

## SIMULATED RECRUITMENT OF RIPARIAN TREES AND SHRUBS UNDER NATURAL AND REGULATED FLOW REGIMES ON THE WISCONSIN RIVER, USA

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### ABSTRACT

Models that link ecological responses to hydrologic changes are important for assessing the effects of flow regulation on aquatic and riparian ecosystems. Based on the Recruitment Box Model, a graphical model used to prescribe environmental flows for cottonwood (*Populus* spp.) recruitment, we designed a simulation model to represent the influence of river flow dynamics on seedling recruitment of riparian pioneer woody plants. The model simulates the influence of temporal patterns of river stage on dispersal, germination, initial recruitment and over-winter survival of first-year seedlings of riparian pioneer shrubs and trees. We used the model to simulate seedling recruitment patterns for five species (*Acer saccharinum*, *Betula nigra*, *Populus deltoides*, *Salix nigra* and *Salix exigua*) on the Wisconsin River (Wisconsin, USA) under three flow scenarios: historic (1935–2002), simulated natural (1915–1975) and simulated regulated flows (1915–1975). Simulation results agreed well with field-observed relative differences among years (1997–2000) in seedling densities for the five focal species. Simulated successful recruitment years were highly synchronous among species, but species differed in their sensitivity to flows at different times during the growing season, consistent with among-species differences in seed dispersal timing. Comparison of simulated natural and regulated flows for 1915–1975 showed that flow regulation decreased monthly flow variability, increased late summer to winter baseflow and reduced the magnitude of spring peaks. Simulated recruitment and over-winter survival of tree seedlings of all species was enhanced under the regulated flow scenario, likely due to increased summer baseflow and reductions in peak flood magnitude. Our analyses show the utility of extending the Recruitment Box Model to include multiple species of riparian shrubs and trees, and the effects of post-colonization flows on their recruitment success. However, some key functional relationships between flow patterns and woody seedling demography (e.g. shear stress thresholds for seedling mortality) have not been adequately quantified and merit further study. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: *Acer saccharinum*; *Betula nigra*; *Populus deltoides*; *Salix nigra*; *Salix exigua*; dams; seedling establishment; simulation modelling

### INTRODUCTION

As ecotones between terrestrial and aquatic systems, riparian areas may respond strongly to environmental change (Decamps, 1993; Grimm *et al.*, 1997), functioning as indicators of change in higher-level variables that influence river flow, such as flow regulation by dams, changes in watershed land cover and hydrology and climatic change. The flow regime is the ‘master variable’ influencing ecological dynamics in rivers and their riparian ecosystems (Poff *et al.*, 1997). Regeneration of many woody riparian plants is closely linked with flow, with the temporal pattern of high and low flows particularly important for influencing plant establishment (Fenner *et al.*, 1985; Stromberg *et al.*, 1991, 1993; Johnson, 1994; Auble and Scott, 1998; Dixon, 2003; Lytle and Merritt, 2004).

Of the external stressors influencing riparian habitats, flow regulation may be the most pervasive, with the majority of the world’s large rivers influenced by dams (Nilsson *et al.*, 2005). Dams often result in hydrologic ‘fragmentation’ or disconnection of the fluvial system, decoupling the affected river reach and its biotic systems

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from its natural flow regime and causing spatial disconnection longitudinally of upstream and downstream reaches, and laterally of the river from its floodplain (Stanford *et al.*, 1996; Gergel *et al.*, 2002). Because dams are often managed to ameliorate climate-induced extremes in river discharge (Gleick, 1990), dams may also decouple the natural link between local flows and regional climate or accentuate the role of local, short-term climatic events versus events occurring over the whole watershed on a seasonal or annual basis (Johnson, 1994).

A number of approaches have been used to quantify the impact of river regulation on the flow regime (Richter *et al.*, 1996, 1997) and project its influence on riparian vegetation (Franz and Bazzaz, 1977; Pearlstine *et al.*, 1985; Johnson, 1992; Auble *et al.*, 1994; Richter and Richter, 2000; Gergel *et al.*, 2002). One of the more successful of these, the Recruitment Box Model (Mahoney and Rood, 1998; Rood *et al.*, 2005), is a simple graphical technique that represents the characteristics of a river hydrograph (magnitude, timing, rate of recession) that are ideal for establishment of seedlings of cottonwood (*Populus* sp.). This model has been used successfully to prescribe flow releases suitable for cottonwood regeneration on regulated rivers in Canada (Rood *et al.*, 1998; Rood and Mahoney, 2000) and on the Truckee River in the western United States (Rood *et al.*, 2003). The model may also be amenable for representing recruitment dynamics of multiple riparian tree species, by incorporating differences in dispersal timing (Shafroth *et al.*, 1998), root growth rates and tolerance to water table decline (Horton and Clark, 2001; Amlin and Rood, 2002). The basic version of the model, however, represents only the effect of the spring flood on germination and initial seedling growth; the effects of subsequent flows on seedling growth and survival are not represented explicitly.

Using the Recruitment Box Model as a foundation, we developed a rule-based simulation model to simulate seedling establishment and survival of several species of pioneer riparian trees under historic, simulated natural and simulated regulated flow regimes on the Wisconsin River, Wisconsin, USA. Our goals were (1) to build and test a model prototype that could be adapted to different riparian shrub and tree species and different rivers, (2) to determine the characteristics of the flow regime that most strongly influence recruitment success of five pioneer riparian tree and shrub species and (3) to use the model to assess the influence that river regulation has had on riparian vegetation establishment on the Wisconsin River.

## METHODS

### *Study area*

We studied a 16-km reach of the Wisconsin River between the Wisconsin Dells and the town of Portage, in Sauk and Columbia Counties, Wisconsin, USA. (Figure 1). The river channel has an island-braided morphology (Schumm, 1985; Knighton, 1998), with a high width-to-depth ratio, numerous mid-channel islands and large sandbars. The gradient of the channel is low (approximately 0.3 m/km), flowing through the lake plain of former glacial Lake Wisconsin (Clayton and Attig, 1989). Flow is modified by a series of upstream dams and reservoirs operated for power generation and water level stabilization. Although extensive alteration of flows occurred before 1900, much of the reduction in peak flows (10–20% at Wisconsin Dells, Krug and House, 1980) was due to the increase in storage capacity in the system (Figure 2) from 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 years. Much of the length of the study reach is bounded by levees on the north and south sides of the river, generally offset from the riverbank into the floodplain by 50–500 m. Because of the set-back position of the levees, however, their influence on flood heights and channel shear stress are likely minimal (Gergel *et al.*, 2002).

Floodplain vegetation includes areas of oak savanna, sedge meadows, and low and mixed floodplain forest (Ware, 1955; Liegel, 1988; Turner *et al.*, 2004). Silver maple (*Acer saccharinum* L.) and river birch (*Betula nigra* L.), and to a lesser degree cottonwood (*Populus deltoides* Bartr.) and black willow (*Salix nigra* Marsh.), dominate the swales and other areas of low floodplain forest, particularly areas that have converted from river channel to woodland since the 1930s. These species, along with sandbar willow (*Salix exigua* Nutt. ssp. *interior* (Rowlee) Cronq.), are the dominant species colonizing young sandbars and thus were the focal species in this study.

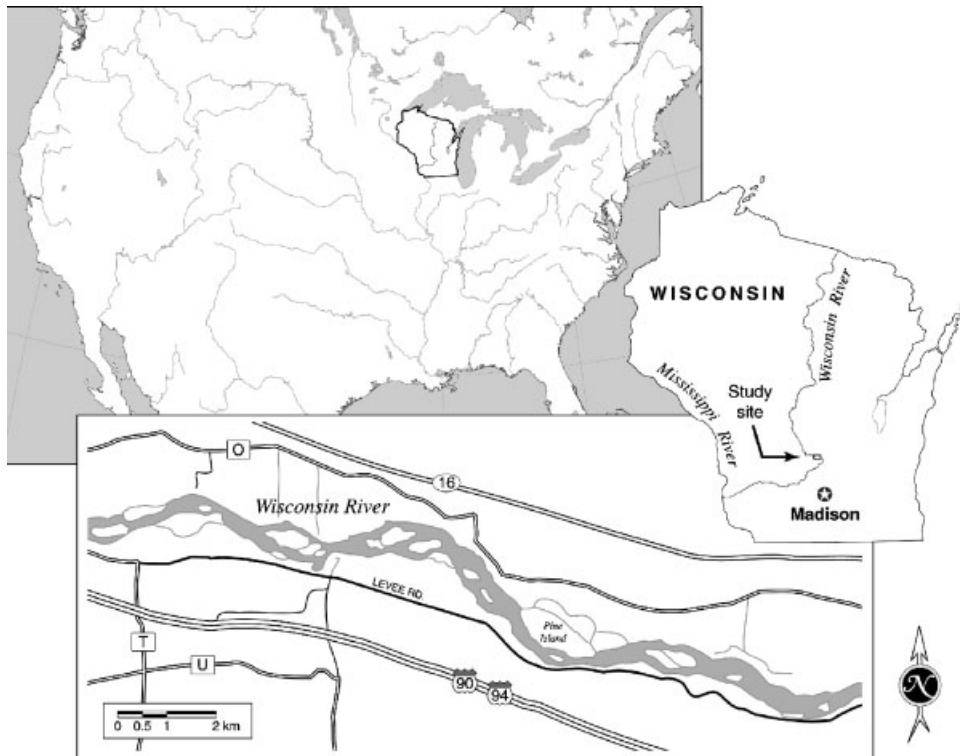


Figure 1. Map of study area (reproduced from Dixon et al., 2002)

#### *Flow, climate and ice data*

Historic daily discharge data were obtained from the Wisconsin Dells gauge (USGS # 05404000) for 1935–2003. The average daily flow over the period of record is  $195 \text{ m}^3/\text{s}$ , with the maximum and minimum daily flows on record at  $2044 \text{ m}^3/\text{s}$  (14 September 1938) and  $30 \text{ m}^3/\text{s}$  (19 August 1936), respectively. The average annual peak flow is

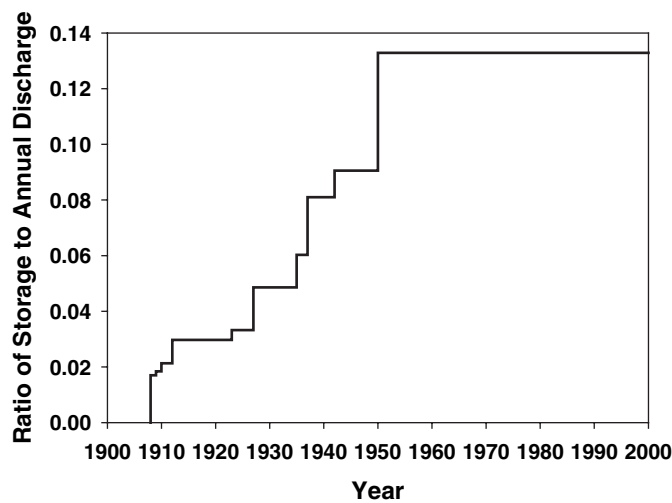


Figure 2. Cumulative changes in reservoir storage capacity on the Wisconsin River, upstream of Wisconsin Dells, Wisconsin since 1908, relative to annual average discharge (1935–2002) at Wisconsin Dells

approximately 1020 m<sup>3</sup>/s. Annual peak flows 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.

