in 1997, 30 in 1998, 32 in 1999, and 20 in 2000. Sandbars were chosen through a stratified random procedure to ensure geographic dispersion of sites and representation of different channel positions. Channel positions included sandbars attached to an island or the mainland, isolated mid-channel bars, and the bed of side channels that were inactive at low flow (Dixon et al. 2002). Sampling of seedlings and of sandbar topography was conducted in two ways: 1x1m demography plots placed within patches of seedlings, and belt transects placed either randomly within the sandbar or in proximity to patches of seedlings.

Demography Plots. On each sandbar, three 1x1m demography plots were established within patches of first year seedlings (Figure 2). On sandbars for which seedling densities were too low to establish three plots, no plots were established. Plot locations were chosen in

stratified random fashion to cover the variability in elevations and seedling composition within the patch. If necessary, plot locations were adjusted to capture at least 2–3 seedlings per plot. Plots were marked with a rebar and revisited seasonally or annually (generally twice per year, once in the following spring or summer and once in the fall) for as long as live seedlings still occurred. All seedlings were counted within the plot, with one side of the quadrat always aligned to the north so that it could be set up in the same orientation on revisits. Herbaceous and litter cover and type of sediment (silt, sand, gravel, cobble) were also noted for each plot. Altogether, demography plots were established on 12 (34 plots) sandbars in 1997, 23 (69 plots) in 1998, and 25 (75 plots) in 1999. No plots were established in 2000.

Demography plots were established to track seedling survival over time, particularly in relation to seasonal mortality factors (e.g., floods or drought during the summer, effects of ice over winter, effects of spring peak flows). Totals from demography plots were also combined with transect totals to quantify species composition for the new seedling cohort of each year. However, because of their non-random placement within observer-defined patches of seedlings and the requirement that each plot initially have at least 2–3 seedlings, the demography plots could not be used for providing unbiased estimates of areal seedling densities on the sandbars.

Transects. Transect-sampling protocol varied somewhat between years due to changing data needs. One to three transects were established per sandbar (Figure 2). Transects were oriented perpendicular to the direction of river flow and extended from the water-sandbar shoreline to the opposite shoreline (on mid-channel bars) or to a permanently vegetated bank (on bars connected to an island or the mainland). In 1998–2000, seedlings were counted continuously within a 2-m belt (sequential 1×2 m quadrats) centered on the transect. The sandbar was divided longitudinally into thirds, with a transect placed a random distance within at least one of the thirds. In 1998, a transect was randomly placed within each of the thirds. In 1999 and 2000, only one random transect was established per sandbar. However, if a seedling patch was present but occurred within a different section (third) of the sandbar than the random transect, then a second (seedling) transect was established at a random distance within the third of the sandbar that contained the seedling patch (Figure 2). These “random” and “seedling” transects were treated differently in subsequent analyses.

On each sandbar sampled in 1997, a single transect was established in the vicinity of the seedling patch that contained the demography plots (Figure 2). Seed-

ling densities obtained from this method were assumed to be comparable with those obtained from the seedling transects in 1998–00 because both methods estimated seedling densities within or in the vicinity of seedling patches. The transect was established at a stratified random distance along the channel margin, oriented perpendicular to river flow, and continued to the other shore or to permanent vegetation (Figure 2). The transect was then divided into thirds, and individual 1×1 m plots were established at random distances along each third (thus, three plots per transect). These plots were sampled in the same fashion as the demography plots and were resampled in subsequent visits.

From 1998 to 2000, data from “random” transects were used to provide estimates of seedling densities per m^2 of sandbar habitat across the study area. “Seedling” transects were established for two reasons: (1) to increase the number of seedlings sampled for estimates of cohort species composition because of the sparse and highly patchy distribution of seedlings in most years and (2) to provide seedling density estimates comparable to those obtained in 1997, when transects were placed only in the vicinity of seedling patches (no “random” transects in 1997). Thus, “seedling” transects measured seedling density in the vicinity of (within the same third of the sandbar) or within seedling patches. “Random” transects that occurred within the same third as the seedling patch were used in both sets of density calculations (considered both a “random” and “seedling” transect).

Calibration of Plot Elevations

Along each transect and at each demography plot, elevation was measured relative to the water surface using a surveying level and rod. Because 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. River discharge at the time of sampling was estimated for each site based on provisional 15-minute 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 (Hydrologic Engineering Center 1998) model results, river cross-section data, and a National Weather Service stream gage at the downstream end of the study area, I calculated the difference in water-surface elevation between the flow at the time of sampling and a reference flow of $99 \text{ m}^3/\text{s}$. I used this difference in stage to adjust the field surveys to express all plot and transect elevations relative to the reference flow of $99 \text{ m}^3/\text{s}$. All plots or portions of the transects below this reference water-surface elevation were deleted from the analyses, since these locations were in-

undated the majority of the time and were unlikely to contain seedlings.