Scenarios of regulated and unregulated flow were obtained from the output of a flow-routing model developed by Krug and House (1980) for the Wisconsin River at Wisconsin Dells, for the period of 1915–1975. The unregulated or ‘natural’ scenario simulates flow without flow impoundment by upstream reservoirs. The ‘regulated’ scenario simulates daily and peak flows that would have occurred had the present number and storage capacity of dams been in existence throughout the entire record. The original model outputs for both scenarios were obtained from William Krug at the USGS in Middleton, Wisconsin. The model was not rerun for flows after 1976 because of the absence of data on reservoir operations and dam releases needed to estimate the influence of the dams on contemporary river flow (William Krug, personal communication). Daily mean flows were used for all model inputs.

We obtained data on historic ice conditions for the Wisconsin River at Portage, Wisconsin, based on daily field observations made at a National Weather Service wire gauge by multiple observers from 1945 to 2003. We transcribed data from copies of original field data sheets, on file in the Wisconsin State Climatologists Office at the University of Wisconsin, on which observers characterized the ice conditions in the vicinity of the gauge into one of several categories. We aggregated all ice conditions into ice versus no ice present.

Ice data were missing for individual months or days (6% of days in November to March, 1945–2002) within the historic record and no data were available prior to November 1945. For months or days with missing data after 1983, we examined USGS gauge records at Wisconsin Dells for days in which discharge estimates were noted as potentially ice affected. Using daily climatic data for the period of record at the Portage (NWS 476718) and Wisconsin Dells (NWS 479319) weather stations, we assumed that ice cover was present if those days of missing ice data corresponded to intervals with cold air temperatures (cumulative 15- and 25-day mean temperature at or below 0°C) and relatively stable flows. For other intervals with missing data (including the entire interval from 1915 to 1945), we calculated 25- and 15-day running means of daily mean temperature at the Portage weather station to estimate the daily presence or absence of ice cover for November through March. For dates with missing weather data at Portage, we estimated temperature based on a linear regression between Wisconsin Dells and Portage winter daily temperature records. For ice to be considered present, both the 25- and 15-day running mean temperatures had to be 0°C or lower. Using these rules correctly classified presence and absence of ice on 88.6% of the 8126 winter days with ice records, with 89.9% of actual ice days and 85.8% of non-ice days correctly classified, for an overall kappa value of 0.74.

#### *Sandbar topography data and hydrologic modelling*

Seedling and topographic data were obtained by extensive surveys of seedling distribution and sandbar elevation during 1998. Seedling densities and topography were surveyed on 30 sandbars spread throughout the study area, with three belt transects per sandbar. Elevations were standardized relative to water level at a discharge of 99 m<sup>3</sup>/s (see Dixon *et al.*, 2002 for details).

We used HEC-RAS software (Hydrologic Engineering Center, 1998) to model the relationship between simulated (and historic) daily discharge and hydrologic variables, particularly river stage and energy slope, at a series of cross-sections spread at 0.8-km intervals throughout the study reach. HEC-RAS simulates 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*) at each cross-section (A. Lulloff, personal communication). We used estimated stage–discharge relationships for a National Weather Service gauge near the downstream end of the study area and discharge estimates at the Wisconsin Dells gauge, upstream of the study area, to provide boundary conditions for the model (Dixon *et al.*, 2002).

Stage-discharge and energy slope estimates for the 30 sampled sandbars were based on the nearest river cross-section or on the average of the nearest upstream and downstream cross-section. For the seedling model, equations for converting river discharge to energy slope and river stage at each sandbar were derived by polynomial regression of stage-discharge and energy slope output from HEC-RAS model runs (Dixon *et al.*, 2002). These regression equations were used to determine the water surface elevation on every day in the flow record at each sandbar (and

relative to each 1-m transect segment). For transect segments (plots) that were modelled as inundated on a given day, the flow depth and energy slope were used to compute estimates of shear stress.

#### *Seedling recruitment simulation model*

We constructed a rule-based computer model in FORTRAN (GNU FORTRAN, G77) to simulate plot-level establishment and survival of riparian tree seedlings, given the plot elevation, stage–discharge relationship at the channel cross-section, the date of the year and the actual or simulated flow conditions on that day (Table I, Figure 3). The model contains functions for dispersal of seeds by wind and water, deposition of seeds, germination, survival during the first growing season (1 May to 30 September), and survival during the subsequent non-growing season (1 October to 30 April of the following year). A new seedling cohort is simulated beginning with 1 May of each year. Details of model structure and parameter choice are provided below.

#### *Dispersal function*

Temporal patterns of seed dispersal were simulated solely as a function of date, based on observed dispersal phenology within the study reach. Dispersal curves for each of the five species (Figure 4) were constructed by manually fitting halves of two different normal curves (same mean, different standard deviations) to field data on seed dispersal dates and seed numbers from 1999 to 2000 (Dixon, 2003). We assumed a maximum of 100 seeds per day during the period of peak dispersal for each 1 m segment on each study area transect (Table II). We made peak dispersal equal for all species because we did not have rigorous estimates of actual seedfall per m<sup>2</sup> in the study area, seed viability or relative differences in the number of seeds dispersed by the different species. Hence, differences in relative recruitment success of different species could not be compared.

#### *Seed deposition function*

Daily seed deposition rates for a given plot were based on the simulated availability of seeds, the height of the plot relative to river level on that day and the river stage on the previous day (Table Ij). We assumed that most dispersal occurred via hydrochory, with seed deposition concentrated close to river level and declining with higher plot elevations. We assumed that 100% of available seeds (up to 100 per day) were deposited on plots that had been inundated on the previous day (to simulate the process of seed deposition during receding flows), 20% (up to 20 seeds per day) on plots 0.0–0.2 m above river stage on a given day and 10% (up to 10 seeds per day) on plots higher than 20 cm above river stage (Table Ij). We assumed no deposition of seeds on plots that were below river stage (inundated) on the day following dispersal. Both the number of seeds dispersed and the number deposited per plot were simulated as integers, so that values less than one were assumed to be zero.

#### *Germination function*

Germination of deposited seeds (Table Ik) was modelled as an inverse function of the number of consecutive days (starting from 1 May) that the plot had been dry (not inundated). We assumed that germination followed seed deposition by 1 day (and thus seed dispersal by 2 days). We further assumed that no germination could occur under water, with inundation washing away all seeds deposited on the previous day on a given plot. Because we did not have estimates of seed viability, we assumed that all seeds were potentially viable. As with densities of dispersed seeds, estimates of germinated numbers of seeds on each plot were truncated to an integer.

#### *Seedling survival function*

Seedling survival was modelled as a function of several factors, including plot age (number of days seedlings were present on plot), tractive shear stress exerted by higher flows (scour), river level relative to simulated root depth (drought) and the number of consecutive days that the plot was underwater (inundation) (Table Im, l). During the first growing season (1 May to 30 September), daily seedling survival was modelled as a function of drought, excessive inundation and scour (Table II). During the non-growing season (1 October to 30 April) survival was

Table I. Documentation of model equations, variables and parameters

Equations (and sources)	Variables	Parameters (and sources)	Descriptions
a. Calculation of shear stress $T = pgRS$ Friedman and Auble (1999) Knighton (1998)	$T$ = Shear stress ( $N/m^2$ ) $g$ = Acceleration due to gravity ( $m/s^2$ ) $p$ = Density of water ( $kg/m^3$ ) $R$ = Hydraulic radius (depth of flow) (m) $S$ = Slope or river energy gradient (m/m)	$g = 9.807$ $p = 1000$	
b. Critical shear for sediment movement $T_{sand} = kg(p_s - p)d50$ Friedman and Auble (1999) Knighton (1998)	$T_{sand}$ = Critical shear stress to move medium sand ( $N/m^2$ ) $k$ = Shield's parameter $g$ = Acceleration due to gravity ( $m/s^2$ ) $p_s$ = Density of mineral soil ( $kg/m^3$ ) $p$ = Density of water ( $kg/m^3$ ) $d50$ = Median particle diameter for sediment (m)	$k = 0.045$ $g = 9.807$ $p_s = 2650$ $p = 1000$ $d50 = 0.00044$ Friedman and Auble (1999)	$d50$ is from field samples, used intermediate Shield's parameter value
c. Critical shear for vegetation mortality $T_{veg} = T_{sand} + r(\text{age})$	$T_{sand}$ = Critical shear stress to move medium sand ( $N/m^2$ ) $T_{veg}$ = Critical shear stress at which seedling mortality is 100% ( $N/m^2$ ) $r$ = Rate of increase of critical shear stress with seedling age ( $N/m^2/\text{day}$ ) age = Number of days seedlings present on plot	$T_{sand} = 0.3$ $r = 0.076$ max ( $T_{veg}$ ) = 7	Equation and parameters based on field data: 100% mortality of 30 day seedlings at $T = 2.5 N/m^2$ , 100% mortality of older seedlings at $7 N/m^2$
d. Scour index $I_{scour} = ((T_{veg}^a - T_{veg}^{1/b})/T_{veg})$	$I_{scour}$ = Index of seedling mortality from scour $T_{veg}$ = Critical shear stress at which seedling mortality is 100% $T$ = Shear stress $a$ = Exponents to determine curve shape	$a = 1$	Equation and exponent ( $a$ ) based on hypothesized relationship and curve shape and calibrated to 1997–2000 field data.
e. Inundation index $I_{inund} = (((wday)_{max}^b - wday) / (wday)_{max}^b) / (wday)_{max}$	$I_{inund}$ = Index of mortality from inundation $wday$ = Consecutive days of inundation > 0.1 m deep $wday_{max}$ = Threshold consecutive inundation days $b$ = Exponents to determine curve shape	$wday_{max} = 15$ or 30 Hosner (1960); Loucks (1987) $b = 2$	Equation and exponent ( $b$ ) based on hypothesized relationship and curve shape and calibrated to 1997–2000 field data. $wday_{max}$ is only loosely based on cited sources

<p>f. Depth of capillary fringe  <math>D_{\text{cap}} = \text{Elev}_{\text{plot}} - (\text{stage} + \text{cap})</math></p>	<p>cap = 0.50            Mahoney and Rood (1998)</p>	<p><math>D_{\text{cap}}</math> = Depth to capillary fringe  <math>\text{Elev}_{\text{plot}}</math> = Elevation of plot above river stage at flow of 99 m<sup>3</sup>/s            stage = Daily river stage above 99 m<sup>3</sup>/s            cap = Width of capillary fringe above river stage (m)</p>	<p>Capillary fringe estimate for sand</p>
<p>g. Drought index  <math>I_{\text{drought}} = (D_{\text{cap}} - D_{\text{root}}) / D_{\text{cap}}</math></p>	<p><math>I_{\text{drought}} = 0</math> if <math>D_{\text{root}} &gt; D_{\text{cap}}</math></p>	<p><math>I_{\text{drought}}</math> = Index of mortality from drought  <math>D_{\text{cap}}</math> = Depth to capillary fringe  <math>D_{\text{root}}</math> = Depth of root growth</p>	<p>Hypothesized relationship</p>
<p>h. Root depth  <math>D_{\text{root}} = \text{age} \times \text{rootgro}</math></p>	<p>rootgro = 0.01  <math>\text{Max}(D_{\text{root}}) = 0.6</math> m            Mahoney and Rood (1998)</p>	<p><math>D_{\text{root}}</math> = Depth of root growth            age = Age of seedlings (days)            rootgro = Daily rate of root growth (m/day)</p>	<p>Hypothesized relationships using maximum growth rate and average 1st year rooting depth of cottonwood</p>
<p>i. Seed release and dispersal  <math>\text{seeds} = \text{seeds}_{\text{max}} \times \text{EXP}(-0.5 \times (\text{day} - \text{day}_{\text{max}})^2) / 2 \times \text{SD}_{\text{days}}</math>            Auble and Scott (1998)</p>	<p><math>\text{seeds}_{\text{max}} = 100</math>  <math>\text{day}_{\text{max}}</math>  <math>\text{SD}_{\text{days}}</math></p>	<p>seeds = Daily number of seeds dispersed  <math>\text{seeds}_{\text{max}}</math> = Peak daily number of seeds dispersed            day = Day of the growing season            (1 May = 1, 30 September = 153)  <math>\text{day}_{\text{max}}</math> = Growing season day of peak dispersal  <math>\text{SD}_{\text{days}}</math> = Standard deviation of dispersal interval</p>	<p>Parameters for individual species determined from field observations in 1999 and 2000</p>
<p>j. Seed deposition  <math>\text{depos} = \text{seeds}/x</math></p>	<p><math>x = 1</math> if lagstage &gt; <math>\text{Elev}_{\text{plot}}</math>  <math>x = 5</math> if <math>(\text{stage} - \text{Elev}_{\text{plot}} &lt; 0.2 \text{ m})</math>  <math>x = 10</math> if <math>(\text{stage} - \text{Elev}_{\text{plot}} &gt; 0.2 \text{ m})</math></p>	<p>depos = Daily number of seeds deposited on a plot            seeds = Daily number of seeds dispersed to a plot  <math>x</math> = Modifier of deposition based on plot elevation relative to stage and previous day's stage            stage = Water surface elevation of river (m)            lagstage = River stage the previous day (m)  <math>\text{Elev}_{\text{plot}}</math> = Plot elevation (m)</p>	<p>Hypothesized relationship and parameters, fit so that deposition is highest after receding flows and closer to the river stage</p>

(Continues)

Table I. (Continued)

Equations (and sources)	Variables	Parameters (and sources)	Descriptions
<p>k. Seed germination  <math>germ = 2depos/(dry + 1)</math></p>	<p>germ = Number of germinating seedlings  depos = Daily number of seeds deposited on plot  dry = Consecutive number of days that plot is not inundated</p>		Hypothesized relationship, based on higher germination rates on moist surfaces
<p>l. Seedling daily survival rate, growing season  <math>Surv_{sum} = I_{scour} I_{inund}(1 - I_{drought})</math></p>	<p><math>Surv_{sum}</math> = Growing season daily seedling survival  <math>I_{scour}</math> = Index of seedling survival in relation to scour  <math>I_{inund}</math> = Index of seedling survival in relation to inundation  <math>I_{drought}</math> = Index of seedling mortality due to drought</p>		Hypothesized relationships
<p>m. Seedling daily survival rate, non-growing season  <math>Surv_{win} = I_{scour} Ice\_Factor</math></p>	<p><math>Surv_{win}</math> = Non-growing season daily seedling survival  <math>I_{scour}</math> = Index of seedling survival in relation to scour  Ice_Factor = Influence of ice on scour mortality</p>	<p>Ice_Factor = 1 if no ice  Ice_Factor = 5 if ice present</p>	Hypothesized relationships. Ice influence is based on the assumption that ice cover substantially increases scour mortality



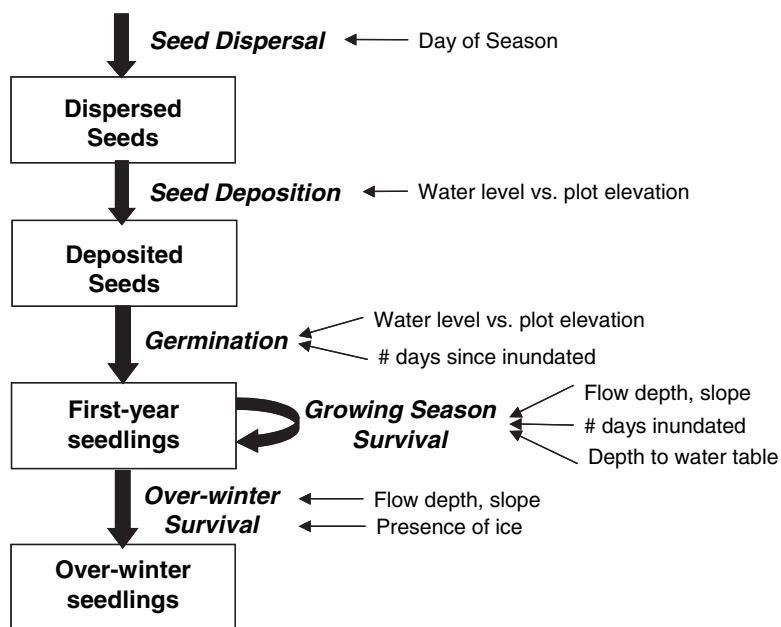


Figure 3. Flow chart of recruitment model structure and important variables

assumed to be only a function of scour from flowing water and/or ice (Table Im). All seedling numbers were reset to zero at the end of each simulation year (30 April), prior to simulation of a new cohort.

Drought mortality was modelled as a function of plant rooting depth relative to the range of capillary movement of water (the phreatic or vadose zone) above the river level. We assumed that the water table on a given day was equivalent to river stage, with the vadose zone extending 0.5 m above stage (Table If). Root growth was modelled as a linear function of seedling age (assumed 1 cm per day), up to a maximum first year root depth (0.6 m) (Table Ih). Mortality was modelled as a function of the difference between the plant rooting depth and the top of the capillary fringe, with zero drought mortality if roots intersected the capillary fringe (Table Ig).

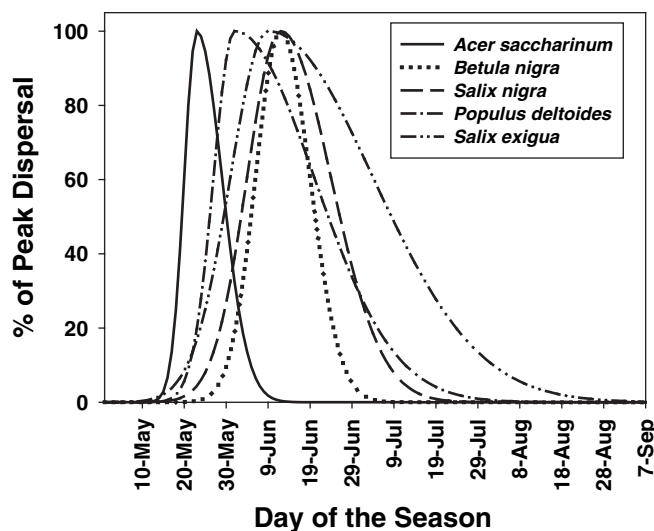


Figure 4. Model curves used to represent temporal patterns of seed dispersal for riparian tree and shrub species in seedling recruitment simulations

Table II. Life history parameters for tree and shrub species represented in the model

Species	Max seeds dispersed per plot, per day	Day of peak dispersal (day 1 = 1 May)	SD of dispersal interval before peak (days)	SD of dispersal interval after peak (days)	Rate of root growth (m/day)	Max 1st year rooting depth (m)	Max survivable inundation period (days)
<i>A. saccharinum</i>	100	23	3	6	0.01	0.6	30
<i>B. nigra</i>	100	43	6	7	0.01	0.6	15
<i>P. deltoides</i>	100	32	5	19	0.01	0.6	15
<i>S. nigra</i>	100	43	8	12	0.01	0.6	30
<i>S. exigua</i>	100	40	9	25	0.01	0.6	30

Flows that inundated plots were assumed to cause seedling mortality from anoxic conditions due to prolonged inundation (Table Ie) and from removal of seedlings by erosion (Table Id). The effect of each on survival was simulated using indices scaled from 0 to 1, relative to thresholds of maximum survivable inundation or scour, with 0 representing values equalling or exceeding the thresholds (100% mortality) and 1 representing no effects of inundation or scour (0% mortality). Seedling survival was modelled as the product of the inundation and scour indices (Table II).