Statistical Analyses

PC-SAS (SAS Institute, Inc. 1990) was used for all analyses. Contingency table chi-square analysis was used for comparing relative abundances of seedling species by cohorts, years, or sampling visits based on seedling totals across all sites. If more than 20% of the cells in the contingency table had expected values of less than 5, rarer groups were lumped, so that the chi-square would be a valid statistic. Because statistical significance of the chi-square is partly a function of sample size, Cramer's V values (scale of 0–1) were examined to assess the strength of association among rows and columns (e.g., species composition and years) in specific contingency table analyses. Mean plot elevations and plot-inundating discharges were compared between years using analysis of variance. Because of the highly non-normal distribution of quadrat-level seedling densities, densities across years were compared using a one-way analysis of variance conducted on the ranks of the quadrat-level values. Thus, individual quadrats were treated as the sampling units. Post-hoc multiple comparisons of rank densities between years were conducted using Tukey's test, which controls for experimentwise error. For all analyses, statistical significance was defined as $P < 0.05$.

RESULTS

Seed Dispersal

Total seed counts in sticky traps were dominated by *Betula nigra* and *Salix* spp., which together made up over 90% of the seeds sampled in each year, with nearly equal numbers of each (not shown). *Betula* dominated the total seed counts during the first two weeks of June in both years, constituting over 2/3 of all seeds collected during that time period. Temporal patterns of seed dispersal were similar in 1999 and 2000 (Figure 3c,d), except for longer periods of dispersal for *S. exigua* and *S. nigra* and an apparent seed crop failure of *Acer saccharinum* in 2000 (Figure 3c,d). Traps contained maple seeds only on one sampling date in 2000 and at very low densities. Few seeds were observed on the ground, and of these, most had malformed samaras or unfilled seeds.

Species showed considerable overlap in dispersal timing but differed in the breadth of their dispersal periods (Figure 3c,d). *Acer* and *Betula* had narrow periods of peak dispersal, concentrated in a 2–3 week period in the early part of the growing season. Peak dispersal by *Populus* and the *Salix* species (particularly

S. exigua) began shortly after *Acer* but extended over a 4–10 week period. Small numbers of *Populus* and *Betula* seeds, however, continued to be found in seed traps until August in 1999 and 2000, well beyond the peak dispersal period. Dispersal patterns differed among willows, with *S. eriocephala* having the earliest and shortest dispersal period. *Salix exigua* had the longest dispersal interval of any species.

Density and Composition of Seedling Cohorts

Density. On randomly-placed transects, ranks of total (all species combined) quadrat-level seedling densities did not differ significantly among years (1998–2000), although individual species showed significant year-to-year variation (Table 1a). On transects placed within or in the vicinity of seedling patches (seedling transects), ranks of quadrat-level seedling densities varied significantly among years (1997–2000), with greatest densities overall and for most species (particularly *Betula nigra*) in 1997 (Table 1b). Differences in sampling protocol among years may have inflated the 1997 density estimates on seedling transects, although total seedling and *Betula* densities were also very high (but with high variance) on the demography plots in 1997 (Table 1c). Mean total seedling densities in 1997 were strongly influenced by very high densities of *Betula* seedlings on individual quadrats: one quadrat on a seedling transect had 501 seedlings (500 of them birch) and one demography plot had 1089 seedlings (785 of them birch).

Composition. Across transects and demography plots, species composition differed strongly among years ($\chi^2 = 9659$, $df = 12$, $P < 0.0001$ for transect totals, with Cramer's V = 0.66), with a different dominant species in each year (Table 1d). *Betula nigra* accounted for over 80% of the seedlings sampled in 1997 but was nearly absent (2 seedlings total) in 1999. *Salix* species accounted for nearly 2/3 of all seedlings in 1998 (*S. nigra* 39%, *S. exigua* 24%) but were a negligible component of the seedling cohort in 1999. *Acer saccharinum* accounted for 89% of all seedlings in 1999 but occurred at very low densities in 2000 (2 *Acer* seedlings out of 238 total seedlings). *Salix exigua* accounted for 71% of the seedlings and *Betula* 23% in 2000. The 2000 proportions, however, were heavily influenced by one seedling transect that contained 3/4 of all the *Salix* seedlings. Without this transect, *Salix exigua* and *Betula nigra* each accounted for 48% of the total seedlings in 2000.

Elevation and Inundating Discharge of Seedling Quadrats

On random and seedling transects, the river discharge required to inundate 50% of the seedlings

Table 1. Mean densities (#/m²) (and standard error) and species composition of new seedling cohorts by year and sampling method. Different letters within a row designate statistically significant ($p < 0.05$) differences in rank mean density among years according to analysis of variance and post-hoc multiple comparisons (Tukey's test). Individual quadrats were considered the sampling units.

Sampling Method	Species	Year			
		1997	1998	1999	2000
a. Random transects	<i>Acer saccharinum</i>	—	0.007 (0.001) ^a	0.073 (0.019) ^b	0.001 (0.001) ^a
	<i>Betula nigra</i>	—	0.008 (0.003) ^a	0 ^a	0.029 (0.008) ^b
	<i>Populus deltoides</i>	—	0.005 (0.001) ^a	0.004 (0.002) ^a	0.002 (0.002) ^a
	<i>Salix exigua</i>	—	0.013 (0.002) ^a	0.001 (0.001) ^b	0.010 (0.004) ^{ab}
	<i>Salix nigra</i>	—	0.015 (0.003) ^a	<0.001 (<0.001) ^b	0 ^b
	Other	—	<0.001 (<0.001) ^a	0.006 (0.001) ^b	0 ^a
	Total	—	0.048 (0.005) ^a	0.084 (0.020) ^a	0.042 (0.011) ^a
	# quadrats (# sandbars)	—	5060 (30)	1429 (32)	868 (20)
b. Seedling transects	<i>Acer saccharinum</i>	0.294 (0.116) ^a	0.009 (0.002) ^b	0.134 (0.030) ^c	0.001 (0.001) ^b
	<i>Betula nigra</i>	29.38 (17.26) ^a	0.026 (0.009) ^b	0 ^c	0.059 (0.017) ^d
	<i>Populus deltoides</i>	0.353 (0.152) ^a	0.008 (0.002) ^b	0.008 (0.003) ^b	0.001 (0.001) ^b
	<i>Salix exigua</i>	0.588 (0.529) ^{ab}	0.035 (0.007) ^{bc}	<0.001 (<0.001) ^c	0.191 (0.057) ^a
	<i>Salix nigra</i>	2.824 (2.263) ^a	0.035 (0.007) ^b	<0.001 (<0.001) ^c	0.008 (0.004) ^c
	Other	0.029 (0.029) ^{ab}	<0.001 (<0.001) ^a	0.009 (0.003) ^b	0 ^a
	Total	33.47 (17.76) ^a	0.115 (0.018) ^{bc}	0.152 (0.032) ^b	0.260 (0.060) ^c
	# quadrats (# sandbars)	34 (12)	1369 (22)	1025 (24)	443 (8)
c. Demography plots	<i>Acer saccharinum</i>	1.06 (0.22) ^a	0.90 (0.17) ^a	18.93 (3.30) ^b	—
	<i>Betula nigra</i>	75.62 (32.96) ^a	0.61 (0.17) ^b	0.03 (0.02) ^c	—
	<i>Populus deltoides</i>	2.85 (0.86) ^a	0.86 (0.15) ^a	1.83 (0.64) ^a	—
	<i>Salix exigua</i>	2.09 (1.04) ^a	1.58 (0.30) ^b	0.01 (0.01) ^c	—
	<i>Salix nigra</i>	10.76 (8.79) ^a	3.38 (0.86) ^a	0.05 (0.03) ^b	—
	Other	0.06 (0.06) ^a	0.01 (0.01) ^a	0.27 (0.08) ^b	—
	Total	92.44 (39.10) ^a	7.33 (1.00) ^b	21.12 (3.25) ^a	—
	# quadrats (# sandbars)	34 (12)	69 (23)	75 (25)	—
d. % Total Seedlings	<i>Acer saccharinum</i>	1.1	12.9	88.9	0.8
	<i>Betula nigra</i>	83.4	12.8	0.1	22.9
	<i>Populus deltoides</i>	2.5	11.2	8.2	2.1
	<i>Salix exigua</i>	2.1	23.8	0.2	71.3
	<i>Salix nigra</i>	10.8	38.8	0.3	2.9
	Other	0.1	0.5	2.3	0

(mean inundating discharge) varied from approximately 180 to 270 m³/s among years (Figure 4). Mean quadrat elevation varied from 0.29 to 0.59 m above the reference water surface (at discharge of 99 m³/s) among years. Seedlings occurred lowest in the river bed in 1998 and highest, with the greatest range, in 1999. Similar patterns held among years for the demography plots (not shown), although they occurred at slightly (but significantly) lower inundating discharges and elevations than transect quadrats in 1998 and 1999.

Influence of Growing Season Flow Pattern on Seedling Recruitment

Growing season flow patterns varied strongly among years (Figures 4). Flows in 1997 receded in mid-April, prior to the beginning of seed dispersal, and

remained relatively low and constant throughout the growing season. In contrast, summer flow pulses of 390 m³/s or greater (flows that inundated greater than 90% of the 1998 sandbar quadrats) occurred at various times during or after the seed dispersal period in 1998, 1999, and 2000 (Figure 4).

Data from demography plots resampled before and after the summer flow pulses in 1998 and 1999 suggested that these flows may have strongly influenced the composition and density of new seedlings (Table 2). The 1998 flow pulse occurred on June 29, after the peak dispersal period of *Acer* and *Betula* and near the end of peak dispersal for *Populus* and *Salix nigra*. Plots visited before (early June) and after (late July) the flow pulse did not differ significantly in relative species abundances ($\chi^2 = 1.021$, $df = 2$, $P = 0.60$, Cramer's $V = 0.06$, with the *Populus* and *Salix* totals lumped to increase expected cell frequencies) but