The inundation index was a function of the number of consecutive days inundated, the age of the seedlings and a maximum number of days of inundation beyond which survival of seedlings was assumed to be zero (Table Ie). For these simulations, the maximum survivable inundation interval was assumed to vary by species (Table II) and seedling age. The shape of the function relating mortality to inundation was chosen to simulate little reduction in seedling survival until the number of consecutive days of inundation approached the 100% mortality threshold. We assumed that a plot was functionally inundated when the flow depth was at least 0.1 m.

The scour index was a function of seedling age and the tractive shear stress experienced at the plot from the flows on a given day (Table Id). As with the inundation index, the critical threshold (of shear stress) for 100% mortality was scaled according to seedling age (Table Ic). Seedlings at age 0 were assumed to suffer 100% mortality at a shear stress of  $0.3 \text{ N/m}^2$ , approximately the critical shear stress at which medium sand particles ( $d_{50} = 0.00044 \text{ m}$ , obtained from sediment samples in the study area) are moved by flowing water (Table Ib). Based on field data, we assumed that the critical shear stress necessary for complete seedling removal increased linearly with seedling age to  $2.5 \text{ N/m}^2$  for month-old seedlings and to a maximum of  $7 \text{ N/m}^2$  after about 3 months (88 days) of seedling growth. We simulated the effect of ice on seedling mortality by assuming that the presence of ice led to a fivefold decrease in seedling survival, for a given inundation depth and calculated shear stress value (Table Im).

Seedling numbers were updated on each day of the simulation for each plot, with new seedlings added by germination and removed by mortality. Plot age was based on the oldest seedlings remaining on the plot, even if new germinants were added. When only one seedling remained on a plot, seedling survival became probabilistic, with mortality values representing the probability of seedling removal. Because of this probabilistic component, we conducted 30 replicate runs for each model scenario and used the mean values of projected seedling numbers in our analyses.

To determine if model projections were consistent with seedling recruitment in the field, we compared model projections with relative densities of first-year seedling cohorts sampled in the field (1997–2000) and over-winter seedling mortality rates for 1997–1998, 1998–1999 and 1999–2000 (Dixon, 2003). We used relative seedling densities and over-winter mortality rates to determine which sets of model parameter settings provided the best fit to observed patterns in the field. Because model projections were not calibrated to represent true plot-level seedling densities, for comparison we scaled both the simulation results and measured seedling densities for 1997–2000 by the year of maximum recruitment within that interval (1997) for each species.

### *Sensitivity and uncertainty analysis*

Analyses of model sensitivity and uncertainty runs suggested that projected seedling densities were most sensitive to parameter choices involving the width of the capillary fringe, the maximum seedling rooting depth and the exponents used in the inundation and scour mortality functions. In particular, over-winter seedling densities and survival rates were disproportionately sensitive to the choice of exponent for the scour mortality function, which influences the shape of the relationship between seedling mortality and tractive shear stress as the threshold for 100% mortality is approached. This was also the parameter with the highest inherent uncertainty, as there is a paucity of data in the literature on shear stress thresholds for plant mortality. A full description of the methods and results of the uncertainty and sensitivity analyses are available on request from the corresponding author.

### *Statistical analysis*

We compared the average monthly maximum, minimum, mean and coefficient of variation of daily flows between the natural flow and regulated flow scenarios using *t* tests (with adjustment for unequal variances when necessary). Differences by year in projected seedling totals and over-winter mortality rates between flow scenarios were compared using paired *t*-test, signed rank tests and sign tests. We used Spearman rank correlation coefficients to quantify correspondence between monthly flow patterns and seedling densities. We used Pearson correlation coefficients to measure the degree of synchrony in temporal patterns of seedling recruitment between species, the degree of correspondence between simulated and observed seedling densities for 1997–2000 and the strength of association between simulated first-year and over-winter seedling densities within species.

We used multiple linear regression to model the influence of flow variables on simulated first-year (growing-season) and over-winter seedling densities, and survival under the regulated and natural flow scenarios. Prior to analysis, the projected seedling totals were log-transformed and over-winter survival rates were arc-sine transformed to improve their fit to a normal distribution. The strength of individual models was quantified and compared using the coefficient of determination ( $R^2$ ), and the strength of association with individual variables was compared using standardized regression coefficients (SAS Institute, 2001).

## RESULTS

### *Model performance*

Model projections of first-year seedling recruitment for 1997–2000, based on historic flows, strongly matched observed temporal patterns of seedling abundance from the field (Figure 5(a–e)). Under both the model projections and field surveys (Dixon, 2003), the highest densities of all five focal species occurred in the 1997 cohort, with much lower densities of *Betula*, *Populus*, and the two *Salix* spp. in 1998–2000. Model projections also matched interannual differences in *Acer* densities well, with the second highest densities occurring in 1999. Relative to field surveys, the model over-predicted the proportional densities (relative to 1997) of *Populus*, *S. nigra*, and particularly *S. exigua* in 1998 and 1999. Pearson's correlation coefficients between field and model proportions, by species, ranged from 0.8 for *S. exigua* ( $p = 0.20$ ) to  $>0.99$  for *Betula*, *Acer*, and *S. nigra* ( $p < 0.01$ ), and 0.98 for *Populus* ( $p = 0.02$ ).

Lumped across species, patterns of over-winter seedling mortality differed between model projections and field estimates for the 1997–1999 cohorts (Figure 5(f)). The model simulated higher seedling mortality rates in 1998–1999 than 1997–1998, while field measurements suggested much higher mortality rates in 1998–1999 than 1997–1998. This discrepancy persisted under a range of alternative parameter choices for ice, scour and inundation mortality in the model. The model did reproduce the occurrence of much lower mortality rates in 1999–2000, although modelled mortality was lower than observed values.

### *Model projections—historic time series*

Model runs using the historic daily flow record at Wisconsin Dells (1935–2002) showed high variation among years in simulated first year seedling establishment, over-winter survival and the density of seedlings the following

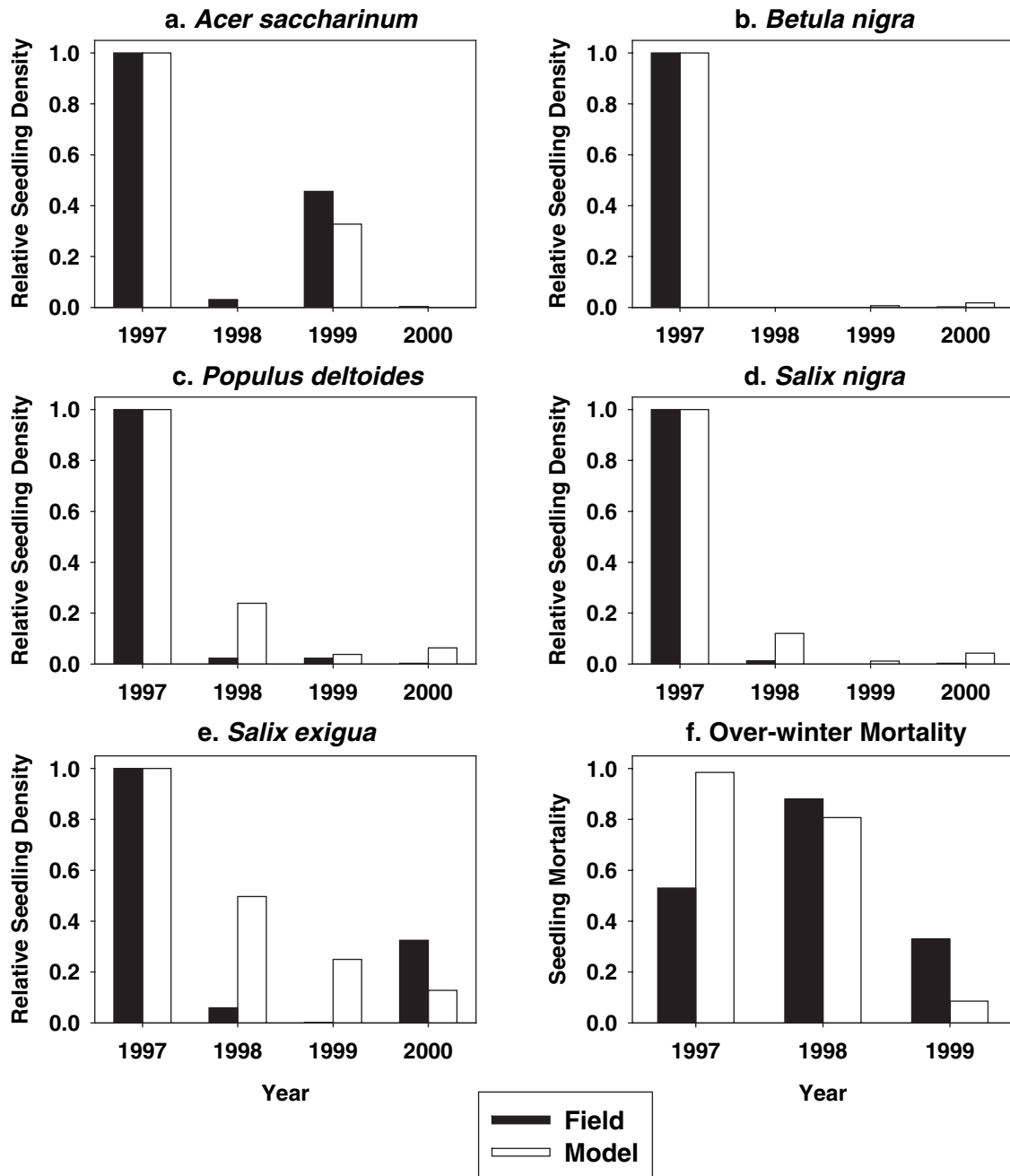


Figure 5. Observed and simulated relative first-year seedling densities, by species (a-e), and observed and simulated over-winter seedling mortality rates (f), lumped across species. Seedling densities for each species are scaled relative to the observed or simulated values in 1997

spring (Figure 6). Across species, simulated over-winter mortality rates were very high in most years (means ranged from 73% in *Acer* to 88% in *S. exigua*), with the bulk of successful establishment concentrated into only a few years and high synchrony in successful initial (first year) and final (over-winter) seedling establishment among species (Table III, Figure 6). Strong recruitment events, across species, occurred in years with low, stable or receding flows throughout June to October and no substantial floods during the late fall and winter (e.g. 1957, 1963, 1976) (Figure 7(top)). Years without successful seedling recruitment, in contrast, were characterized by more chaotic