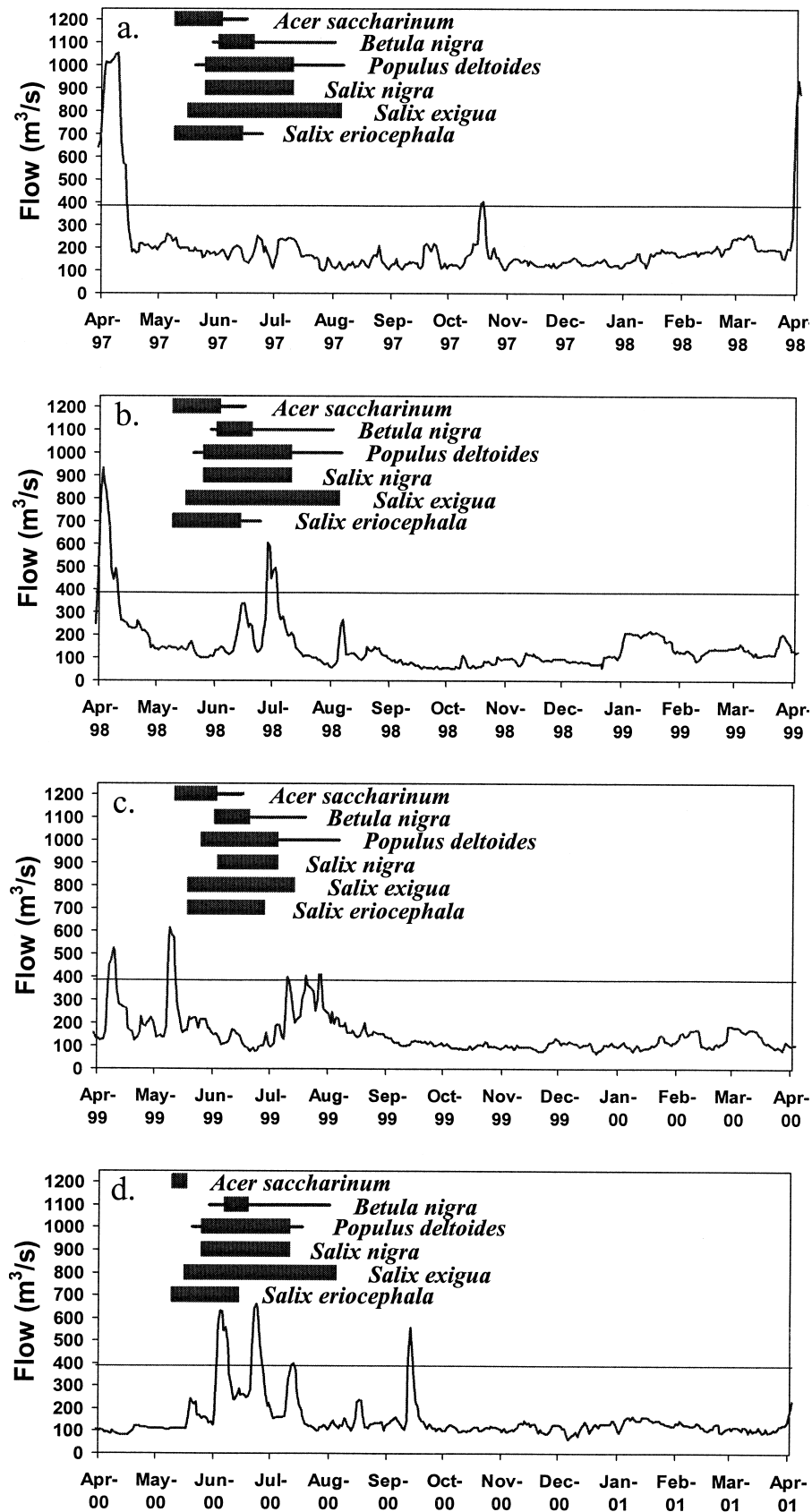


Figure 3. River discharge (m³/s) for April 1997–March 2001 from the Wisconsin Dells gaging station and seed dispersal intervals of focal tree species. For each species, the thicker bar indicates the interval of peak dispersal (10% – 90% of the

showed a 78% reduction in total (1998 cohort) seedling numbers (Table 2). If seedlings known to have established between sampling periods (plots that showed post-flood increases in seedling numbers) are removed from the post-flood totals, then actual mortality rates for new seedlings exceeded 92%. Plot mortality (complete loss of seedlings) was 44%. In contrast to the species composition on new transects and demography plots established at the end of the season in 1998 (Table 1), willows (*S. exigua*, *S. nigra*) made up only a small proportion of the new seedlings that established on resampled demography plots.

Three separate flow pulses exceeding 390 m³/s occurred in July of 1999. This period of high water, although of lower magnitude than in 1998, occurred after a June with very low flows, after peak dispersal had ended for most species, and inundated the majority of the plots for 2–3 weeks (Figures 3 and 4). As in 1998, new seedling numbers were greatly reduced, with post-flood seedling numbers only 4% of the pre-flood totals and with 74% of the plots losing all new seedlings. Unlike 1998, species composition of new seedlings (1999 cohort) within 1998 demography plots changed dramatically from pre-flood (early July) to post-flood (late August) ($\chi^2 = 45.498$, $df = 1$, $P < 0.0001$, Cramer's $V = 0.31$, with the *Betula*, *Populus* and *Salix* totals lumped) (Table 2). The pre-flood 1999 seedling cohort was dominated by *Salix nigra* and *Betula*, with *Acer* constituting only 20% of the seedlings. In contrast, *Acer* constituted 89% (16 of 18) of the seedlings remaining after the flood. Survival by new maple seedlings, although low (18%), was significantly greater than that of *Salix*, *Populus*, and *Betula* (0.5%, totaled across species) (Table 2). Although based on very low seedling numbers, this post-flood dominance by *Acer* on resampled demography plots matches well with the observed dominance by *Acer* on the transects and demography plots established at the end of the season (Table 1).