Table III. Spearman rank correlations in simulated first-year and over-winter seedling densities between species. All correlations are significant at  $p < 0.0001$

Species	<i>A. saccharinum</i>	<i>B. nigra</i>	<i>S. exigua</i>	<i>S. nigra</i>	<i>P. deltoides</i>
First-year seedling densities					
<i>A. saccharinum</i>	1.00	0.57	0.46	0.53	0.56
<i>B. nigra</i>	0.57	1.00	0.82	0.94	0.90
<i>S. exigua</i>	0.46	0.82	1.00	0.94	0.97
<i>S. nigra</i>	0.53	0.94	0.94	1.00	0.97
<i>P. deltoides</i>	0.56	0.90	0.97	0.97	1.00
Over-winter seedling densities					
<i>A. saccharinum</i>	1.00	0.60	0.60	0.55	0.61
<i>B. nigra</i>	0.60	1.00	0.72	0.78	0.77
<i>S. exigua</i>	0.60	0.72	1.00	0.97	0.97
<i>S. nigra</i>	0.55	0.78	0.97	1.00	0.96
<i>P. deltoides</i>	0.61	0.77	0.97	0.96	1.00

hydrographs, with mid-summer (1978) or autumn flood events (1985, 1995) and/or moderate-large spring floods (1978, 1985, 1995) (Figure 7(bottom)). Successful recruitment was generally limited to years with summer (post-dispersal) flows lower than 400–500 m<sup>3</sup>/s and subsequent winter-spring peak flows lower than 600 m<sup>3</sup>/s (Figure 8; *Betula* shown as an example, but other species show similar patterns).

#### *Influence of historic flow patterns on simulated recruitment*

Differences in monthly flow patterns among years influenced initial (first-year) seedling recruitment and subsequent over-winter survival among species. In general, first-year recruitment was negatively correlated with maximum daily flows by month during the growing season (Figure 9(a)). Similar patterns were obtained with mean daily flows and the coefficient of variation in daily flows by month; only the maximum flow results are reported here. Initial recruitment of *A. saccharinum* was most strongly negatively correlated with maximum flows in June, while *B. nigra* was most strongly limited by July maximum flows. These differences are consistent with the periods of dispersal and germination in these species, with *Acer* dispersal concentrated in mid-May to early June and *Betula* in June (Figure 4). First-year seedling densities by *S. exigua* and *P. deltoides*, the latest dispersing species with the broadest dispersal peaks, were most strongly correlated with September maximum flows, with the rank correlation between maximum monthly flow magnitude and recruitment becoming increasingly strong and negative from May to September. Growing season flow conditions were much less strongly correlated with over-winter seedling densities and the direction of the correlation switched for some months (Figure 9(b)). June flows, in particular, were weakly negatively correlated with initial recruitment in the four later dispersing species (*Betula*, *Populus* and the two *Salix*), but positively correlated with over-winter seedling densities. Overall, across species, over-winter seedling densities were most strongly and negatively correlated with October to April peak flows or September peak flows.

#### *Influence of flow scenarios on flow and seedling densities*

Monthly flow patterns differed strongly between the regulated and natural flow scenarios for 1915–1975. Relative to the natural scenario, the regulated scenario had substantially lower spring peak flows, lower within-month flow variability (coefficient of variation) and higher minimum flows during most months of the year (Figure 10). Minimum daily flow under the regulated scenario averaged 47% higher for May to September (growing season) and 39% higher for October to April (non-growing season), compared to the natural flow scenario. Non-growing season peak flows under the regulated scenario averaged 42% lower than the natural flow scenario. Monthly and overall peak flows during the growing season (May to September), however, did not differ significantly between flow scenarios.

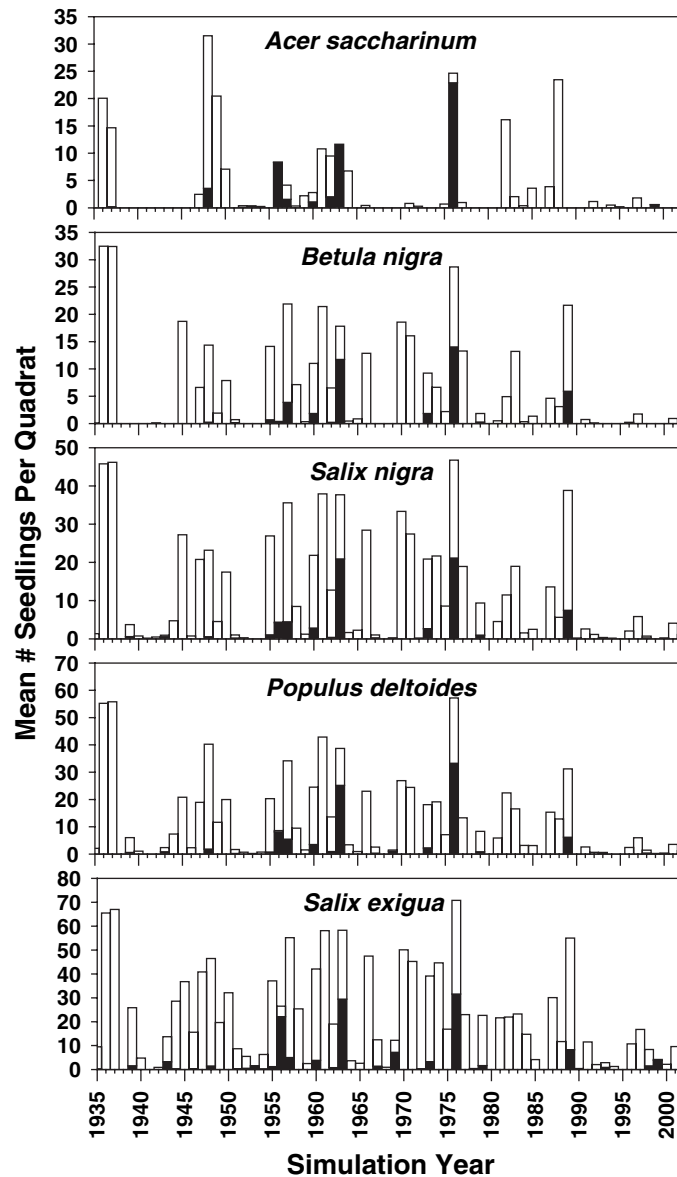


Figure 6. Model projections of first-year (white bars) and over-winter (black bars) seedling abundances under the historic flow conditions (1935–2002) at Wisconsin Dells

Simulated seedling establishment differed significantly between the natural and regulated flow scenarios (Figures 11 and 12). Paired by year, first-year establishment, over-winter seedling densities and over-winter seedling survival were significantly lower under the natural flow regime than under regulated flows for all species (Table IV). Over-winter survival averaged 6–13% higher under the regulated scenario, among species (Figure 13).

#### *Relationship between flow patterns on simulated seedling recruitment*

Regression models relating monthly and seasonal flow variables to first-year and over-winter seedling densities and over-winter survival rates explained 55–91% of the variation, across the five focal species and two flow

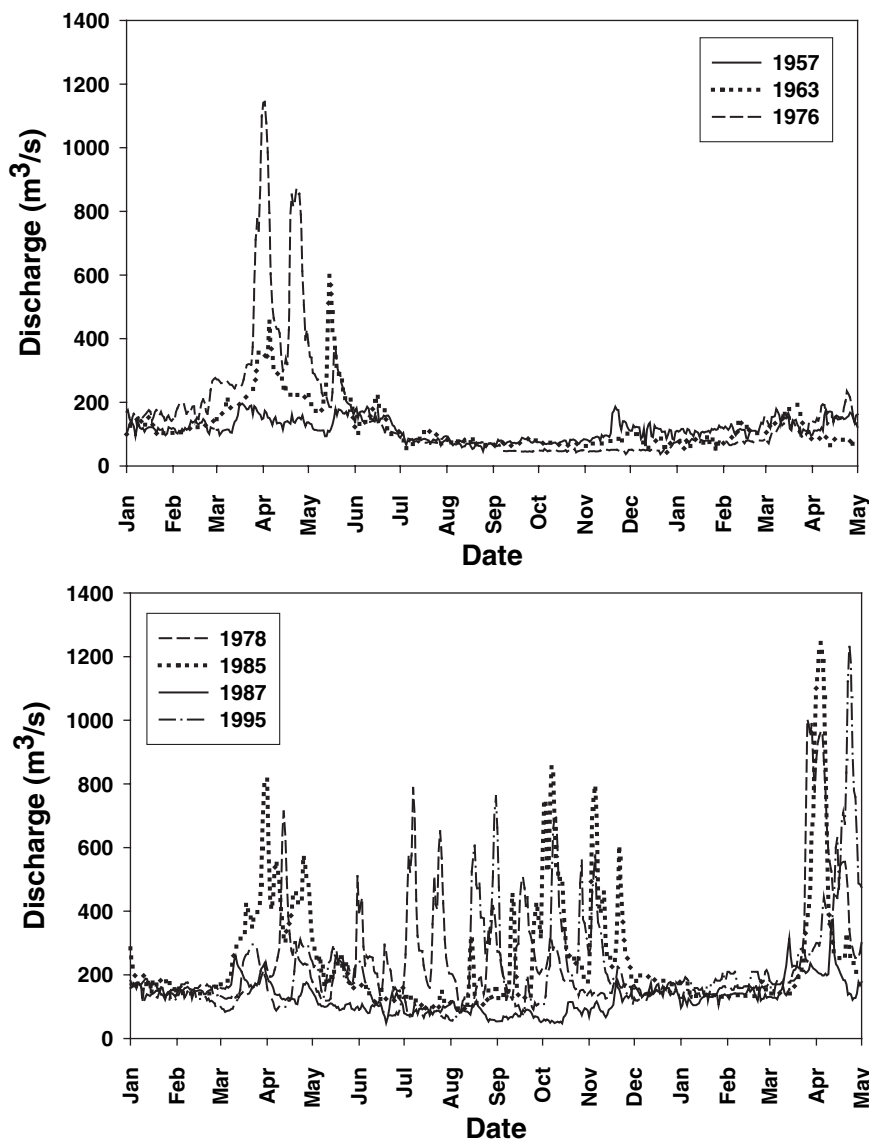


Figure 7. Hydrographs from selected years with strong (top) and poor (bottom) simulated seedling recruitment from the historic (1935–2002) flow record

scenarios (Table V). Flow-seedling regression models were generally stronger (higher  $R^2$ ) for the regulated scenario, particularly for over-winter seedling densities and survival.

Across species, first-year seedling establishment was negatively related to the magnitude (median) and variability (CV) of daily flows during specific months of the growing season. As in the analysis of recruitment patterns under historic flows, the particular months of importance varied among species consistent with differences in their dispersal phenologies. Initial establishment of *Acer* was negatively related to the median and CV of June and September flows. Establishment by *Betula* was negatively related to flow variability in July, as well as to the magnitude and variability of flows in August and September. First-year densities of *P. deltoides* and *S. nigra* were negatively correlated with median flows or flow variability in July, August and September. Establishment of *S. exigua* was negatively correlated with the median and CV of flows in August and September. First-year densities of all five species were positively correlated with median daily flows in May.

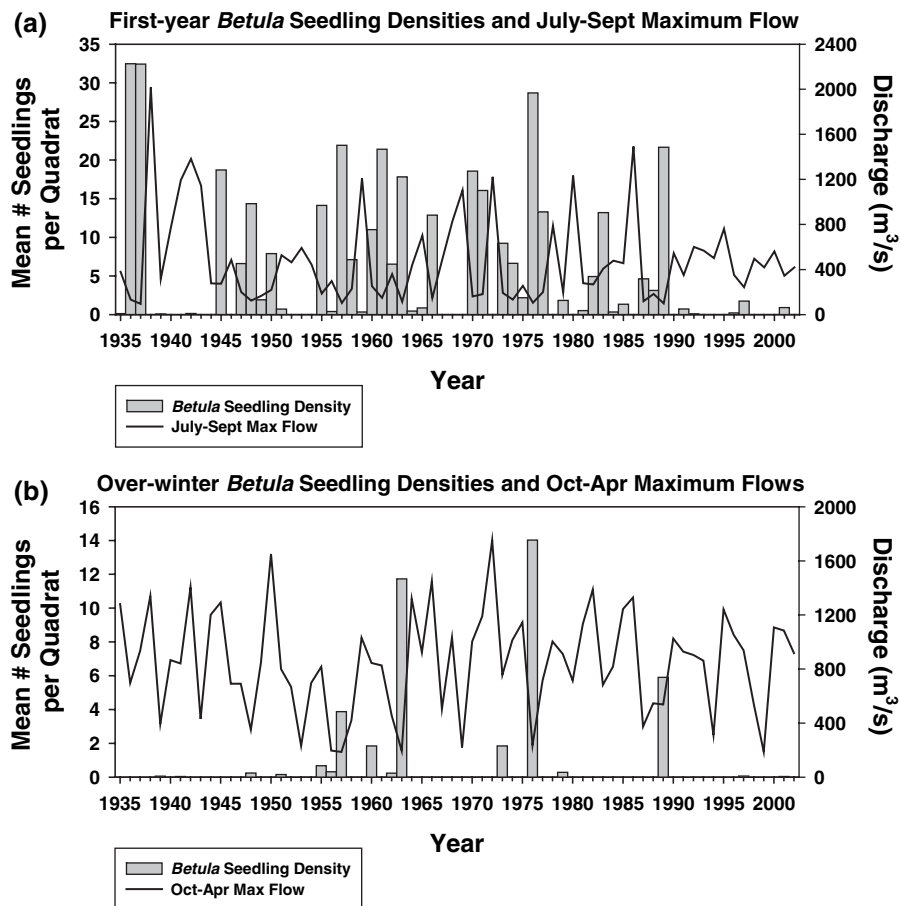


Figure 8. Relationship between post-dispersal maximum growing season flows and simulated first-year seedling densities (top) and between October and April peak flows and over-winter seedling densities (bottom) for *Betula nigra* under historic (1935–2002) flows

Survival between the first-year and over-winter seedling classes was strongly negatively related to October to April peak flow across species and scenarios (Table V). Survival was also negatively related to October to April median flow, but only significantly so for the regulated flow scenario. Across species and flow scenarios, survival was positively related to higher median flows during specific growing season months, particularly August and September. The positive correlation of these variables with over-winter seedling survival and their negative relationship with first-year seedling totals suggest that higher late summer flows may restrict recruitment to higher sandbar surfaces where seedlings are less vulnerable to scour from subsequent winter or spring high flows.

Consistent with the strong negative relationships between over-winter survival and peak flow, over-winter seedling numbers were negatively related to peak flow magnitude during the non-growing season across all species and both scenarios (Table V). Under the natural flow scenario, October to April peak flow was the strongest predictor (highest standardized regression coefficient) of over-winter seedling densities for all five species. Under the regulated flow scenario, however, median flow magnitudes or variation during specific growing-season months (June, July) were comparable or stronger predictors for *Betula* or *Acer* seedling density. Correlation analyses indicated that over-winter seedling densities of *Betula*, *Acer*, *Populus* and *S. nigra* were more strongly correlated with initial first-year densities under the regulated (Pearson's  $R = 0.37, 0.54, 0.33$  and  $0.29$  respectively) than under the natural flow scenario ( $R = 0.19, 0.28, 0.17$  and  $0.15$ ). Initial densities of *S. exigua*, in contrast, were only weakly correlated with over-winter densities under both scenarios (regulated:  $R = 0.20, p = 0.11$ ; natural:  $R = 0.17,$



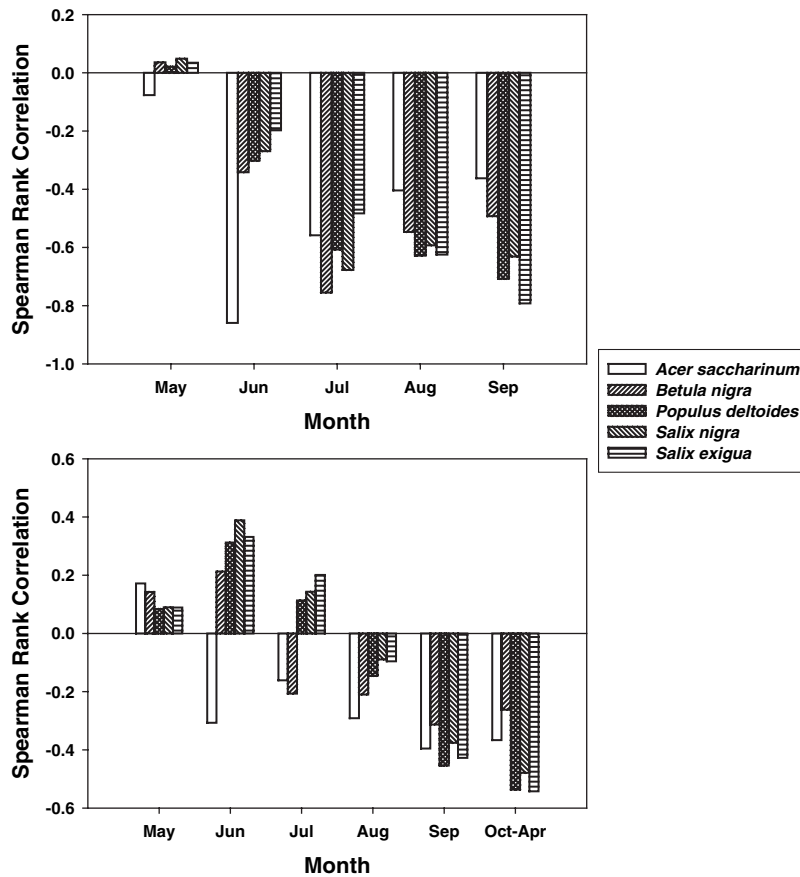


Figure 9. Spearman rank correlations between simulated first-year (top) and over-winter (bottom) seedling recruitment and monthly or seasonal maximum flows, under historic (1935–2002) flow conditions

$p = 0.18$ ). August and September flow variables, which were significantly correlated to first-year establishment in all five species and both scenarios, were only weakly related to final over-winter seedling numbers (Table V).

## DISCUSSION

Based on differences between the natural and regulated flow scenarios (Krug and House, 1980), the effects of flow regulation on Wisconsin River flows are qualitatively similar to those found on other regulated rivers, with reduced peak flows, higher base flow and lower flow variability. The severity of these impacts, however, is less than on many rivers in the western US, such as the Missouri (Johnson, 1992), the Green (Cooper *et al.*, 1999) and the Colorado (Schmidt *et al.*, 1998). In contrast to these western rivers, the storage capacity (Figure 2) and annual drawdown of the reservoirs on the Wisconsin are not large. The dams are operated on a run-of-the-river basis, more or less following natural, climate-induced seasonal patterns of flow, but reducing their amplitude through some capture of flood waters in the spring and release of extra flow during late summer, fall and winter (Krug and House, 1980).