Overwinter and Other Subsequent Mortality

Species composition of seedling cohorts remained relatively stable over the year following establishment (Figure 5), with large, rapid compositional changes limited to the first growing season (Table 2). Although contingency table analyses suggested highly significant changes ($P < 0.0001$ for each cohort) in relative species abundances across sampling dates in all three

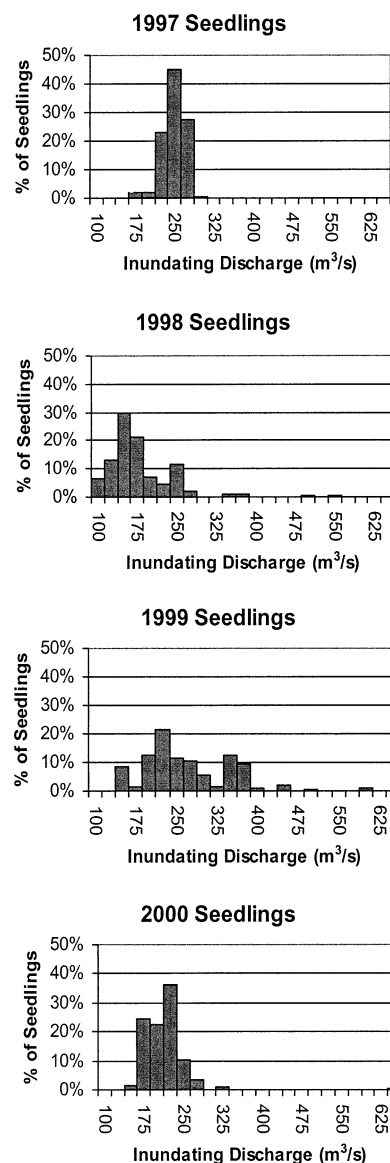


Figure 4. Distribution of new seedlings on transects (both random and seedling) in 1997–2000, relative to estimated inundating discharge (m³/s).

cohorts, the effect of year on species composition was weak (Cramer's $V = 0.09$, 0.17 , and 0.12 for 1997, 1998, and 1999 cohorts, respectively) and the identity of the most abundant species did not change. Mortality over winter and in subsequent erosive flows seemed to be relatively non-selective across species, although in some cohorts there was evidence for increases in rel-

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seeds) and the thinner bar line indicates earliest to latest dispersal dates. Dispersal intervals for 1997 and 1998 were estimated, based on a composite of the 1999 and 2000 observations. The horizontal line indicates the discharge (390 m³/s) above which >90% of the sandbar quadrats in 1998 would have been inundated.

Table 2. Total numbers of new seedlings and resampled demography plots containing new seedlings before and after summer flow pulses in 1998 and 1999.

Year	Species	Plots with Seedlings		Seedling Totals	
		Pre-flood	Post-flood	Pre-flood	Post-flood
1998	<i>Acer saccharinum</i>	13	5	95	17 (4)**
	<i>Betula nigra</i>	7	3	116	29 (12)**
	<i>Populus deltoides</i>	1	1	1	1
	<i>Salix exigua</i>	1	0	2	0
	<i>Salix nigra</i>	4	2	12	2 (1)**
	Other	0	0	0	0
	Total	16	9	226	49 (18)**
1999	<i>Acer saccharinum</i>	14	4	89	16
	<i>Betula nigra</i>	12	0	126	0
	<i>Populus deltoides</i>	11	0	56	0
	<i>Salix exigua</i>	3	1	4	1
	<i>Salix nigra</i>	17	1	190	1
	Other	3	0	5	0
	Total	23	6	470	18

** Seedling numbers increased on some plots due to establishment after pre-flood sampling. Numbers in parentheses indicate maximum numbers of seedlings that may have been survivors from pre-flood sampling.

ative abundance for *Salix* spp. or *Acer* (1998 cohort) and decreases for *Betula* (1997 and 1998 cohorts) with time. Overwinter mortality across species was greatest for the 1998 cohort, at 88%, and lowest for the 1999 cohort, at 33% (Figure 6). Higher mortality rates for the 1998 cohort may have been related to the low mean elevation of seedlings in the riverbed (Figure 4), followed by moderate spring peak flows in 1999 (Figures 3c). The particularly low mortality rate for the 1999 cohort occurred over a winter with relatively low, stable flows (Figure 3c) and with seedlings distributed at higher plot elevations (higher inundating discharges) than in other years (Figure 4). Seedlings from prior year cohorts (2nd year seedlings) also experienced high mortality during the mid-summer flow pulses in 1998 (77%) and 1999 (48%) and moderate mortality (30%) during summer of 2000 (Figure 6). The proportion of seedlings surviving after one full year was 47% for the 1999 cohort and only 6% for the 1997 and 1998 cohorts (Figure 6).