In contrast to the effects of regulation on meandering rivers (Williams and Wolman, 1984; Rood and Mahoney, 1990; Johnson, 1998), flow regulation on the island-braided Wisconsin may create more favourable conditions for vegetation establishment and persistence. In the model runs, regulation increased annual seedling recruitment by reducing the magnitude of winter and spring peak flows, resulting in lower scour mortality. In addition, changes in summer flows (increased baseflows, decreased flow variation) also increased initial seedling establishment. In these

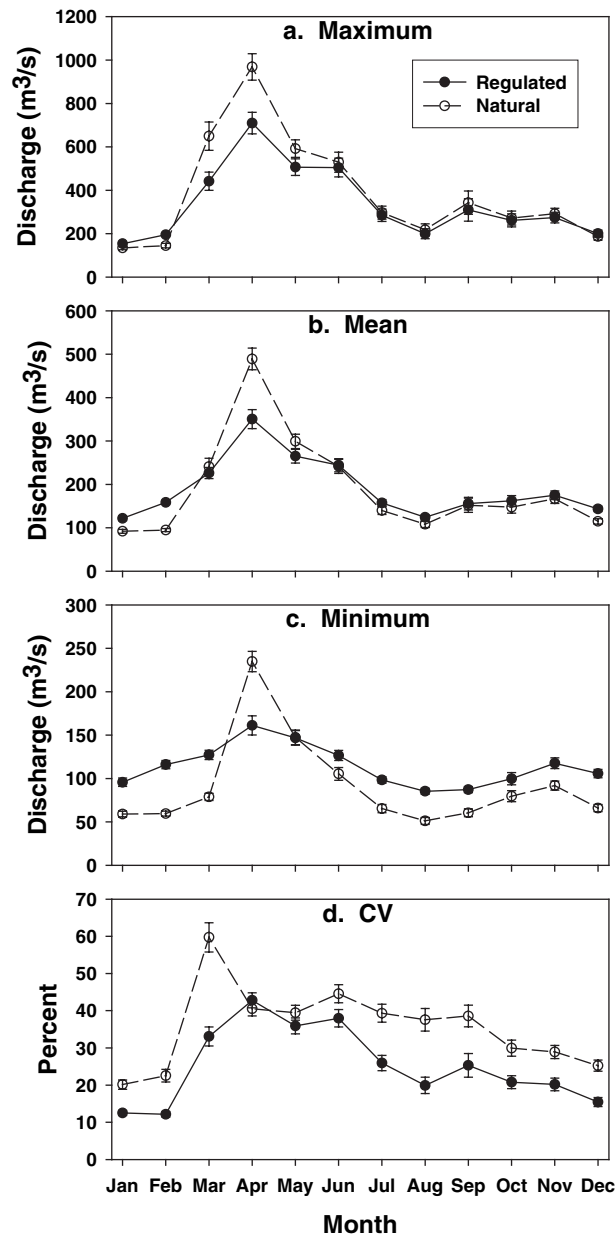


Figure 10. Differences in flow regime (monthly maximum, mean, minimum and coefficient of variation of daily flows) between regulated and natural flow scenarios

respects, the effects of regulation on the Wisconsin resemble that of the Platte (Johnson, 1994), the Colorado (Johnson, 1991; Schmidt *et al.*, 1998) and the Snake River in Idaho (Dixon and Johnson, 1999), all of which show evidence of reduced peak flows, accompanied by encroachment by woody vegetation along the channel. These differences among rivers in response to flow regulation underscore the importance of considering a river's geomorphic setting (e.g. channel morphology), flow conditions that promote or limit vegetation establishment and persistence and the specific effects of regulation on the flow regime, for predicting the response of riparian vegetation to regulation (Williams and Wolman, 1984; Scott *et al.*, 1996; Friedman *et al.*, 1998; Johnson, 1998). On the Wisconsin, the wide, shallow channel, the sandy riverbed, the island-braided channel morphology and the

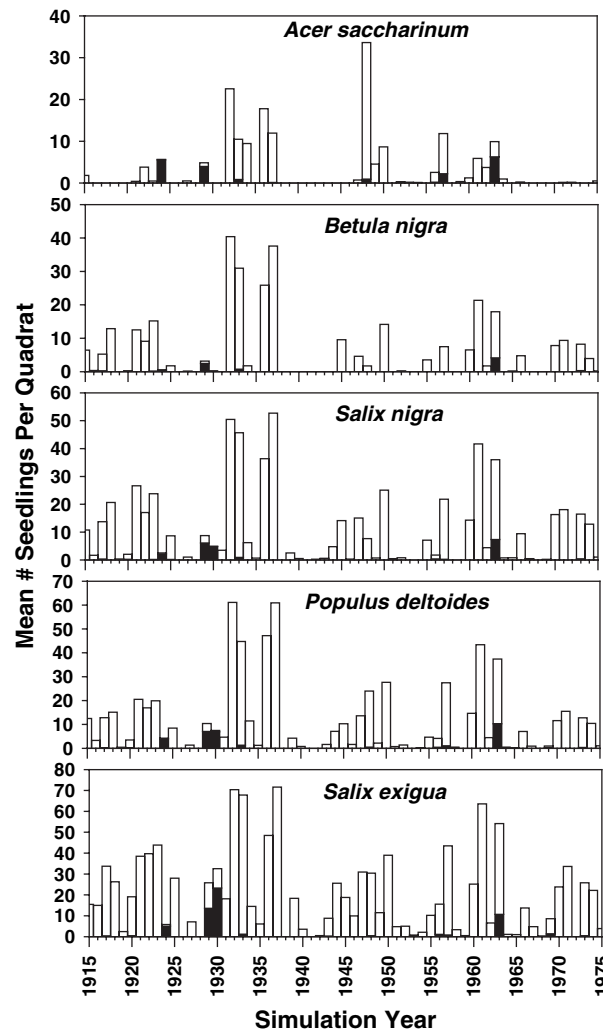


Figure 11. Model projections of first-year (white bars) and over-winter (black bars) seedling abundances under the simulated natural flow regime (1915–1975)

reduction of spring peak flows by regulation create conditions conducive to vegetation establishment within the channel during prolonged low flow conditions. Projections of higher seedling recruitment under regulated flows are consistent with estimated declines in channel area (and concomitant increases in riparian vegetation) of 11.5% from 1937 to 1968 in the study area, based on analysis of historic aerial photographs (Dixon *et al.*, 2002).

Successful recruitment of tree seedlings in the river channel may be highly sensitive to specific types of flow events at specific times of the year. Initial establishment of seedlings was strongly influenced by flows during specific months of the growing season, which differed between species in ways consistent with species differences in the timing and duration of seed dispersal. Initial establishment of *A. saccharinum*, which concentrated its dispersal in mid-May to early June (Dixon, 2003), was most strongly related to June flows, with lower recruitment in years with higher or more variable June flows. For *B. nigra*, which concentrated dispersal in June, first-year seedling establishment was lowest in years with higher or more variable flows in July and subsequent months. Seedling establishment of *S. exigua*, which had the longest dispersal duration of any species, was more strongly related to flows later in the summer (August and September). The importance of summer high flows for limiting establishment matches well with our field observations on the Wisconsin (Dixon *et al.*, 2002; Dixon, 2003) and

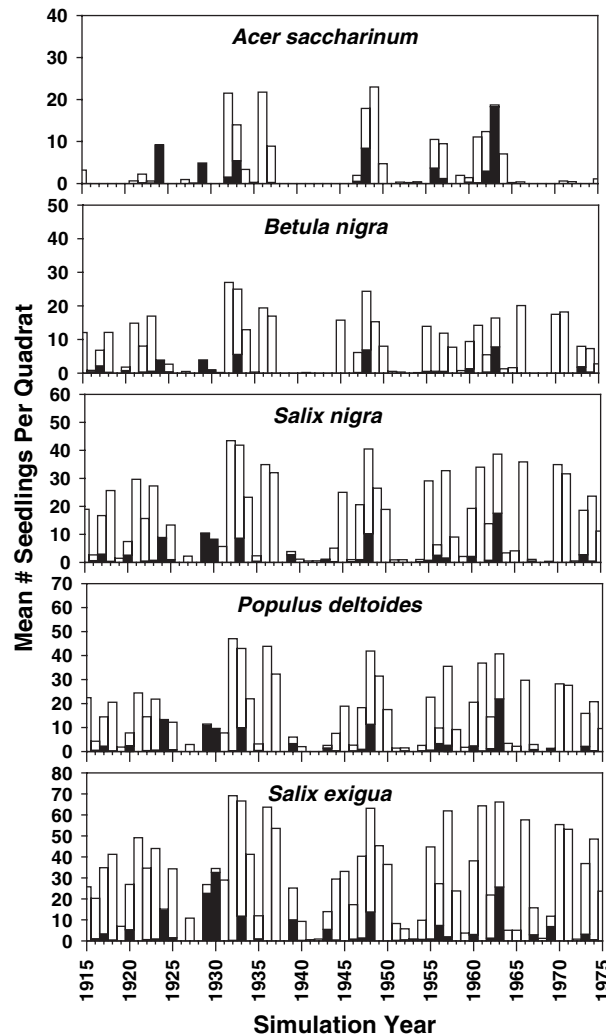


Figure 12. Model projections of first-year (white bars) and over-winter (black bars) seedling abundances under the simulated regulated flow regime (1915–1975)

those of Johnson on the Platte River in Nebraska (Johnson, 1994, 1997, 2000). Our model results suggest that flow regulation may have heightened the importance of summer flow events for enhancing or limiting seedling recruitment on the Wisconsin, as the dams reduce spring peak flow magnitude and increase the probability that first-year seedlings will survive until the following spring.