DISCUSSION

Across the four years of the study (1997–2000), the magnitude and timing of flows during the growing season influenced the species composition, elevation distribution, and density of each year's seedling recruitment. Several factors may have had important influences on cohort composition and density. First, periods

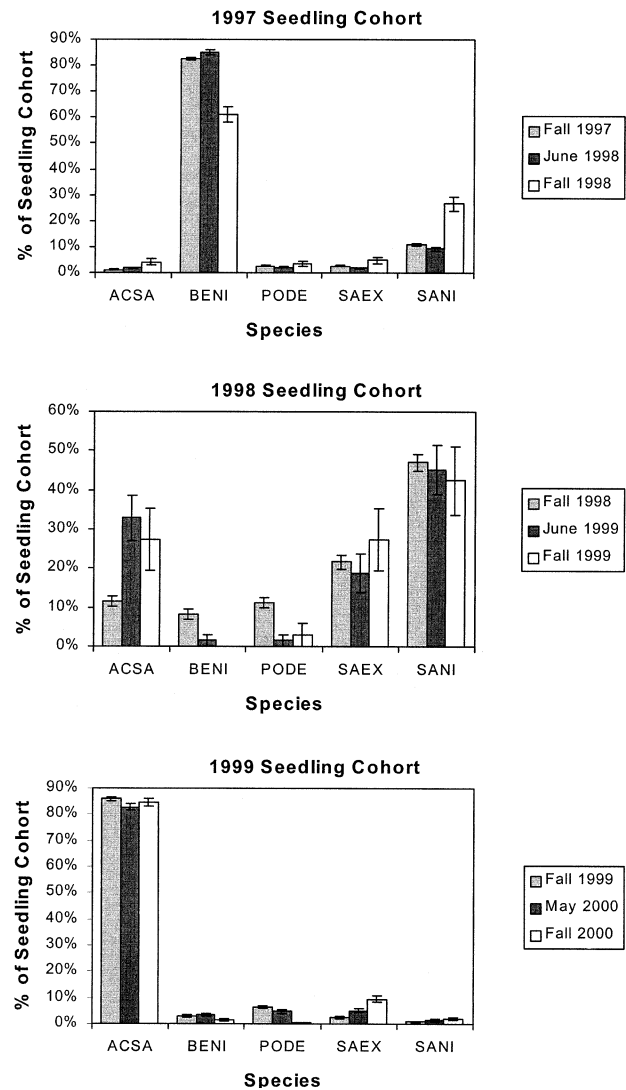


Figure 5. Changes in species composition (proportion and standard error) on demography plots of 1997, 1998, and 1999 seedling cohorts during the first year after establishment. Species codes are as follows: ACSA = *Acer saccharinum*, BENI = *Betula nigra*, PODE = *Populus deltoides*, SAEX = *Salix exigua*, SANI = *Salix nigra*. Standard errors are based on the equation: $SE = [(p*(1 - p)/(n - 1))^{0.5}]$, where p = proportion of the cohort composed of a given species, and n = total number of seedlings in the cohort (Zar 1984).

of high flow may have prevented germination and establishment of some species by covering suitable recruitment sites (open, bare sediment bars) during the time that the seeds were being dispersed. Second, summer peak flows caused high mortality of newly germinated and older seedlings, presumably by the combined effects of erosion from high shear stress and anoxia from prolonged inundation (Friedman and Auble 1999). The timing of seedling establishment, however, may influence stress-induced mortality, with vul-

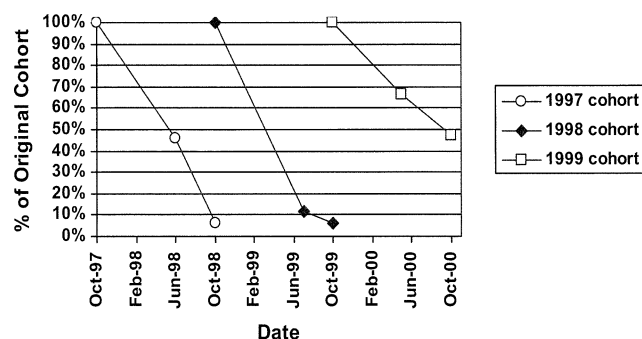


Figure 6. Changes in relative seedling numbers (% of original total) on demography plots for 1997, 1998, and 1999 seedling cohorts during the first year after establishment.

nerability to environmental stress often decreasing with seedling age (Streng et al. 1989, Jones et al. 1994). In 1999, the earlier dispersal date of *Acer* may have given its seedlings a head start of one to three weeks in seedling growth relative to the other species. *Acer* dispersal also coincided with the receding limb of the mid-May peak flow in 1999 (Figure 3c). Greater seedling age, and possibly higher establishment elevation, of *Acer* may in part explain its lower mortality rates and the shift in new seedling dominance from *Betula*, *Populus*, and *Salix nigra* to *Acer* after the flow pulses in July of 1999 (Table 2, Figure 3). Third, differences among species in the breadth of the dispersal period may have influenced their relative sensitivities to summer pulse flows. Species with a wide dispersal period (e.g., *Salix exigua*) may be more buffered from the effects of unfavorable environmental conditions at a particular time, whereas species with a more concentrated dispersal peak (e.g., *Acer saccharinum* or *Betula nigra*) may be more vulnerable to short-duration stress or disturbance, dominating the cohort in years with suitable flows but being virtually absent if unsuitable flows occur during that specific period. Finally, variability among years in both the size of the seed crop and the dispersal period for a given species may also have influenced recruitment success. The paucity of *Acer* recruitment in 2000 may have been jointly linked to unsuitable flows (Figure 3) and to a seed crop failure.

Although growing season flow pulses appeared to influence species composition, the strongest effects of the 1998 and 1999 growing season flow pulses were to reduce seedling densities. For most species, densities of new seedlings on seedling transects were substantially greater in 1997 than all other years (Table 1b), with low overall seedling densities in the three years with growing season flow pulses (1998–2000). On seedling transects, *Salix nigra* seedling densities were significantly greater in 1997 than in 1998, despite the fact that black willow constituted a minor part of

the cohort in 1997 (11%) and was the dominant species, at 39% of the cohort, in 1998 (Table 1b,d). *Salix exigua* densities did not differ significantly between 1997 and 2000, but this species made up only 2% of the 1997 cohort versus 71% in 2000. For *Acer saccharinum*, seedling transect densities were significantly greater in 1997 than 1999, even though maple made up 89% of the cohort in 1999 and only 1% of all seedlings sampled in 1997. Thus, proportional dominance of a cohort does not necessarily correspond to a strong recruitment year for a given species.

Because of the small sample size (only 34 quadrats over 12 sandbars) and different protocol employed for transect placement, comparisons with the estimate of seedling density on the 1997 seedling transects should be treated with caution. The absence of random transect sampling precludes estimation of true seedling densities throughout the study reach in 1997. The seedling transect data for 1997 and the other years represent seedling densities within or in the vicinity of seedling patches and, thus, are not unbiased estimates of seedling densities over the entire study reach. However, differences in density estimates on seedling transects were very large between 1997 and the other years (nearly two orders of magnitude), and densities were greater on demography plots than in any other year (but differences with 1999 not significant) (Table 1). Field observations also suggest that the 1997 cohort was still well-represented among surviving seedlings on river sandbars at the end of the study in 2000.

Conditions over the year following establishment strongly influenced seedling densities but did not strongly alter seedling composition, at least not in terms of dominant species. Patterns of species composition established during the first growing season persisted at least through the following year. However, mortality from winter and spring flows and from summer peak flows in the following year reduced seedling densities of the 1997 and 1998 cohorts by 94% (Figure 6). Thus, even if initial seedling densities are high, mortality within the first or subsequent years may virtually eliminate the contribution of that cohort to long-term successional trajectories.

Several years of suitable flow conditions, until seedlings or saplings become relatively resistant to erosive flows, may be necessary for long-term persistence of a cohort. Over longer time scales, traits other than dispersal timing may exert important influences on relative survival of different species of seedlings and saplings. Differences in vegetative reproduction, sprouting (Barnes 1985), inundation tolerance (Hosner 1960, Loucks 1987, Amlin and Rood 2001), and tolerance to burial may influence the relative success of species exposed to flooding; rooting depth and photosynthetic physiology may influence responses to drought (Coo-

per et al. 1999, Horton and Clark 2001, Amlin and Rood 2002); and these factors and shade tolerance may influence the outcomes of competitive interactions among seedlings. For the willows, particularly *Salix exigua*, the ability to reproduce vegetatively by root or stem sprouts (Barnes 1985, Krasny et al. 1988, Burns and Honkala 1990, Craig and Malanson 1993) and a large tolerance for inundation (Amlin and Rood 2001) may favor their survival and eventual dominance on sites with high disturbance frequency and intensity (Karrenberg et al. 2002). Thus, the influence of variation in flow timing on long-term species composition in the system remains unclear, as does the degree to which tree population dynamics are influenced by conditions during the first growing season (dispersal, germination, and growth) vs. those in subsequent years (ice scour, erosion or burial from floods, drought mortality).

Although it is difficult to compare across studies because of differences in species, environment, and sampling procedure, measured densities in the 1998–2000 cohorts (<0.1 seedlings/m² on random plots, 0.11 – 0.26 seedlings/m² on seedling transects) seem low compared to many other studies of seedling demography in riparian systems. The 1997 densities (33 seedlings/m² on seedling transects) seem more in line with other studies, at least with those that concentrated sampling within seedling patches (Stromberg 1997, Auble and Scott 1998, Rood et al. 1998, Cooper et al. 1999, Rood and Mahoney 2000, Kalischuk et al. 2001). Seedling densities in most of these studies ranged from 5 to 100 seedlings/m², with sometimes much greater local densities (e.g., Rood et al. 1998, Cooper et al. 1999). Most of these other studies were in the semi-arid western United States or Canada and were focused on *Populus* or *Salix* species. Extremely high local densities have also been observed in the Upper Midwest, with nearly 20,000 first-year seedlings of *Betula nigra* counted on one 3.3 m² plot along the Mississippi River in Wisconsin (Koevenig 1976).