The sensitivity of seedling recruitment in the model to both summer and winter/spring flow conditions suggests that riparian vegetation dynamics may be sensitive to shifts in climate that influence the relative importance of snowmelt and summer rainstorm floods, or that influence the frequency of summer droughts. In the upper Midwest, even modest shifts in climate can lead to major changes in flood timing and magnitude, due to shifts in seasonal storm tracks and the boundaries of continental air masses. Knox (1988, 2000) found that short-term anomalous climatic conditions in the months of June and March particularly influenced the occurrence of floods in the upper Mississippi basin. Our analyses of the links among flow, climate and simulated seedling recruitment on the Wisconsin suggest that summer floods and first-year seedling recruitment are strongly linked to June precipitation, while over-winter survival and spring peak flows are linked to winter precipitation (Dixon, 2001). Hence, riparian

Table IV. Tests of paired differences, by year, in quadrat-level densities of first-year and over-winter seedlings between 'natural' (Nat) and 'regulated' (Reg) flow scenarios

Seedling age	Species	Median seedling densities			Signed rank	$p >  S $	Sign Test	$P >  M $
		Nat	Reg	Nat-Reg				
First-year	<i>Acer</i>	0.13	0.28	-0.02	-386.5	0.0003	-15.5	<0.0001
	<i>Betula</i>	0.31	2.75	-0.28	-449.5	0.0003	-18	<0.0001
	<i>Populus</i>	4.49	9.80	-1.95	-646.5	<0.0001	-22.5	<0.0001
	<i>S. nigra</i>	3.50	9.04	-1.96	-666.5	<0.0001	-21.5	<0.0001
	<i>S. exigua</i>	14.99	26.85	-8.93	-822.5	<0.0001	-24.5	<0.0001
Over-winter	<i>Acer</i>	0.0001	0.012	-0.008	-531	<0.0001	-21	<0.0001
	<i>Betula</i>	0.0004	0.052	-0.051	-641	<0.0001	-23.5	<0.0001
	<i>Populus</i>	0.010	0.249	-0.220	-760	<0.0001	-25.5	<0.0001
	<i>S. nigra</i>	0.006	0.147	-0.118	-744	<0.0001	-24.5	<0.0001
	<i>S. exigua</i>	0.030	0.392	-0.269	-839.5	<0.0001	-27	<0.0001

Each comparison is based on a sample size of 61 years.

vegetation dynamics on the Wisconsin, as well as on other midwestern rivers, could be highly sensitive to the effects of climatic change or variability.

Differences among species in dispersal timing and monthly flow-recruitment relationships suggest that shifts in flood timing could influence the relative recruitment success of *Acer* versus later dispersing species. Regionally, the abundance of *A. saccharinum* has increased, relative to other pioneer riparian species, during the last century (Nelson *et al.*, 1994; Barnes, 1997; Yin *et al.*, 1997; Knutson and Klaas, 1998). We speculate that regional hydrologic changes, particularly shifts in flood timing due to climate, earlier snowmelt from land cover change, or flow regulation could be contributing factors to the expansion of *A. saccharinum* in the midwest. These relationships have not, to our knowledge, been investigated rigorously and merit further study.

Here we have developed a formalized simulation model based on the Recruitment Box Model and have used it to project the potential effects of flow regulation on woody seedling recruitment on a north temperate river. This model provides an advance over more qualitative examination of hydrographs by providing a more explicit, mechanistic expression of how flow magnitude, timing, and pattern influences initial establishment and survival of seedlings of pioneer riparian tree and shrub species. As such, a wider range of different hydrographs can be explored through the eyes of the model, to forecast the potential effects of, for example, environmental flow

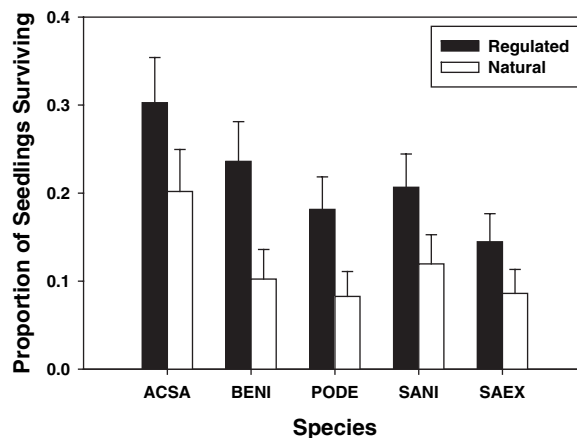


Figure 13. Mean and standard error of over-winter seedling survival rates under the regulated and natural flow scenarios, by species (*Acer saccharinum* = ACSA, *Betula nigra* = BENI, *Populus deltoides* = PODE, *Salix nigra* = SANI, *Salix exigua* = SAEX)

Table V. Standardized regression coefficients for multiple regression analyses of first-year and over-winter simulated seedling numbers and seedling survival with flow variables (median and coefficient of variation of daily mean flows, by interval), under 'natural' and regulated flow scenarios

Species and flow scenario	Standardized regression coefficients by month and flow variable												R <sup>2</sup>			
	May		June		July		August		September		October to April					
	MED	CV	MED	CV	MED	CV	MED	CV	MED	CV	MED	MAX				
<b>First-year densities</b>																
ACSA																
NAT	+0.18**		-0.64**	-0.54**											NA	0.86
REG	+0.18**		-0.60**	-0.57**											NA	0.84
<b>BENI</b>																
NAT	+0.16				-0.20	-0.45**	-0.16	-0.16	-0.16	-0.20*					NA	0.73
REG	+0.11					-0.59**	-0.17	-0.17	-0.21**					NA	0.84	
<b>PODE</b>																
NAT	+0.15*				-0.15*					-0.23**	-0.55**			NA	0.87	
REG					-0.14	-0.14*				-0.24**	-0.55**			NA	0.87	
<b>SANI</b>																
NAT	+0.18*				-0.40**	-0.22**				-0.27**	-0.40**			NA	0.81	
REG	+0.11				-0.32**	-0.34**				-0.28**	-0.37**			NA	0.87	
<b>SAEX</b>																
NAT	+0.15**									-0.26**	-0.53**			NA	0.89	
REG	+0.09									-0.15*	-0.27**			NA	0.91	
<b>Over-winter densities</b>																
<b>ACSA</b>																
NAT			-0.41**	-0.31**											-0.48**	0.64
REG			-0.37**	-0.40**	+0.29*	-0.17									-0.38**	0.74
<b>BENI</b>																
NAT										-0.19	-0.24				-0.39**	0.57
REG										-0.72**	-0.21				-0.39**	0.71
<b>PODE</b>																
NAT	+0.18*														-0.51**	0.74
REG										-0.29**	-0.24**				-0.52**	0.76
<b>SANI</b>																
NAT															-0.52**	0.66
REG										-0.39**					-0.48**	0.69
<b>SAEX</b>																
NAT															-0.52**	0.69
REG										-0.22*					-0.53**	0.77

Over-winter Survival							
ACSA							
NAT							-0.57**
REG							-0.58**
BENI							-0.30*
NAT							-0.54**
REG							-0.53**
PODE							-0.54**
NAT							-0.61**
REG							-0.59
SANI							-0.52**
NAT							-0.59**
REG							0.62
SAEX							0.71
NAT							-0.51**
REG							-0.59**
							0.63
							0.69

*Acer saccharinum* = ACSA, *Betula nigra* = BENI, *Populus deltoides* = PODE, *Salix nigra* = SANI, *Salix exigua* = SAEX).

+ Positive coefficient (and  $p < 0.10$ ), - Negative coefficient (and  $p < 0.10$ ).

\* $p < 0.05$ .

\*\* $p < 0.01$ .

prescriptions or dam operating rules. The uncertainties in the model also point out key areas of research for better understanding the link between flow variation and plant recruitment, such as the post-dispersal flow thresholds for removal of seedlings and the effects of winter ice on seedling survival.

Weaknesses or limitations of the model include its static treatment of geomorphology, crude treatment of ice scour effects, fixed seed dispersal curves and minimal inclusion of spatial heterogeneity in channel conditions and recruitment processes. For instance, although seedling recruitment may be limited by large spring peak flows on an annual time scale, formation of the geomorphic surfaces needed for recruitment may require periodic large floods. Differences in species recruitment were simulated solely on the basis of differences in dispersal timing and inundation tolerance. The model does not simulate successional processes or survival past the first year, does not include competitive or facilitative interactions among seedlings (Walker *et al.*, 1986), and does not include the effects of vegetative reproduction or clonal spread, which can be very important to vegetation dynamics in rivers. Population demography of willows, particularly *S. exigua*, may be dominated by clonal processes, especially on regulated rivers (Douhovnikoff *et al.*, 2005) and vegetative propagation by branch fragments may be an important mode of colonization for many riparian species (Krasny *et al.*, 1988; Burns and Honkala, 1990; Craig and Malanson, 1993). Because of these simplifications, recruitment processes within sandbars already colonized by woody vegetation may be quite different than those projected by the model. The model is probably best designed for simulating initial colonization on previously unvegetated sediment bars. Inclusion of clonal spread, successional interactions and geomorphic dynamics would be a significant improvement for further development of a linked vegetation-geomorphology model of channel dynamics (Malanson, 1993; Murray and Paola, 1994; Richards *et al.*, 2002; Douhovnikoff *et al.*, 2005).

Despite these caveats, we believe that this initial application of our simulation approach suggests promise in use of this or other models based on the Recruitment Box Model (Rood *et al.*, 2005) for projecting the effects of environmental change on river vegetation dynamics. The Recruitment Box Model, particularly with extensions to represent multiple species and the effects of flows on post-establishment survival, provides a useful framework for modelling the relationship between altered river flows and demography of riparian plants (and possibly other organisms). With the global pervasiveness of flow regulation (Nilsson *et al.*, 2005), the potential impacts of global climatic change on rivers (Arnell, 2004), and increasing interest in river restoration and environmental flow prescriptions (Richter and Richter, 2000; Richter *et al.*, 2003; Tharme, 2003; Palmer *et al.*, 2005), process-based models linking ecology and hydrology will become increasingly important tools for exploring flow management options for restoration of riparian ecosystems or for projecting the ecological effects of large water projects.

#### ACKNOWLEDGEMENTS

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