The results of this study are similar to those of Johnson (1994, 1997, 2000) on the braided Platte River, in that mid-season flow pulses had an important impact on cohort species composition and overall seedling density. Mortality rates observed from summer pulse flows on the Platte ranged from 95 to 100% of new germinants (mostly *Populus* and *Salix*), similar to the $>90\%$ mortality rates estimated for Wisconsin River seedlings from the 1998 and 1999 summer pulse flows. On the Platte, winter mortality rates, probably related to scour by ice drives, were also high, usually exceeding 50% for first-year seedlings and occasionally as high as 85%. Large spring peak flows sometimes caused substantial mortality of second-year seedlings as well. In some years, a combination of high mortality

in consecutive summers and winters virtually eliminated the entire cohort (Johnson 2000).

First-year mortality rates in the range found on the Platte and Wisconsin were also common in other studies of riparian seedling demography (commonly 70–100%), although in many other systems, drought seemed to be the dominant mortality factor (Cooper et al. 1999, studies cited in Karrenberg et al. 2002). Streng et al. (1989) also found high mortality rates associated with post-germination flood events in southern bottomland forests, especially for light-seeded pioneer species (e.g., *Acer rubrum*), with timing of seedling emergence also influencing mortality rate. She also found that periods of high flooding frequency led to shifts in species composition to larger-seeded species, whereas light-seeded pioneers increased in years with few floods.

Only a portion of the full range of conditions that influence seedling establishment and vegetation succession on the Wisconsin River was observed in the four years of this study. None of these years had prolonged drought or large, erosive floods. The incidence of mid-growing season flow pulses, however, has been quite common over the last 30 years and emerged as a strong limiting factor in a simulation model of recruitment for the same system (Dixon 2001). Thus, interactions between species dispersal phenology and flow timing may have had an influence on historic recruitment dynamics of riparian trees on the Wisconsin River. This sensitivity of seedling recruitment to mid-eason flow patterns suggests that both dam operation and the incidence of summer rainstorms could strongly influence species composition or the occurrence of successful seedling establishment at all.

Implications

These results, as well as those from other studies, suggest that riparian vegetation dynamics (tree recruitment and the composition and age structure of riparian communities) could function as an indicator of the cumulative or ongoing impacts of environmental changes, such as river regulation, climatic trends, and land-use change, that cause shifts in flow regime (Decamps et al. 1988, Decamps 1993, Nilsson and Berggren 2000). In western North America, the recruitment of cottonwood species (*Populus*) has been shown to be highly sensitive to flow timing and magnitude (Fenner et al. 1985, Rood and Mahoney 1990, Scott et al. 1997, Mahoney and Rood 1998). In the upper Midwest, dam-induced changes in flow regime (flow stabilization, increased duration of flooding, reduced low flow periods, reduced geomorphic activity) may have contributed to large increases in silver maple (*Acer saccharinum*) since pre-settlement times, relative to other

early successional species (*Populus deltoides*, *Betula nigra*, and *Salix nigra*) that are more dependent on bare mineral soils or are less tolerant of long duration flooding (Nelson et al. 1994, Barnes 1997, Yin et al. 1997, Knutson and Klaas 1998). Changes in historic climate and land use may also have influenced species composition of riparian trees, with snowmelt and spring floods in the Upper Mississippi River basin now occurring earlier than historically, possibly due to conversion to agriculture (Knox 2001). Given the strong effect of summer floods on the density and composition of seedling cohorts in this study, future shifts in climate that alter the relative frequency of snowmelt and summer thunderstorm-induced floods (Knox 2000) could have a strong effect on riparian vegetation composition and dynamics.

The sensitivity of seedling recruitment to flow pattern suggests that human management of flows may also be used in a prescriptive fashion to intentionally manage or restore riparian systems (Rood and Mahoney 1990, Johnson 1994, Rood et al. 1998, Schmidt et al. 1998). For management of riparian vegetation, the regeneration niche (including recruitment phenology) of the species of interest must be considered when designing flow prescriptions. In addition to managing spring flood magnitude, timing, and recession rate (Mahoney and Rood 1998, Rood et al. 1998), summer pulse flows may be used to inhibit (or remove) vegetation establishment in general (Johnson 1994), or inhibit or favor particular species (Gladwin and Roelle 1998). Prescribed drawdowns to expose mudflats or sediment bars to colonization may be a tool to use in systems like the upper Mississippi where stabilized flows have reduced recruitment of pioneer species (Knutson and Klaas 1998). Under all of these scenarios, an understanding of how vegetation recruitment is linked to flow may be critical for using riparian vegetation as an indicator of change and for restoring (or managing) structure and function in riparian ecosystems.

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